Acta Bot. Neerl. 23(4), August 1974, p. 493–503.

MEGASPORANGIUM, NUCELLUS, OVULE AND PRESEMEN: THEIR NOMENCLATURE AND HOMOLOGY

A. D. J. MEEUSE

Hugo de Vries-laboratorium, Universiteit van Amsterdam

SUMMARY

Palaeobotanic studies of remains of megasporangiate organs of early Cycadophytic forms of Palaeozoic age, carried out in the last few decades, have contributed a sufficient amount of new data to enable the complete reconstruction of the phylogenetic history of the ovule. The evolution of the ovule took place as a continuous (orthogenetic) process in which nine successive phases can be distinguished. The morphological evaluation and homologisation of parts of the ovule and its accessory organs is complicated by the 'ontogenetic' changes taking place between the initiation and the shedding of the ovule (in the more primitive presemen stage of evolution) or between its initiation and the completion of the fertilisation process (in more advanced ovules). In spite of this difficulty the homologisation of certain parts is clear and unambiguous at both the pre- and post-fertilisation stage. Our increased knowledge has strengthened the case for a pteridospermous affinity of the so-called water-ferns appreciably, so that some, or all, of their morphological features and their life-cycles may serve as a yardstick for the conditions prevailing in the pteridosperms currently regarded as quite extinct since Palaeozoic times.

1. INTRODUCTION

Our knowlege of the female reproductive organs of palaeozoic Spermatophytes has increased very rapidly in the last few decades, mainly through the efforts of American and British palaeobotanists (compare, e.g., LONG 1966, PETTITT 1966, 1969, PETTITT & BECK 1968, STIDD & HALL 1970, ROTHWELL 1971, and the papers cited by these authors). Some in a phylogenetic sense far-reaching additions to our cognisance of the ovular structures are, among other ones, the discovery of "pteridophytic" features in the megasporangial organs of early seed ferns (PETTITT 1969) and the reconstruction of the ontogeny of pteridospermous ovules (ROTHWELL 1971).

The phylogenetic significance of such new discoveries has been emphasised by LONG (1966) and, in connection with integument homologies, by MEEUSE & BOUMAN (1974). There are a few points which need some comment, and a warning must be sounded against the danger of semantic inconsequences caused by the rather indiscriminate use of some terms applicable to reproductive structures in Higher Cycadophytes but hardly to those of the earliest cycadophytinous Gymnosperms of Upper Devonian and Lower Carboniferous age. The present contribution deals exclusively with the precursory stages of the ovules and with the ovular structures of cycadophytinous forms. The ovules of coniferophytinous taxa underwent a separate semophyletic evolution since, probably, Late-Devonian eras.

2. THE EVOLUTIONARY SEQUENCE IN OVULE PHYLOGENY

After a discovery by BECK (1960), confirmed and extended by him and various other workers, it became clear that from about the beginning of the Middle Devonian onwards, there appeared on the scene a group of forms named *Progymnospermopsida* by BECK and by others, but perhaps better called *Prae-* or *Protospermatophyta* because they gave rise to all spermatophytic plants including the Angiosperms. Although the evolution from more or less clearly "pteridophytic" to truly spermatophytic conditions is revealed in fossil remains of decreasing geological age as a gradual and continuous process, it is possible approximately to define the various stages of phylogenetic advancement as more or less discrete, successive semophyletic steps by their attainment of a certain level of progressive organisation. This is of course a matter of definitions and requires a consensus of opinion as regards the qualification and the nomenclature of certain essential, structural features on which the distinction of levels of evolutionary progress is to be based. As I have pointed out before (see, e.g. MEEUSE 1963, 1966) the most logical definition of a *seedplant* (a Spermatophyte) is: "*A cormophyte which exhibits a characteristic type of secondary growth (or shows clear signs of having descended from a group of plants with this peculiarity) and bears ovules; the secondary xylem is initially characterised by tracheidal water-conducting elements provided with bordered pits (or is likely to have originated from such a primitive type of secondary wood) and the ovule is to be defined as a (whole or partial) megasporangium homologue surrounded by at least one integument*".

This emended formulation does away with the apparently rather generally accepted notion that "seed plants" bear seeds, which idea, reversedly applied, has presumably led to the indiscriminate use of the term "seed" for various tegumented macrosporangial organs which, if one wishes to preclude any adulteration of semantics, do not deserve this qualification at all.

The other extreme is the distinction made by EMBERGER (1949, 1952) between his "*préphanérogames*" and "*phanérogames*", groups supposed to be in the pre-seed and the seed phase, respectively, but this classification is too rigid because there are transitional stages (compare MEEUSE 1966, chapter 8, p. 61–71, on the confusion of lines and levels). The whole sequence of phylogenetic changes in the ovular morphology, with the corresponding nomenclature, was set forth by the present author (MEEUSE 1963, 1964), but novel evidence added another intervening phase. Our sequential palaeobotanic records indicate the following transitional phases:

Stage a): homosporous plants of the "*Protopteridium*" (*Rellimia*) and *Svalbardia* type were succeeded by heterosporous forms (*Svalbardia* can also be regarded as a primitive *Archaeopteris* with homospory and with deeply "dissected" phyllomic organs precursory to the pseudomicrophylls of the more advanced *Archaeopteridales*);

Stage b): the sporangia of both sexes tended to form synangial aggregates; the megasporangium was presumably still dehiscent before or after shedding and released the functional megaspores it contained (as in phase *a*);

Stage c): the number of megaspores contained in each megasporangium decreased and ultimately the MS (= megasporangium) only produced a single tetrad of which only one spore was functional and the other three abortive; at about the same time the MS became surrounded by an integument, almost certainly derived from the other megasporangia of the gynosynangium (BENSON 1904, MEEUSE 1963, MEEUSE & BOUMAN 1974), but the functional sporangium still opens at the top (in the stages *a*, *b* and *c* the original contents of the sporangium were used up during the formation of the megaspores); at stage *c* only the remains of the MS wall and the tapetal membrane preserved as a thin layer surrounding the single functional megaspore which was retained for some time and was not shed as a separate entity but became detached, together with the enveloping integument, as a presemen (see below);

Stage d): the MS wall formed an apical extension, the lagenostome, which surrounds a pollen chamber; the pollen grains (pluricellular semophyletic derivatives of microspores) were caught by the micropylar area and reached the pollen chamber; at, or directly before, this stage the megaspore tetrad did not develop directly at the cost of the contents of the sporangium but the latter, as the diploid nucellus, first grew out and formed a mass of tissue in which, at a later stage of development, a small tetradic linear arrangement of four haploid cells formed of which only one gradually developed into a large megaspore at the cost of the nucellar tissue: see ROTHWELL (1971, fig. 21–26);

Stage e): the tegumented MS is not shed before the actual fertilisation process has taken place (as in the typical pteridospermous stage *d*), but a zygotic nucleus is formed inside the sporangial or megagametophytic tissue before the ovule becomes detached, and the level of the *true seed* has been attained: the previous stage (or stages) can, if necessary, be distinguished by the name of *presemen* (plural: *presemina*) the transition to stage *f* is characterised by an initial increase in bulk of the nucellar (= sporangial) and megagametophytic tissues;

Stage f): the ovule becomes a seed before being shed, and this seed contains an embryo of some appreciable size, whereas the gametophytic tissue gradually becomes reduced in bulk and, although growing out at the cost of the contents of the nucellus, as a rule does not replace it completely before fertilisation as in stage *d*; zoidiogamy has become obsolete; ultimately archegonia are mostly no longer formed in the megagametophyte;

Stage g): the megagametophyte is further reduced; embryo well-developed at the time of shedding at the cost of nucellar and tegumentary tissues; ultimately the seed can germinate very soon after having been shed (in Angiosperms there is no longer any post-shedding growth of the embryo inside the testa as a rule); after further reductions, and after pre-shedding embryo development had become more pronounced, only the advent of double fertilisation and of the "new" form of feeding tissue, the secondary endosperm, was needed to attain:

Stage h): gametophyte reduced to (mostly) 8-nucleate embryo sac; double fertilisation; secondary endosperm apparently (almost) always initiated even if not copious at a later stage; embryo mostly full-grown and seed in a resting phase at the time of seed- or fruit-shedding; germination taking place without previous "internal" growth after seed has become detached; atropous (orthotropous) type of ovule usually replaced by anatropous or campylotropous type; and, finally:

Stage i): reductions in bulk of the nucellus (crassinucellate → tenuinucellate) and of the integuments; reduction of one integument or of both (or a fusion of the two integuments), etc., in the most advanced and in some (ecologically) highly specialised angiospermous taxa, such as *Orchidales* and *Santalales*, and in several groups of gamopetalous Dicots.

The series of figures (see *fig. 1*) illustrates a number of these phases, some of which have been reconstructed from fossil remains and others are still extant.

Fig. 1. Ovule phylogeny, precursory and initial stages.

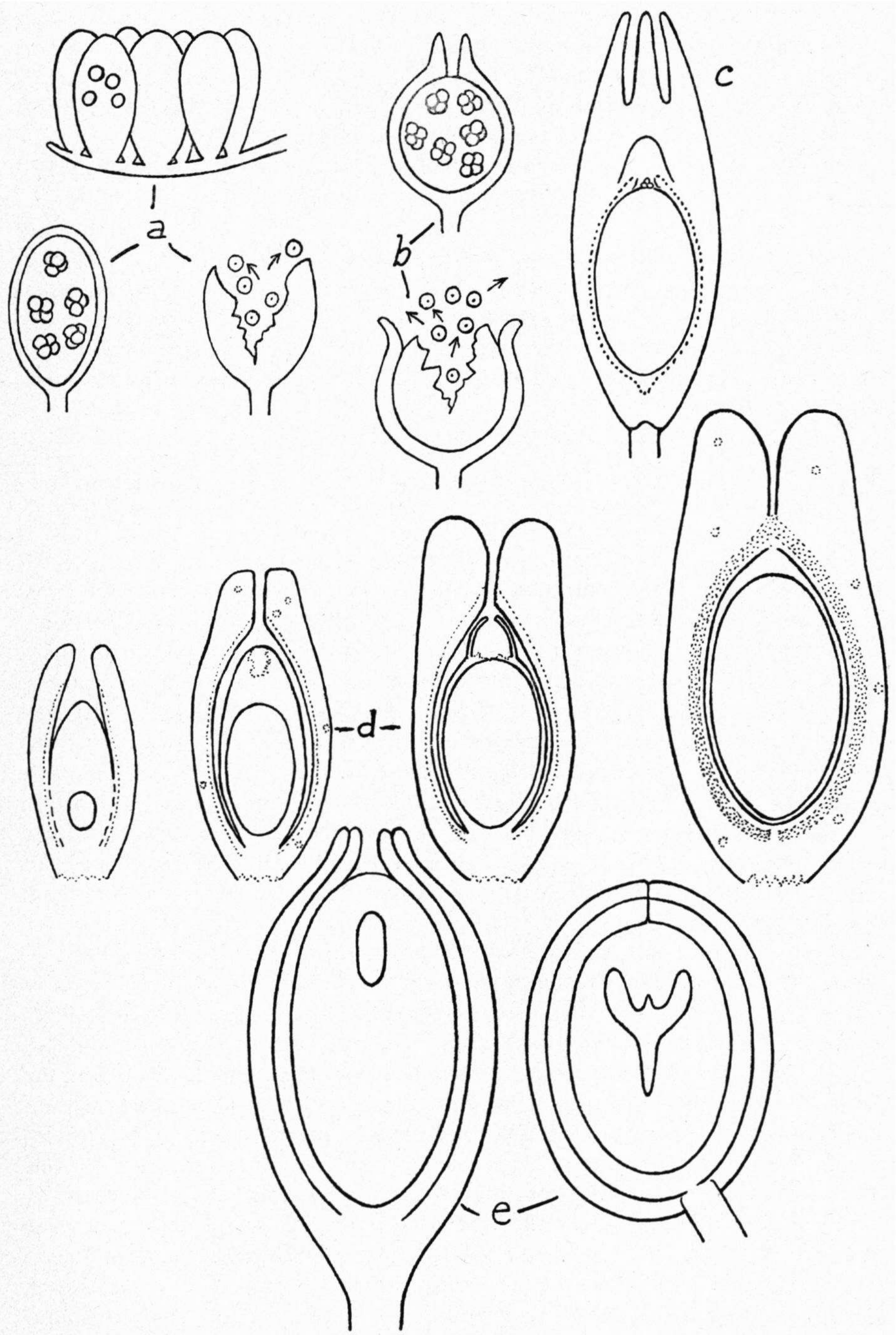
a: Cluster of homosporous sporangia in early progymnospermous forms (top), each sporangium forming tetrads of spores released when the sporangium wall dehisces or desintegrates (bottom left and right)

b: Sporangium enveloped by the (future outer) integument (it is not improbable that this condition developed out of the phase shown in *a*, top, so that the OI is synangial in origin); the spores (here already megaspores, but still numerous) were initially released by dehiscence.

c: Cupulate ovule of an early (Late-Devonian) type *(Archaeosperma)*, adapted from Pettitt & Beck 1968. Only one spore tetrad formed of which three spores abort immediately, the whole ovule (or the single functional megaspore) perhaps released before germination (= before archespore formation); beginning of lagenostome formation (by apical opening or local disintegration of the m.sp.wall).

d: Four stages in the development of a pteridospermous presemen of the *Callospermarion* type (adapted from Rothwell 1971); at left: young stage with gametophyte initiation, followed by older stages showing (respectively) apical disintegration of m.sp.wall, and formation of lateral rim around apical part (lagenostome); last stage but one about fertilisation stage, gametophyte large, original macrosporangial contents almost completely used up in its formation; and finally (at right) maturation taking place, lagenostome etc. crushed flat between the enlarging inner part of the presemen and the testa, the micropyle becoming closed.

e: At left, bitegmic (atropous) angiospermous ovule with nucellus and embryo sac; after fertilisation (at right) the testa is formed and embryo has developed in secondary endosperm, micropyle squashed tight (N.B.: this figure is not in proportion to the left one; the two principal seed coat layers are almost invariably derivatives of the outer integument alone; the inner one becoming crushed to a very thin layer: compare also the last stage of *Callospermarion* shown in *d*).


a
b
c
d
e

All these phases are of course transcendent and gradually pass into one another in an uninterrupted orthogenetic sequence which started in the Devonian eras and probably did not reach its culmination before the Lower Cretaceous or even later, but we can distinguish three main semophyletic phases which represent fundamentally different levels of advancement, viz.,
(α) *a "pteridophytic" phase*, including the stages *a* and *b*, *c* being transitional to β
(β) *a presemen phase*, chiefly including only stage *d*; and
(γ) *a seed phase*, comprising all later stages.
I have previously contended, and still maintain, that all ovular structures not evolved beyond the evolutionary level of stage *d* do not deserve the name of seed at any stage of pre- or post-fertilisation; a fairly advanced, precursory stage could be referred to by the name of *presemen* (roughly corresponding with the terminal part of stage *c* and with stage *d*, and found in nearly all Carboniferous seed ferns).

3. ON THE TERMINOLOGY OF CYCADOPHYTINOUS MEGASPORANGIATE ORGANS

It is quite clear that the origin of the "primary" integument (the single "gymnospermous" integument, "primary" in the sense of MEEUSE & BOUMAN 1974) preceded the retardation of megaspore development: the Upper Devonian form genus *Archaeosperma* described by PETTITT & BECK (1968) contains a tetrad of four, tetrahedrally arranged, megaspores of which only the largest was functional, and stayed enclosed in the remains of the MS wall which had opened or degenerated at the apex before or just after megasporogenesis commenced. This condition must originally have been concomitant with an early shedding of the MS (with its adhering integument), conceivably even before megasporogenesis was completed (as we may deduce from the situation in some living pteridophytes, but this is perhaps irrelevant here; see, however, sub 5!). This stage, also recognisable in fossil material by the trilete (triradiate) apical suture of such megaspores and/or a reticulate impression of the tapetum on the megaspore wall, still prevailed in some Lower Carboniferous Pteridosperms (among which megasporangiate structures included in the form genus *Cardiocarpus*, and possibly also some described as *Pachytesta*: PETTITT 1969).

We may assume that these presemina of Carboniferous seed ferns did not become detached from the mother plant so early as they must have done in the Devonian progenitors of these pteridosperms, and that at least some megagamethophytic tissue developed (and presumably pollen grains were caught) before the time of shedding of the ovule. It is only of academic interest if one does not apply the qualification "ovule" to the tegumented and functionally monosporangiate organ of *Archaeosperma* for some technical reason, because in *Cardiocarpus* this term must be admitted. The application of the term "seed" to the ovule-like structure of *Archaeosperma* is, at any rate, utterly misleading, because at the time of shedding it contained, most probably, only a uninucleate megaspore, and no megagametophytic tissue at all, let alone egg cells contained in archegonia (not to mention an embryo!). If we define an ovule as a MS derivative enclosed in an integument, the situation in *Archaeosperma* and in some early Carboniferous seed ferns with trilete megaspores is marginal. Without the integument, the organ in question would have to be called a MS, but the advent of the integument was such an important evolutionary happening that there is, to my mind, every reason to call this early type of tegumented reproductive organ an ovule.

What exactly is a nucellus (or *the* nucellus)? If we start from the "wrong" end and consider the morphology of the ovule of the most advanced cycadophytinous forms, the Angiosperms, as more representative, the nucellus is a more or less ellipsoid body of diploid cells surrounded by the (inner) integument and at some later stage of development forming an archespore (megaspore mother cell), but retaining its cellular structure for an appreciable length of time, at least until the early phases of embryogenesis. Working "backwards" we apparently have no problem in locating the nucellus in the *Gnetatae*. In the *Cycadales*, presumably representative of the condition in mesozoic cycadopsids, the nucellus includes the "roof" of the original pollen chamber, i.e., a future tegumentary structure (MEEUSE & BOUMAN 1974). In the more advanced seed ferns the nucellus is present as a cellular structure at first, but it is rather soon completely destroyed by resorption to be replaced by the massive megagametophyte which is, to all intents and purposes, ultimately surrounded (except at its apex) by the remains of the MS (= nucellus?) wall alone (ROTHWELL 1971).

The nucellus, as found in the Higher *Cycadophytina*, is, therefore, undoubtedly the (partial) homologue of the *contents* of the MS that became an ovule in Late Devonian and Early Carboniferous periods. The current definition of the nucellus as "the homologue of the megasporangium" is, consequently, not quite correct, because the MS wall (or every other derivative of the sporangium: lagenostome, inner integument) is not represented in what is called "the nucellus" in the most advanced cycadophytinous ovules. In *Gnetatae* and in Angiosperms (presumably also in at least some cycadeoid taxa) the inner integument is once more separated from the "megasporangial nucellus" of the early cycadophytinous forms. The semophyletic history of the original sporangial wall and its derivatives must, accordingly, have some bearing on the question of nucellar homology. In pteridophytic and hemigymnospermous forms the sporangia are normally dehiscent to release the (mega)spores which subsequently start leading an independent existence. As we have seen, the contents of the MS are completely used up in all early forms, and in at least the majority of the presemina, to be digested and gradually replaced by the uninucleate megaspore and, later on, by the pluricellular gametophyte, the original MS wall remaining more or less intact and forming a conspicuous apical differentiation (the lagenostome) around the zone where the sporangial tissue has disappeared during the early ovule ontogeny (i.e., where it has "dehisced" or opened up, no longer to release the megaspore(s), but to give the pollen grains, and consequently the antherozoids, a direct access to the female gametophyte). The so-called nucellus of the seed ferns is, in a later stage of development (viz., at the time of shedding actually the uninucleate megaspore surrounded by the apically perforated skin of the sporangium (including the "tapetal membrane" of PETTITT 1966). The lagenostome is the semophyletic precursor of the inner integument of the Higher Cycadophyta (MEEUSE & BOUMAN 1974); in *Cycadales* the lagenostome exists at the pollination phase after which it closes up again and forms part of what is conventionally called the nucellus, in *Gnetatae* the lagenostome = inner integument persists as a discrete entity.

4. ONTOGENY, SECONDARY PROCESSES, AND OVULE MORPHOLOGY

The difficulties encountered in the morphological (and semantic) evaluation of ovular structures are mostly caused by the rapid structural changes during the ontogenetic development leading up to a certain well-defined level of advancement (such as the time of severance of the ovule or its derivative from the mother plant, the pollination or fertilisation stage, the completion of gametophyte development, the cessation of embryo growth, etc.), and by various "secondary" phenomena (particularly the post-fertilisation development of the embryo, of the seed-coat and accessory organs, including the formation of the future testa, of the endosperm, etc.). The typical ontogenetic sequence in the presemina of the seed ferns, as sketched above is: the MS, after "internal germination" produces a diploid (nucellar) mass of tissue, but this is soon used up by the developing megaspore, leaving only the sporangial (and tapetal) wall. In the first stage there is only diploid sporangial tissue, in the intermediate stage the nucellus contains some diploid tissue and an enlarging megaspore, and ultimately the contents consists only of prothallial cells (after the complete resorption of the nucellar tissue and the subsequent "internal germination" of the spore).

In Higher *Cycadophytina* the ovule contains diploid nucellar tissue up to the time of fertilisation or even thereafter, the diploid tissue never becoming completely replaced by the megaspore and the gametophyte until the development of the embryo and the perisperm or endosperm is well on its way. In some angiospermous taxa (*Nelumbo*, *Laurales*, *Magnoliaceae*, etc.) the mature seed contains a large embryo with massive cotyledons, all other internal tissues having become depleted and crushed flat against the testa. It thus becomes somewhat awkward to homologise the "nucellus" of a pteridospermous presemen, normally shed after pollination but before fertilisation with the nucellus of the angiospermous ovule, shed long after zygotic fusion has taken place, unless one takes the different evolutionary levels into account (and distinguishes for instance, a macrosporic ovule or presemen, a macrosporangial presemen, and a seed-forming ovule), and adapts the terminology accordingly. It is quite clear, on the other hand, that the homology relations are unambiguous if one distinguishes a sporangial wall (and diploid sporangial tissue, "nucellar" tissue), a tapetal membrane and a megaspore membrane (or their derivatives), the megaspore, the haploid megagametophyte, the diploid embryo and the (frequently triploid) secondary endospermal tissue. A complication is that in eoand also in the mesocycadophytinous forms (such as *Cycadales*) the development of the second (inner) integument originated as a special apical differentiation of the MS (= nucellus s.l.). For easy reference one may still refer to the inner part of the ovule as the "nucellus", meaning (as stated above) that this term usually comprises every kind of solid, ovoid to globose structure contained within the MS wall (the 'nucellus" representing the contents of the macrosporangium and/or all its sporangial and prothallial derivatives), and occasionally (as in the young ovules of *Cycadales*) represents the whole megasporangium.

5. THE OVULES OF THE "WATER-FERNS": PHYLOGENETIC AND TAXONOMIC CONSEQUENCES

Ovules are by definition megasporangia (or their derivatives) enclosed in at least one individual cover or integument leaving a "micropylar" region. Another characteristic of the mature ovule is the exposed area of the megasporangial tissue (= nucellus) surrounded by the distal part of the sporangium wall (lagenostome, later becoming nucellar beak, outer wall of pollen chamber, and ultimately inner integument: Meeuse & Bouman 1974). If, conversely, megasporangiate structures are found in plants up to now considered to be pteridophytes, but otherwise fulfill the requirements to qualify as ovules on account of their singular pattern of organisation and of their ontogeny, the taxonomic groups in which these structures occur must be seed plants. Palaeobotanists have, at any rate, regarded several megasporangiate form genera (such as *Archaeosperma*) as the ovules ("seeds"!) of early Spermatophytes although the vegetative parts of the plants bearing such primitive ovular organs are not always known. If this typological interpretation is extended to include the megasporangiate ovule-like organs of *recent* forms, one must accept the consequences and conclude that these extant taxa, even if hitherto classified as pteridophytes, must be ranked with a group of the *Spermatophyta*.

There are two examples of such groups of pseudo-Pteridophytes, viz., the *Marsileales* and the *Salviniales*. A suggestion that they are the very much reduced, aquatic derivatives of seed ferns (Meeuse 1961) was pooh-poohed even by my own research associates, but if certain fossil organs are classified as "seeds", or "seed megaspores" (Pettitt 1969), and prove to be provided with a cupule even in the primitive condition corresponding with stage *c* (i.e., the MS or the nucellus contains a single megaspore at the time of shedding of the ovule as in the Devonian fossil *Archaeosperma*: Pettitt & Beck 1968), typologically similar organs in recent forms can, to my mind, only be interpreted as ovules or presemina.

The *Marsileales* have attained stage *c* of ovule and seed evolution, the sporangium containing, at the time of shedding, a one-celled megaspore formed after a meiotic process during which a tetrad originated of which only one spore is functional and the other ones are abortive. The accompanying diagrams (with the old names and the new names of the constituting parts of the preseminal ovule) show the development (see *fig. 2*). At the time of shedding or shortly

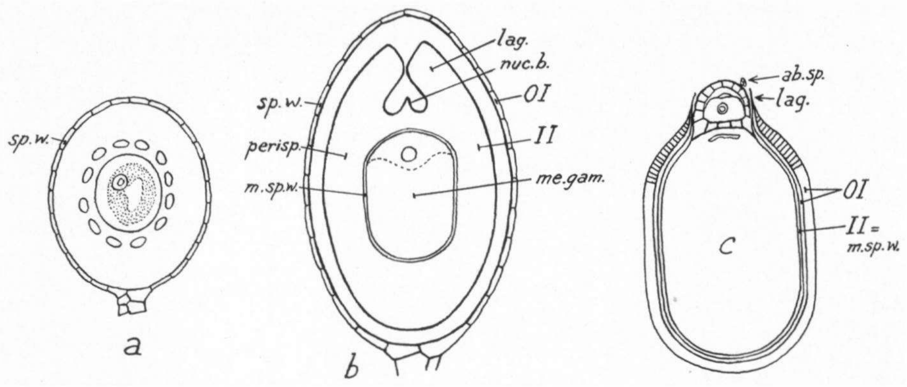


Fig. 2. Presemina of "water-ferns".
a and *b*: Two stages of development of a so-called megasporangium of *Salvinia*;
a: the gametophyte develops at the cost of the sporangial (= nucellar) tissue (compare Fig. 1 *d* of *Callospermarion*),
b: "mature" stage just before shedding (with conventional names of parts indicated at the left-, and the new interpretation at the right-hand side,
c: So-called megasporangium of *Marsilea* with new interpretation of parts (conventionally there was just one complex megasporangial wall opening at the top where archegonial structure develops). Remains of aborted megaspores and palissade structure of outer layer of OI indicated.
OI = outer; II = inner integument, sp.w. = sporangium wall (closed in *Salvinia*, but initially open in *Azolla*), perisp. = perisporium, m.sp. wall = megaspore wall, lag. = lagenostome, me.gam. = megagametophyte, nuc.b. = nucellar beak.

afterwards the megaspore becomes exposed by the bursting of the apical cover ("roof") of the pollen chamber and forms an archegonium, the burst megaspore membrane forming a forerunner of the lagenostome.

The *Salviniales* represent an offshoot of, presumably, lyginopterid and/or neuropteroid stock. The ovule passes through exactly the same phases of ontogenetic differentiation as the ovules (presemina) of their Carboniferous progenitors (ROTHWELL 1971: *Callospermarion*), as a comparison of *fig. 2* with *fig. 1d* shows. All one has to do for the identification is to replace the conventional terms by those applied to ovular or preseminal structures. The *Marsileales* clearly became arrested at a lower level of ovular phylogeny than the *Salviniales*. There are other differences between the two groups, and the present author has (1961) suggested an affinity between the *Marsileales* and the glossopterid seed ferns on the one hand, and between the *Salviniales* and the pteridosperms of the Euramerican Carboniferous on the other. There is no reason to change this view. If this proposal is accepted (which is, I believe, inevitable), various characters exhibited by the recent *Marsileales* and *Salviniales*, but not or hardly preserved in fossil pteridosperms, may be representative of the conditions that obtained in their Palaeozoic ancestors and may assist us in the reconstruction of the details of their complete life-cycle (such as gametogenesis and shoot ontogeny). The cognisance of these details may well lead to a better understanding of morphological (semophyletic), taxonomic, and phylogenetic relationships among all, living and extinct, cycadophytinous Gymnosperms.

REFERENCES

BECK, C. B. (1960): The identity of Archaeopteris and Callixylon. *Brittonia* **12**: 351–368.

BENSON, M. (1904): Telangium scotti, a new species of Telangium showing structure. *Ann. Bot. (London)* **18**: 161–177.

EMBERGER, L. (1949): Les Préphanérogames. *Ann. Sci. Nat., Bot. (11me Sér.)* **10**: 131–144.

— (1952): Encore sur les Préphanerogames avec remarques générales sur la systématique. *Rec. Trav. Lab. Bot. Univ. Montpellier, Sér. Bot.* **6**: 11–14.

LONG, A. G. (1966): Some Lower Carboniferous fructifications from Berwickshire, together with a theoretical account of the evolution of ovules, cupules, and carpels. *Trans. Roy. Soc. Edinburgh* **66**: 345–375.

MEEUSE, A. D. J. (1961): Marsileales and Salviniales – Living Fossils? *Acta Bot. Neerl.* **10**: 257–260.

— (1963): From ovule to ovary – A contribution to the phylogeny of the megasporangium. *Acta Biotheor. (Leyden)* **16**: 127–182.

— (1964): The bitegmic spermatophytic ovule and the cupule – A re-appraisal of the so-called pseudo-monomerous ovary. *Acta Bot. Neerl.* **13**: 97–112.

— (1966): *Fundamentals of phytomorphology.* New York etc.

— & BOUMAN (1974): The inner integument – its probable origin and homology. *Acta Bot. Neerl.* **23**: 237–249.

PETTITT, J. M. (1966): A new interpretation of the structure of the megaspore membrane in some gymnospermous ovules. *Journ. Linn. Soc. London (Bot.)* **59**: 253–263.

— (1969): Pteridophytic features in some Lower Carboniferous seed megaspores. *Bot. Journ. Linn. Soc. London* **62**: 233–239.

— & BECK, C. B. (1968): Archaeosperma arnoldii – a cupulate seed from the Upper Devonian of North America. *Contrib. Mus. Paleont. Univ. Michigan* **10**: 139–154.

ROTHWELL, G. W. (1971): Ontogeny of the Palaeozoic ovule, Callospermarion pusillum. *Amer. Journ. Bot.* **58**: 706–715.

STIDD, B. M. & J. W. HALL (1970): The natural affinity of the Carboniferous seed, Callospermarion. *Amer. Journ. Bot.* **57**: 827–836.