EVOLUTION OF THE OVULE

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I CONSIDER it a great privilege and an honour to be invited to deliver the Seward Memorial Lecture of 1960. While I did not have the pleasure of knowing Professor Seward personally, I exchanged several letters with him and still treasure a few specimens donated by him, about 26 years ago, in exchange for a number of botanical preparations that I had sent him from Agra.

I must confess at the outset that professionally I am not a palaeobotanist, but a student of the morphology of living plants. However, I am conscious that the morphology of living plants cannot be gainfully studied without some knowledge of the plants that lived in the past (I am sure that the reverse is equally true). In choosing as my subject the evolution of the ovule, I hope to show how the past helps us to understand the present.

THE SEED

Like the mammals among animals, the dominant plants at present are the spermatophytes, more especially the angiosperms. What makes them more successful than others is, no doubt, the presence of ovules enclosed inside an ovary which later becomes a fruit and serves for the dispersal of the seeds. As examples of such fruits are the familiar papaya, tomato, watermelon and pea. Among those features, which appear to be specially significant in the success of this group, one may mention the following:

1. The megaspore (= female gametophyte) is retained in the megasporangium (= nucellus).
2. The nucellus is enclosed in one or two integuments which form highly efficient protective structures.
3. The ovules are enclosed in an ovary, so that the pollen lands on the stigma and not on the nucellus as in the gymnosperms.

4. Fertilization is internal and independent of fluid water.
5. Adequate food reserves are present either in the embryo itself or in the endosperm which serves as nurse tissue for the embryo.
6. The maturation of the seed is followed by a variable period of dormancy, although this is not of universal occurrence.

In the pteridophytes, on the other hand, we sometimes encounter structures which look like seeds but do not fully answer the above description. Most members of the group are homosporous, and even those which are heterosporous have delicate prothalli and motile male gametes requiring free water for their activity. Further, the new embryo is devoid of any substantial food reserves and is parasitic on the gametophyte.

The gymnosperms are in some ways intermediate. Two of the living orders, Cycadales and Ginkgoales, possess swimming sperms, and it is presumed that this was true of all the members of the fossil groups. In the remaining orders the sperms are devoid of cilia. The ovules of all the members of this group have an integument[1].

A notable difference between the majority of gymnosperms and angiosperms is that while in the former the pollen lands on the nucellus, in the latter it alights on the stigma from where a pollen tube leads the male gametes to the embryo sac.

In trying to trace the origin of the ovule and the ovary we must naturally take our clue from fossils, and although vascular plants have apparently been traced as far back as the Cambrian (LECLERCQ, 1956), from

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1. *Nucellangium* (ANDREWS, 1949), a Carboniferous fossil of unknown affinity, has an unintegumented nucellus; however, it is possible that the ovules fell out from a loose integumentary envelope. In the Gnetales there appear to be two integuments, but their exact morphology is problematical.

the point of view of this discussion we shall begin with fossils discovered from the middle Devonian and subsequent periods.

THE DEVONIAN

Ninety years ago, there was a flood in the Catskill region of the New York State which tore away the soil and rocks and exposed a number of fossil trunks. The late Sir William Dawson of Canada referred them, at that time, to the genus *Psaronius* Extensive quarrying operations, carried out in 1920 for the construction of a reservoir, exposed near-ly 50 stumps, some with a diameter of 3.5 ft. Their swollen bases, resembling those of the coconut palm, suggested a swampy habitat. The reconstructed plant was figured as a tree 10 meters high with a swollen base and a crown of leaves 2-3 meters long. Goldring (1924) considered it as the earliest known seed plant and named it *Eospermatopteris*. She interpreted the small oval bodies situated at the tips of the smooth bifurcated rami-fications as seeds. Earlier, Kräusel and Weyland (1923) had described some similar specimens under the name *Aneurophyton* which is, therefore, the valid name. Kräusel and Weyland (1935) also subjected the so-called " seeds " to oxidative maceration and obtained from them masses of cutinized spores. For the present, therefore, this so-called seed-plant has been pushed back among the ferns. It has two kinds of lateral branches : some with short forked appendages and incomplete leaflets, and others with small-er appendages bearing the seed-like bodies which, as already mentioned, are really spore-cases. If true seeds occur, they have not been seen so far.

More interesting than *Aneurophyton*, for our present purpose, is *Archaeopteris latifolia* (ARNOLD, 1935) — a plant so widely distri-buted in the Upper Devonian of Pennsylvania as to earn the name of an " index fossil " of this period. Little is known of its habit, but it was probably a shrub with large fronds reaching a meter or more in length. The sporangia are borne on specialized fertile pinnae forming a part of the frond and are of two kinds. The slender smaller ones contain 100 or more spores, while others which are slightly broader contain 8-16 spores. These are at least 10 times larger and the plant may, therefore, be regarded as a heterosporous fern. This naturally implies the presence of heterothally, i.e. the existence of two different types of gametophytes[2].

THE LOWER CARBONIFEROUS

Twenty years ago, Andrews (1940) re-ported a large cupule named *Magatheca* from the Lower Carboniferous of southern Scotland. He called it the " black tulip " and so it looks in size and form except that the six lobes are more massive than the petals of a tulip. No seeds were, however, found inside it. From another locality in Scotland, Walton (1940, 1949) described a petrified cupule, named *Calathospermum scoticum*, with numerous ovules each having a long stalk and a trumpet-like extension of the salpynx down which the pollen must have passed into the pollen chamber. The cupule is composed of six lobes each with several vascular strands. The stalk has a C-shaped strand pointing to the foliar nature of the cupule which may represent the major part of a frond or even a complete frond.

Some of the cupules of *Calathospermum* contain no seeds but only a few stalks extend-ing to the top. This makes it probable that

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2. Since this was written, Beck (1960) has reported that *Archaeopteris* usually considered to be a fern, and *Callixylon*, classified with the gymnosperms, are parts of the same plant.
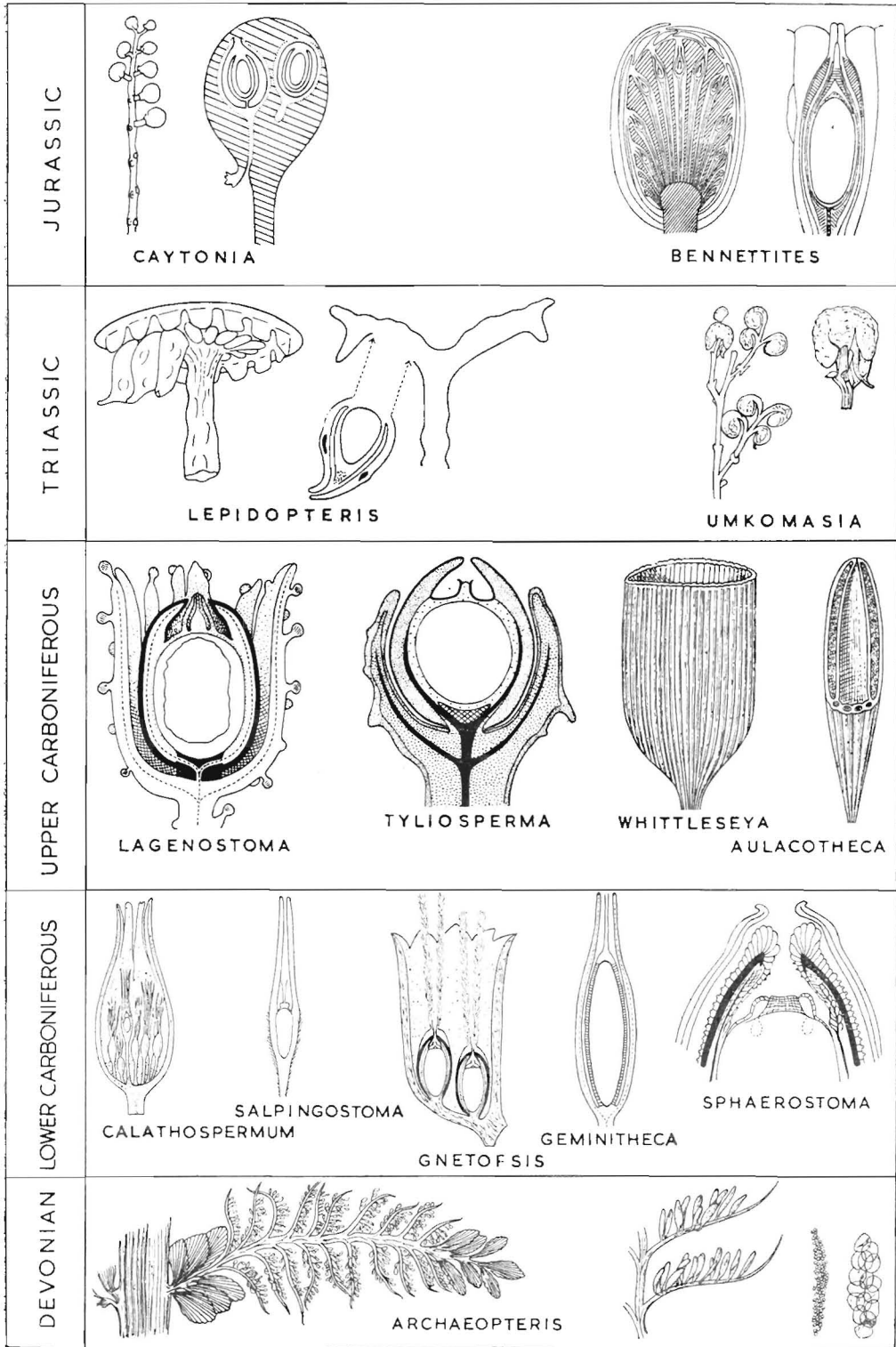

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FIG. 1

the stalks lengthened and extruded the seeds at maturity.

The ovules in the *Calathospermum* cupule match very well with those called *Salpingostoma dasu* and described by Gordon (1941) from the Lower Carboniferous. The lower part of the nucellus contains the megaspore with a cutinized membrane. The upper is differentiated into a dome-shaped pollen chamber which is prolonged into a salpynx. The nucellus is surrounded by six terete integumentary processes, each containing a vascular strand. The processes are fused to the lower part of the nucellus but become free at about the level of the pollen chamber. The space between the salpynx and the integumentary processes is filled with a loose felt of fine hairs. The vascular strand in the pedicel of the ovule is crescent-shaped in section.

Earlier, Benson (1935) described some multi-seeded cupules under the name *Calathiops bernhardti* which are borne on a pinnately branching structure — apparently a modified frond or a portion thereof. Although these are only half the size of *Calathospermum*, the general resemblance is quite appreciable.

Calathiops and *Calathospermum* are forerunners of the type of cupule known as *Gnetopsis* (also Lower Carboniferous) which has only two ovules and was at first believed to belong to some Gnetaceous plant. A characteristic feature of the seeds is the presence of three or four long plumes of hairs at the apex, recalling the stigma of a grass.

Smith (1959) has recorded a new fructification called *Geminitheca scotica* from the Lower Carboniferous of Dunbartonshire. Here the cupules occur in pairs and are borne in bunches at the tips of naked dichotomizing rachides. Each cupule contains two ovules similar to those of *Calathospermum* but possessing a free integument. This has eight lobes which become free at about the level of the base of the lagenostome. Each lobe has a vascular bundle.

Mention may also be made of *Sphaerostoma* (BENSON, 1914) believed to be the seed of *Heterangium grievii*. Here the integument extends beyond the nucellar apex which consists of a flat plinth surface surmounted by an annular pollen chamber or lagenostome. Outside the integument lies the cupule, both having their own vascular supply. In *Sphaerostoma* we thus have a cupule with a single seed.

THE UPPER CARBONIFEROUS

Of the Upper Carboniferous types *Lagenostoma* is the most familiar and so well known that it needs no description. This has a short salpynx which projects slightly beyond the free apices of the integument.

From the Upper Carboniferous of Kansas a new cupulate seed called *Tyliosperma orbiculatum* has been described by Mamay (1954). The cupule almost equals the seed and is deeply divided into at least seven fleshy lobes, each bearing on the outside some irregular parenchymatous processes. The integument is extended into seven lobes forming a canopy over the micropylar region like that of *Conostoma*. The difference between this seed and other members of the Lagenostomales lies in the absence of a vascular system in the integument. On the other hand, several vascular bundles supply the outer margin of the nucellus. The apex of the nucellus is produced into a conical mound, which, like the floor of the surrounding chamber, is enclosed by an epidermal layer continuous with that of the inner surface of the integument.

PERMIAN

Quite a few surprises await us in the Permian. Many geologists believe that at that time and for millions of years afterward there was a large space of water (the Tethys Sea) separating a northern from a southern continent, the latter being known as Gondwanaland. At its maximum development Gondwanaland included nearly the whole of South America, Falkland Islands, most of Africa,

Madagascar, India, Australia, Tasmania and eastern Antarctica.

Important from our present point of view is the wide occurrence in Gondwanaland of certain tongue-shaped leaves long known as *Glossopteris* having a midrib and a network of lateral veins. The stomata are haplochelic and the guard cells have lignine lamellae of the type commonly seen in gymnosperms. The leaves have never been seen attached but from their frequent association with certain branched stems called *Vertebraria* the assumption has often been made that they are parts of the same plant.

While a few pollen grains (*Pityosporites*) and seeds (*Spermatites*) have been assigned to *Glossopteris* (SEN, 1956; PANT, 1958), they have never been found attached. Recently Plumstead (1952, 1956a, 1958) has published a series of rather startling papers based on material collected from southern Transvaal. The fructifications, which are all compressions, have been classified under the following genera; *Scutum, Hirsutum, Lanceolatus, Otto-karia, Cistella* and *Pluma* (FIG. 2). Little of the actual plant tissue has been preserved but some significant observations have been made. In both *Scutum* and *Lanceolatus* a short pedicel arises from the midrib of the leaf and ends in a bivalved envelope. In *Scutum* the valves are round or shield-shaped and provided with a peripheral wing while in *Lanceolatus* they are lanceolate and wingless. Another difference is that in *Lanceolatus* the whole of the pedicel and the valve nearest the lamina are adnate to the leaf. In both genera this valve bears a number of seed-like organs with a stigma-like tip while the other has sometimes been found to bear large bract-shaped pollen-bearing structures. The two halves are believed to have been partly open at least until pollination had taken place after which they fused and the closed cupule served as a fruit. Recently one species of *Scutum, S. dutoitides*, has been transferred to a new genus called *Hirsutum* (PLUMSTEAD, 1958), because the pollen-bearing organs of

this are filamentous rather than flat and bract-like as in most species of *Scutum*.

A fourth fructification, called *Ottokaria*, has been known for many years from the Karharbari beds of India but was found unattached and misinterpreted as a leaf. Plumstead (1956b) now reports two species, *O. buriadica* and *O. transvaalensis*, attached to leaves of the *Gangamopteris* type. There is a strong resemblance between *Ottokaria* and *Scutum*, although it is not known whether the veined half of the bivalved structure had any pollen-bearing organs. The other half, nearest the lamina, shows ovoid sacs with a stigmatic tip. Its peripheral part shows several separate bracts corresponding to the single fluted and dentate wing of *Scutum*.

In *Cistella* the female half again shows well-developed ovoid sacs while the protective half is concave and composed of harder tissue. Neither of the two possesses any wing-like structure and the general resemblance is to a little heart-shaped casket.

The sixth genus *Pluma* is quite different from the above. The male fructification is attached to the base of the lamina and arches outwards in a graceful curve. On the margins there is a fringe, reminiscent of the feathers of an ostrich, and looking like a group of pollen sacs. The female fructification, on the other hand, looks more like a bunch of rounded objects covered by a dark strengthening tissue similar to that in the outer part of a petiole.

Thomas (1958a) has reported yet another fructification called *Lidgettonia* from some specimens collected from a place called Lidgetton in Natal, but this is merely a cupule without any contents.

While the exact nature of the fructifications of *Glossopteris* cannot be considered as fully established, they are undoubtedly of great interest. Plumstead considers them to be more like angiosperms than gymnosperms but better preserved material will, no doubt, be necessary before their true affinities can be determined.
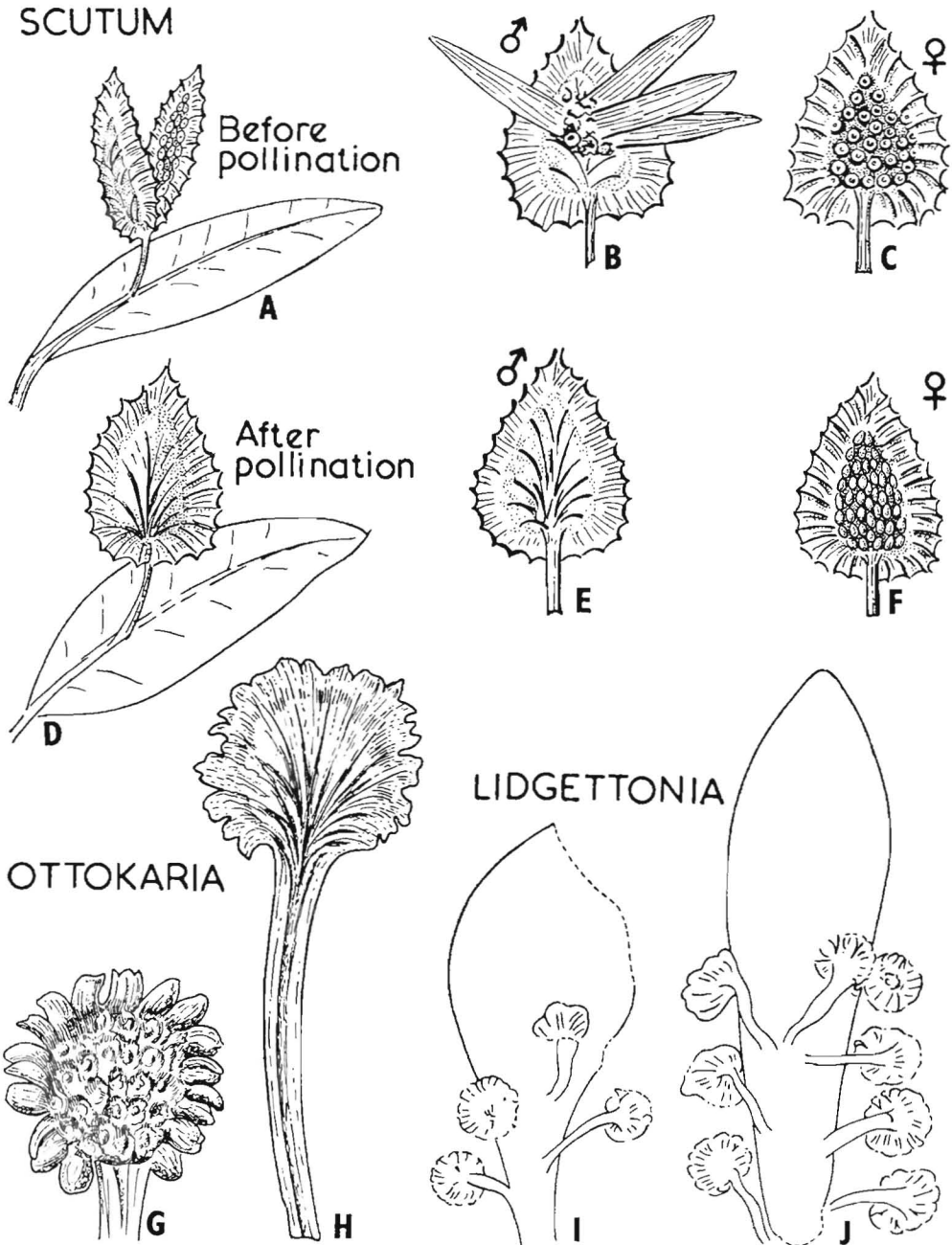
FIG. 2 — Diagrams of fructifications attributed to *Glossopteris*. A. *Scutum*, early stage showing open cupule at the time of pollination. The half nearest the lamina bears the ovules or structures containing ovules; the other half is supposed to bear the microsporangiate organs. B. Enlarged view of " micro-sporophyll " with pollen-bearing " bracts ". C. " Megasporophyll " showing ring-shaped sacs with central " stigma ". D. Closed cupule as seen after pollination. E. Microsporophyll from which the pollen-bearing structures have fallen off and which now performs only a protective function. F. Mega-sporophyll, older stage. G. *Ottokaria*, fertile half of fructification. H. Long, ribbed pedicel bearing veined half of the fructification. I, J. *Lidgettonia*, two fertile leaves bearing stalked cupules. A-F, after Plumstead 1956a; G, after Plumstead 1956b; I-J, after Thomas, 1958a.

If we now review the seed-bearing fructifications of the Palaeozoic, we may say that there are many types of cupules containing one or more seeds. In addition there are other kinds of seeds which have no cupules at all. Those of the Cordaitales belong to this category, although there are also many Pteridosperms which are non-cupular. The valves or cupules of *Glossopteris* are unique in that nothing like them has so far been recorded anywhere in the plant kingdom.

TRIASSIC

Passing on to the Triassic and the Jurassic we come across an interesting genus called *Lepiodopteris* placed under the family Peltaspermaceae. Harris (1932) has assigned to it certain peltate structures bearing seeds having a curved and beak-shaped micropylar canal. These peltate heads may be compared with everted cupules.

Another genus *Umkomasia* (Corystospermaceae) shows an axis bearing forked lateral branches terminating in recurved cupules. Each cupule has a single seed with a long curved micropyle.

JURASSIC

In the Jurassic there are the Caytoniales which have been carefully studied by Thomas (1925) and Harris (1957). Confining ourselves to the female fructifications we find here a pinnate structure in which each branch terminates in a recurved cupule which is almost completely closed leaving just a flap of tissue close to the stalk which was originally designated as the " stigma " as it was supposed to serve as the receptive organ for the pollen. Harris was, however, able to show pollen grains even inside the micropylar canals of the ovules contained in the cupule and he, therefore, substituted the name " lip " for the stigma. Thus, while showing some approach to angiosperms, *Caytonia* remains essentially a gymnosperm. A relationship between the Caytoniales and the angiosperms could be accepted only if detailed comparisons were possible between all the organs of the one with those of the other. To point out a few of the differences, in *Caytonia* the leaves do not show the blindly ending veins found in nearly all flowering plants, the anther is radially symmetrical (bilateral in angiosperms), the pollen is winged (it is never so in angiosperms), and the megasporophyll is branched (there is no counterpart to this in the carpel of any angiosperm). Nevertheless, *Caytonia* does show us the manner in which angiospermy might have been brought about and Thomas (1934) has tried to present some possible stages in the evolution of the angiosperm carpel from *Caytonia*.

CRETACEOUS

The angiosperms appear suddenly in the Cretaceous but there is no clear indication of earlier types (*see* KRAUSEL, 1956) unless we accept the evidence recently brought forward in favour of the existence of certain palm-like plants in the Triassic (BROWN, 1956). More recently Thomas (1958b) has reported some specimens from the Triassic rocks of South Africa which look like inflorescences bearing flowers but no pollen-bearing or ovule-bearing organs have been identified. In one form, *Pykea*, the flower-like structures seem to show " two whorls of free perianth segments, possibly surrounding some fruits or seeds " However, the evidence is not conclusive and we do not know anything about the ovules and ovaries of any undoubted angiosperms of Pre-cretaceous times.

Walton (1949) writes: " If we imagine a *Calathospermum* cupule in which only one segment bears marginal ovules, the central system being suppressed, a cupule somewhat similar to the *Caytonia* fruit would be formed " A cupule of the *Calathospermum* type, he adds, might also serve as a better starting point for the ovary of an angiosperm. It may well be that the integument also originated similarly and we can consider an angiosperm
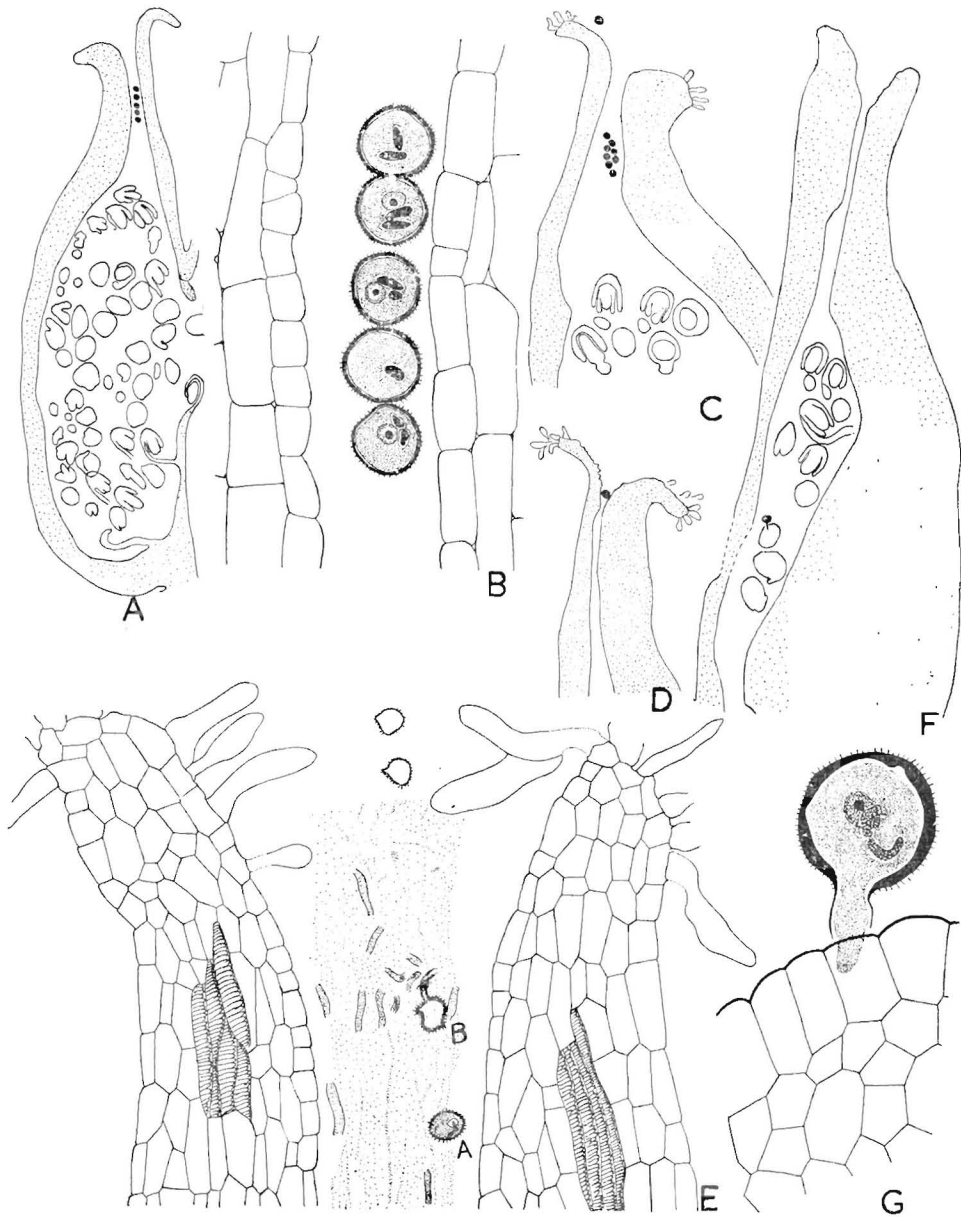
FIG. 3 — *Butomopsis lanceolata*. A. L.s. carpel showing pollen grains in stylar canal. × 25. B. Upper part of same enlarged to show structure of pollen grains. × 375. C. Upper part of a carpel showing a group of eight pollen grains in the stylar canal. × 37. D. One pollen grain lodged at the tip of the stylar canal. × 37. E. Upper end of a carpel showing the stylar canal with irregularly cut pollen tubes and pollen grains; the one at ' B ' has put out a germ tube. × 162. F. L.s. ovary (the section has passed near the surface) showing a pollen grain germinating directly on an ovule. × 25. G. Same, highly magnified × 1125. After Johri, 1936

ovule as a nucellus surrounded by one or two small cupules (integuments) enclosed within a supercupule (*see* also TAKHTAJAN, 1959).

The question arises as to how the cupules originated. An attractive hypothesis is that in a bunch of sporangia a single fertile sporangium became the seed while the others surrounding it became sterilized and fused to form a collective protective structure or integument. This view also receives support from some microsporangiate fructifications of the Upper Carboniferous. They form a group united into a radially companulate flower. In these the microsporangia are elongated and fused to form a single ring. In others they are more or less free and enclose other sporangia (*see* FIG. 1).

It is also possible that too much importance has been attached to the place where the pollen germinated. Depending upon the diameter of the cupular opening or other channel (the stylar canal of angiosperms) it is possible that pollen grains may either enter inside to varying distances or be withheld at the top.

This will be clear from Johri's (1936) work on *Butomopsis* in which he recorded pollen grains in the stylar canals and even the ovaries (FIG. 3). Intracarpellary pollen grains have also been identified in *Anona* (ADATIA, 1946), *Erythronium* (HAQUE, 1951), *Amianthium* (EUNUS, 1951), *Ottelia* (ISLAM, 1950), *Limnocharis* (FIG. 4), *Butomus,* *Hydrocleis*, *Bootia* and *Trillium* (JOHRI & BHATNAGAR, 1957). In three plants—*Butomopsis lanceolatus*, *Trillium sessile* and *Limnocharis emarginata* — pollen grains have even been found to germinate in the ovary.

The mechanism by which the pollen grains gained entrance into the ovary has not been investigated but it may be conjectured that the hollow-styled forms secrete some kind of a " pollination drop " from the stigma as in the gymnosperms including forms like *Ephedra* and *Gnetum* which have a long micropylar canal. In fact *Gnetum* is quite interesting in another respect. Here the pollen grains

may germinate either on the nucellus as in the majority of gymnosperms or at some distance from it in the stylar canal (*see* VASIL, 1959).

It may also be mentioned here that in my laboratory Miss Kusum Kanta has recently succeeded in artificially injecting pollen grains into the ovaries of *Papaver* and bringing about
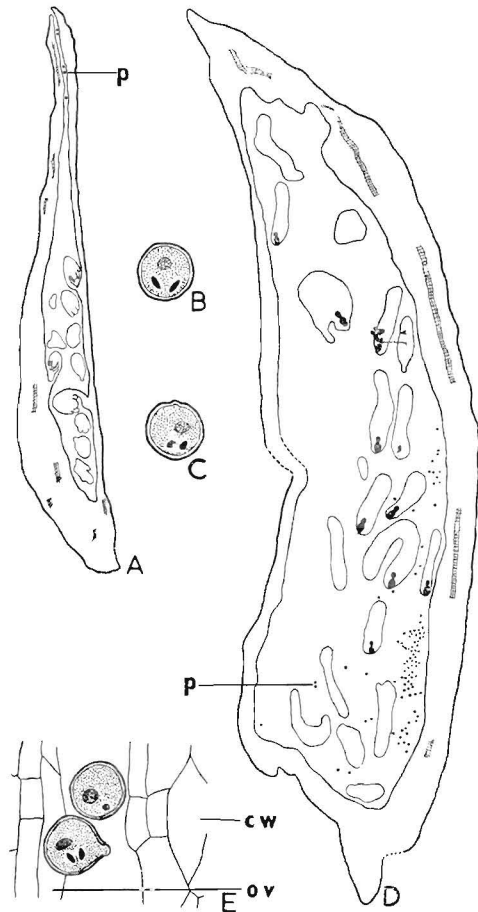

FIG. 4 — *Limnocharis emarginata*. (*cw*, carpel wall; *ov*, part of ovule; *p*, pollen grain.) A. L.s. carpel showing pollen grains in style. × 11. B. One of the pollen grains from A. × 353. C. Mature pollen grain from the anther. × 353. D. L.s. old carpel with numerous pollen grains in ovary; the ovules contain young proembryos. × 11. E. Enlarged view of a portion of the ovary showing a germinated pollen grain adjacent to an ovule. × 353. After Johri and Bhatnagar, 1957.

fertilization followed by maturation of seeds. She prepared suspensions of pollen grains in sterile distilled water containing traces of boric acid and injected them by means of a hypodermic syringe into the ovaries. The seeds obtained by this method proved to be fully viable.

CONCLUSION

In conclusion one may say that while the work already done with ovules of living plants is quite considerable, we still know very little that is really definite and certain about the ovules and ovular envelopes of the primitive fossil angiosperms. The origin of flowering plants remains the abominable mystery as Darwin termed it. However, there are leads here and there and it should be possible to make new and more substantial contributions. Unworked material is abundant in our country and with modern techniques progress can be made much more rapidly than at any time in the past. There is only one thing we cannot ordinarily hope for in palaeobotany. This is a satisfactory knowledge of the gametophytes and fertilization. Perhaps we shall never know the origin of " double fertilization ", which is such a peculiar feature of angiosperms. In dealing with fossils we come across fallen leaves, ripe seeds, and empty husks, and these, too, in a disintegrated condition. Their study demands a great deal of patience, ingenuity and caution.

Before closing one must call attention to the tremendous importance of the discovery of the reproductive structures of a really primitive angiosperm of the Jurassic, Triassic or Carboniferous, whenever the group made its humble beginnings. Almost overnight it would give a new orientation to our systems of classification.

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