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# Evolutionary trends in the reproductive biology of angiosperms\*

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Which embryologic characters are *primitive*, and which are *advanced*, has long been a controversial issue? The comparative embryology of angiosperms and gymnosperms does not provide any useful clue. Single embryological characters are not as useful for phylogenetic and evolutionary considerations as are a group of characters. Moreover, some of the characters may be merely adaptive without any evolutionary significance. The numerous variations cause further complication.

This article is devoted to (a) distribution and phylogeny of anther tapetum, (b) affinities of megagametophyte, (c) can the angiosperm embryo sac be derived from the archegonium in gymnosperms?, (d) primitive and advanced embryological features, and (e) embryological features in Magnoliiflorae s.l. and certain Liliiflorae.

**Key-words**—Evolutionary trends, Reproductive biology, Embryology, Angiosperms.

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## सारांश

आवृतबीजीयों के जननांगी अवयवों में वैकसिक प्रवृत्तियाँ

बी० एम० जौहरी

यह एक विवादास्पद विषय रहा है कि कौन भूणीय लक्षण आद्य हैं तथा कौन समुन्नत। आवृतबीजी एवं अनावृतबीजी पौधों के तुलनात्मक भूणीय अध्ययन से भी कोई महत्वपूर्ण निष्कर्ष नहीं निकलता। लक्षणों के एक समूह की अपेक्षा एक भूणीय लक्षण से जातिवृत्तीय एवं वैकसिक रहस्यों का अध्ययन नहीं किया जा सकता। अत्याधिक विविधता से और जटिल समस्यायें उत्पन्न हो जाती हैं।

प्रस्तुत शोध-पत्र में (अ) परागकोश टेपीटम का जातिवृत्त एवं वितरण, (आ) गुरु-गैमीटोफाइट की सजातीयता, (इ) क्या आवृतबीजीयों में भ्रूण-कोष की उत्पत्ति अनावृतबीजीयों की स्त्रीधानी से हुई है? (ई) आद्य एवं समुन्नत लक्षण, एवं (उ) मैग्गोलिफलोरी एवं कुछ लिलीफलोरी में भूणीय लक्षणों की विवेचना की गई है।

## DISTRIBUTION AND PHYLOGENY OF ANTHETAPETUM

Pacini *et al.* (1985) discuss the form, function and possible phylogeny of tapetum in the Embryophyta. The tapetum is of considerable physiological significance because all nutritional material entering the sporogenous cells/microspores/pollen grains originates or passes through it. Between the 'secretory' (glandular) and 'amoeboid' (intrusive, plasmodial) types, an intermediate 'pseudoamoeboid' type is also recognized. The tapetal protoplasts extend into the pollen sac but do not fuse to form a true periplasmodium as in Dipsacaceae (Kamelena, 1980) and Triuridaceae (Rubsamen-Weustenfeld, 1991).

According to Pacini *et al.* (1985) in 207 angiosperm families the type of tapetum is a family character. The amoeboid type occurs mostly in monocots. Both types of tapetum have been reported in at least 12 (either primitive or advanced) families : Caesalpiniaceae, Caprifoliaceae, Chenopodiaceae, Droseraceae, Euphorbiaceae, Gentianaceae, Haemodoraceae, Helleboraceae, Lauraceae, Solanaceae, Vitaceae, Winteraceae, and Zingiberaceae (the only monocot family).

The secretory tapetum is primitive and the amoeboid type advanced. The type of tapetum depends on locule diameter, pollen shape or dry/wet habitats. There is no unequivocal proof that the secretory type is primitive, but it appears to be

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so because of the widespread occurrence in gymnosperms and angiosperms.

#### AFFINITIES OF THE MEGAGAMETOPHYTE

Anton and Cocucci (1984) attempt to establish the affinities of the megagametophyte of the Poaceae (Gramineae) with those of other monocot families.

The Polygonum type of embryo sac with supernumerary antipodal cells (6-300) has been reported in the Poaceae. In *Echinochloa frumentacea* there are three cells, each two- or three-nucleate; in *Eleusine coracana* each of the three antipodal cells is uninucleate (Narayanaswami, 1955a, b).

Proliferation of antipodals—both in dicots and monocots, has arisen independently in unrelated families even in monocots: Amaryllidaceae, Araceae, Hypoxidaceae, Juncaginaceae, Liliaceae, Marantaceae, Restionaceae and Zannichelliaceae (see Johri *et al.*, 1992).

Clayton (1981) considers the possibility of origin of Poaceae from Flagellariaceae. However, *Flagellaria indica* shows bisporic Allium type of embryo sac, and three ephemeral antipodals (Subramanyam & Narayana, 1972). Therefore, the origin of Poaceae—monosporic Polygonum type of embryo sac with supernumerary persistent antipodals—from the Flagellariaceae is doubtful. Other monocot families which may be considered as ancestors of Poaceae are Joinvilleaceae, Centrolepidaceae and Restionaceae—all members (along with Flagellariaceae) of the order Restionales. Of these, Restionaceae is very closely related to Poaceae; Anton and Cocucci (1984) confirm this alliance.

#### CAN THE ANGIOSPERM EMBRYO SAC BE DERIVED FROM THE GYMNOSPERM ARCHEGONIUM/A?

Cocucci (1973) and Favre-Duchartre (1984) consider the homology of a four-celled archegonium with the egg apparatus and the upper polar nucleus in angiosperms. The closest example is of the *Oenothera* type of monosporic embryo sac; the lower polar and antipodal nuclei are not formed. Another good example is *Butomopsis lanceolata* of the Alismaceae (Johri, 1936), the chalazal nucleus of the two-nucleate bisporic embryo sac degenerates. The upper nucleus divides twice and a three-celled egg apparatus and the upper polar nucleus are produced. An eight-nucleate gametophyte is equated to two archegonia, and a 16-nucleate *Penaea* type of tetrasporic embryo sac to four archegonia.

In *Oenothera*, *Polygonum* and *Allium*, the two synergids are sister cells, and so are the egg and upper polar. In *Penaea* type, only the micropylar quartet organizes and functions as in *Oenothera*, *Allium* and *Butomopsis* (see Johri *et al.*, 1992).

The homology is carried further by equating the three antipodals and lower polar nucleus in *Polygonum*, *Allium* and *Adoxa* to a second archegonium. The two lateral three-celled groups and one three-celled chalazal group in *Penaea* are equated to three archegonia (see Cocucci, 1973; Favre-Duchartre, 1984). The above comparison is completely unconvincing; the archegonia in gymnosperms organize in a monosporic gametophyte (after meiosis II of megaspore mother cell, the basal megaspore produces the gametophyte). Moreover, the ventral canal cell always lies above the egg cell. Khan (1943) reported double fertilization (egg nucleus and ventral canal nucleus) in *Ephedra foliata*. Friedman (1990) points out that in *E. nivadensis* there is no wall between the egg and ventral canal nucleus. The latter, at the time of fertilization, migrates to a more central position in the egg cell (simulating the upper polar nucleus in an angiosperm embryo sac). Then, double fertilization takes place, comparable to that in angiosperms. On this basis alone, Friedman erroneously seeks homology between gymnosperms and angiosperms.

Battaglia (1989) discusses the evolution of the embryo sac of angiosperms and devotes considerable attention to (a) female gametophyte of *Welwitschia* and *Gnetum*, (b) concept of the primitive embryo sac, and (c) variations in organization and structure of mono-, bi- and tetrasporic embryo sac in angiosperms. The archegonium in most gymnosperms arises through two mitoses, reduced to a single mitosis in *Taxus*, but both mitoses have been suppressed in *Welwitschia* and *Gnetum*. In *Welwitschia*, as in *Gnetum*, there is no differentiation of the archegonial initials, and the archegonium has been totally suppressed. In spite of the homologies discussed above, the embryo sac in angiosperms can not be derived from the archegonium-bearing female gametophyte of gymnosperms.

The angiosperm embryo sac cannot be distinguished into less evolved (primitive) and more evolved (advanced) types on the basis of (a) the number of nuclear divisions (meiosis followed by mitoses), (b) polarization of the nuclei immediately after meiosis I (tetrasporic), (c) after meiosis II (bisporic), and (d) after two/three mitoses (monosporic gametophytes), (e) total number of nuclei in the embryo sac, and (f) organization of the

embryo sac. It may be emphasized that considerable reduction and elaboration have taken place in the angiosperm embryo sac. However, the origin and evolution of the angiosperm embryo sac still eludes us.

### PRIMITIVE AND ADVANCED EMBRYOLOGICAL CHARACTERS\*\*

The 'Primitive Features' usually comprize: a thick anther wall, widespread endothelial thickenings, several middle layers, secretory (glandular) tapetum; successive cytokinesis in pollen mother cells after meiosis; two-celled pollen grains; anatropous, bitegmic, crassinucellate ovule, micropyle formed by both integuments, massive parietal tissue including nucellar cap formed by division in apical cells of the nucellar epidermis and their derivatives; monosporic Polygonum type of embryo sac; chalazogamy; nuclear type of endosperm, sometimes ruminant; typical dicotyledonous embryo with a conspicuous suspensor; seed albuminous, sometimes perispermous; seed-coat thick, formed by both testa and tegmen.

The 'Advanced Characters' include: a thin anther wall, fibrous thickenings limited mostly to endothecium, ephemeral middle layer, amoeboid (plasmodial, invasive, intrusive) tapetum; simultaneous cytokinesis by furrowing in pollen mother cells after meiosis; three-celled pollen grains; anatropous, unitegmic, tenuinucellate ovule, micropyle narrow and short, the inner epidermis of integument differentiates as endothelium; megaspore haustoria (*Sedum*), mono-, bi- and tetrasporic embryo sac, synergids sometimes absent (*Plumbago*), antiopodal nuclei may or may not organize into cells, ephemeral; embryo sac (*Exocarpos*), synergid and antipodal haustoria (*Quinchamalium*); endosperm of the cellular type, chalazal, micropylar or both micropylar and chalazal haustoria develop, sometimes the haustoria invade the placenta and even pedicel; embryo with a few-celled suspensor, sometimes suspensor haustoria conspicuous; seed exalbuminous, perisperm usually absent; seed-coat exotestal.

These embryological characters cannot be considered to be *strictly* primitive or advanced, since many primitive features have been observed in

advanced families and vice versa. A few examples will illustrate this point (see Johri *et al.*, 1992).

1. *Tapetum*—Secretory and amoeboid tapetum is randomly distributed in Polypetalae, Sympetalae and Monocots.

2. *Pollen grain*—Successive and simultaneous cytokinesis in post-meiosis microspore mother cells, two- and three-celled pollen grain; single pollen grains, and pollen grains in permanent dyads, tetrads, pollinia and massulae occur in primitive as well as advanced taxa. Most of these conditions are known in the Orchidaceae, a highly evolved monocot family.

3. *Ovule*—Since anatropous ovule occurs in Magnoliiflorae, it is considered to be a primitive character. In fact, the simplest (not necessarily the most primitive?) ovule is orthotropous which undergoes curvature to give rise to anatropous, hemianatropous, campylotropous, and sometimes circinotropous condition. Seeking homology with the gymnosperm ovule, the orthotropous angiosperm ovule should indeed be considered primitive.

4. *Embryo sac*—The development and organization of the female gametophyte is highly variable in Polypetalae, Sympetalae and Monocots. Further consideration becomes even more debatable since mono- and bisporic condition may occur in the same species—*Tellima grandiflora* (Ratnaparkhi, 1972); mono-, bi- and tetrasporic embryo sacs develop in *Erigeron* (Harling, 1951), several types of tetrasporic embryo sacs—*Adoxa*, *Drusa*, *Fritillaria* and *Chrysanthemum cinerariaefolium*—occur in the same genus, e.g., *Tamarix* (Johri & Kak, 1954).

5. *Endosperm*—The Nuclear type of endosperm is characteristic of Polypetalae, Cellular type of Sympetalae, and Helobial type of Monocots (Johri *et al.*, 1992). Each of these three types has been observed in all the three groups. Some families like Trapaceae (Ram, 1956), Podostemaceae (Mukkada & Chopra, 1973) lack endosperm altogether. These families have, therefore, developed alternative strategies for the nourishment of the embryo, e.g., pseudo-embryo sac in Podostemaceae, and haustorial suspensor in Orchidaceae (Swamy, 1943).

6. *Embryo*—The embryo is typically dicotyledonous in Polypetalae and Sympetalae, and has only a single cotyledon in Monocots. In a dicotyledonous taxon, *Trapa* (Ram, 1956), one cotyledon is completely suppressed.

7. What about the organless (undifferentiated) embryo as in Lentibulariaceae, Burmanniaceae, Mayacaceae, Xyridaceae, Rapateaceae, Eriocaulaceae, Centrolepidaceae, Orchidaceae, and others? We do not have any knowledge as to why some embryos

\*\*For literature see: Anton and Cocucci (1984), Battaglia (1989), Brewbaker (1967), Canright (1963), Cocucci (1973), Dahlgren and Clifford (1981), Fagerlind (1944), Favre-Duchartre (1984), Johri *et al.* (1992), Pacini *et al.* (1985), Rübssamen-Weustenfeld (1991)—cited in the text already.

have remained arrested? Their germination should be studied to throw light on their differentiation (see Johri *et al.*, 1992).

### Embryological features in Magnoliiflorae s.l. and certain Liliiflorae

Dahlgren and Clifford (1981) compare the embryological features of Magnoliiflorae—especially Annonaceae, Aristolochiaceae, Lactoridaceae, Chloranthaceae and Myristicaceae, and the Liliiflorae—Dioscoreales (Dioscoreaceae, Trichopodaceae, Taccaceae, Trilliaceae) and Asparagales (Smilacaceae, Philesiaceae, Convallariaceae and a few more families). Some of the characters are listed below (see Johri *et al.*, 1992):

1. Anther wall is of the Dicotyledonous type in *Tacca*, the only case known in monocots.

2. Tapetum is of the secretory type in all Magnoliiflorae, as also in all Dioscoreales and most Asparagales.

3. Simultaneous post-meiotic cytokinesis occurs in pollen mother cells of most dicots; successive type is widely distributed in monocots. Both types are known in *Aristolochia*, *Annona*, *Cananga* and certain other Magnoliiflorae. The simultaneous type is known in some species of *Dioscorea* and *Tacca* (monocots).

4. Monoaperturate (often sulcate) pollen are common in Monocots and some Magnoliiferae, although inaperturate, biaperturate types occur as well.

5. Bicelled pollen grains are reported in practically all Magnoliiflorae and nearly all Liliiflorae; three-celled pollen grains occur in both groups.

6. The ovules of Magnoliiflorae are usually anatropous, bitegmic and crassinucellate; in the Dioscoreales and closely related families of Asparagales, the early stages of development are similar although exceptions occur. The ovules are orthotropous in *Stemona*; *Trichopus* lacks a parietal cell. The Polygonum type of embryo sac is common in all these groups; Allium type is known in the Trilliaceae and Orchidaceae.

7. The Magnoliiflorae have Cellular type of endosperm development. The Nuclear type is widespread in Dioscoreales and many berry-fruited Asparagales.

8. In some families, as in Saxifragaceae, all the three types of endosperm are reported.

The initial development of endosperm may be of the Cellular type, but free-nuclear divisions occur in each cell. Finally, the endosperm becomes completely cellular. This type of development is

described as Cellular-Nuclear-Cellular and is rare.

9. Ruminant endosperm, common in Annonaceae, Aristolochiaceae, Canellaceae, Degeneriaceae, Eupomatiaceae and Myristicaceae (Magnoliiflorae), is also known in *Avetra* and *Trichopus* (Dioscoreales).

10. The embryo is small in relation to the endosperm, in most Magnoliiflorae and some of the Liliiflorae (*Paris*, *Trillium*, *Madeola*), and is fairly small in most Dioscoreales. In both monocots and dicots the stem tip is invariably terminal and cotyledon/s lateral. The interpretation of a lateral stem tip in the monocot embryo has been unequivocally disproved (see Swamy & Krishnamurthy, 1977).

11. In the Magnoliiflorae starchy endosperm is reported in several members of Annonaceae, Aristolochiaceae, Myristicaceae and others (see Johri *et al.*, 1992). Starch is occasionally present in the Dioscoreales (*Croomia*, sometimes in *Paris* and *Trillium*) and related Asparagales (*Ripogonum*, *Streptopus*).

12. Polyembryony and apomixis are common to both mono- and dicots.

The above account clearly indicates that the Magnoliiflorae show a number of monocot characters, and Dioscoreales and berry-fruited Asparagales (Liliiflorae) a number of dicot features. Both the super-orders share some common characters. At least on the basis of characters under consideration, the dicots and monocots are not very distinctly demarcated. However, the similarities may not indicate any relationship.

Brewbaker (1967) points out the phylogenetic significance of two- and three-celled pollen grains. Erdtman (1969) refers to the systematic significance of dyads and tetrads of microspores, and the importance of pollen morphology in taxonomy. Canright (1963) uses pollen morphology as a basis of phylogeny of some Ranalian families. Walker and Skvarla (1975) propose a new concept in the evolutionary morphology of angiosperms on the basis of primitively columella-less pollen.

The ovule is considered as an indicator of the evolutionary status of angiosperms: ovular morphology as a basis of classification of dicotyledons; developmental and structural studies of integuments for consideration of taxonomic and phylogenetic problems; micropyle as an indicator of primitiveness in angiosperms.

Fagerlind (1944) refers to the phylogeny of female gametophyte on the basis of tetrasporic embryo sacs. Single embryological characters are not as useful for phylogenetic and evolutionary considerations as a group of characters. Anatomical



and chaemotaxonomic data provide significant support to embryological data.

The assignment of Nymphaeaceae to the monocots has been repeatedly questioned, and it has been emphasized again and again that Nymphaeaceae are a dicotyledonous group with a distinct dicot embryo. In spite of the fact that Dahlgren and Clifford (1981) accept that in Nymphaeaceae the leaves are net-veined, and the embryo has two distinct cotyledons, they still assign this family to the monocots.

### PROSPECTS

I wish to emphasize that a comparative study of the embryological characters of angiosperms and tracing homologies with the gymnosperms does provide a good deal of interesting information, but fails to reflect (convincingly) common evolutionary tendencies between the two groups.

The occurrence of primitive characters in the advanced taxa (even at the species level) and vice versa can be interpreted to indicate that the primitive and advanced characters have independently originated in mono- and di-cots. Whether the intriguing problem of primitive and advanced features in angiosperms can ever be solved, remains to be seen.

It is now time that, based on all the above evidences, separate monographs on different orders are prepared. Every effort should be made to fill up the gaps in our knowledge of reproductive biology. Separate monographs should also be prepared on (a) major crops, including the breeding behaviour of parents and reciprocal crosses, (b) parasites and semi-parasites (see Kuijt, 1955), saprophytes, and (c) insectivorous plants. There are very few such monographs available at present.

The percentage of variations met with during various developmental phases should be studied to determine the dominant condition. Also, the temporal relations of developmental phases. Another important aspect which needs attention is the use of cross- and longi-sections as well as cleared and dissected wholemounts to trace the structure and disposition of extensions of embryo sac, synergid, endosperm and suspensor haustoria. It is also necessary to follow the development of embryo from longisections in various planes and transections of the various tiers. Seed-coat structure requires further study from paradermal, tran- and longisections, and macerations.

The application of histochemical techniques, and electron, fluorescence, interference (Nomarski effect), phase contrast and polarizing microscopy

has already resulted in significant advances in our knowledge. The study of living material by enzymatically isolated generative and sperm cells, embryo sac, central cell, egg cell, synergid, antipodal cells, endosperm and embryo is an excellent method for embryological investigations (see Zhou & Yang, 1985).

These relationships can be further strengthened by using comparative data from (a) morphology and vegetative anatomy, (b) floral morphology and anatomy [attention is invited to two recent publications of Endress (1990a, b)], (c) cytology, (d) palynology, and (e) chemotaxonomy.

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