

EVOLUTIONARY TENDENCIES IN THE REPRODUCTIVE BIOLOGY OF ANGIOSPERMS

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Which embryologic characters are *primitive*, and which ones *advanced*, has been a controversial issue since long? 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 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 archegonium in gymnosperms give rise to the angiosperm embryo sac? (d) primitive and advanced embryological features, and (e) embryological features in Magnoliiflorae s.l. and certain Liliiflorae.

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DISTRIBUTION AND PHYLOGENY OF ANTHER TAPETUM

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.*, 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 so because of the widespread occurrence in gymnosperms and angiosperms.

AFFINITIES OF THE MEGAGAMETOPHYTE

Anton & 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 *Panicum miliare*, each of the three antipodal cells is uninucleate (Narayanaswami, 1955 a, b).

Proliferation of antipodals—both in dicots and monocots — has arisen independently, in unrelated families even in monocots: Amaryllidaceae, Araceae 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 & 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 the *Oenothera* type of monosporic embryo sacs, the lower polar and antipodal nuclei are not formed. Another good example is *Butomopsis lanceolata* (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*.

The homology is carried further by equating the three antipodals and lower polar nucleus to a second archegonium in *Polygonum*, *Allium* and *Adoxa*. The two lateral and one chalazal group in *Penaea* are equated to three archegonia. The above homology is completely unconvincing since the archegonia in gymnosperms organize in monosporic 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 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 seeks homology between gymnosperms and angiosperms.

Battaglia (1989) discusses the evolution of the embryo sac of angiosperms and devotes considerable attention to the female gametophyte of *Welwitschia* and *Gnetum*, concept of the primitive embryo sac, and variations in organization and structure of mono-, bi- and tetrasporic embryo sacs 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 archegonial initials, and the

archegonium has been totally suppressed.

Can the angiosperm embryo sac be distinguished into less evolved (primitive) and more evolved (advanced) types? Can the number of nuclear divisions (meiosis followed by mitoses), polarization of the nuclei immediately after meiosis I (tetrasporic), after meiosis II (bisporic), and after mitoses (monosporic gametophytes), total number of nuclei in the embryo sac, and organization of the embryo sac, provide a satisfactory solution?

In spite of the homologies discussed above, the embryo sac in angiosperms cannot be derived from the archegonium-bearing female gametophyte of gymnosperms. It may be emphasized that considerable reduction and elaboration have taken place in the angiosperms embryo sac. However, the origin and evolution of the angiosperm embryo sac still eludes us.

PRIMITIVE AND ADVANCED EMBRYOLOGICAL CHARACTERS

The Primitive Features usually comprise: a thick anther wall, widespread endothecial 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; 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 (plasmoidal, 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; mono-, bi- and tetrasporic embryo sac, synergids sometimes absent (*Plumbago*), antipodal nuclei may or may not organize into cells, ephemeral; 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.

1. *Tapetum*: Secretory and amoeboid tapetum, two- and three-celled pollen grains, successive and simultaneous-cytokinesis in post-meiosis microspore mother cells are randomly distributed in Polypetalae, Sympetalae and Monocots.

2. *Pollen Grain*: Single pollen grains, and pollen grains in permanent dyads, tetrads, pollinia and massulae occur in primitive as well as advanced taxa. All 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 ovule is orthotropous which undergoes curvature to give rise to anatropous, hemianatropous, campylotropous, and sometimes circinotropous condition. Seeking homology with the gymnosperms, orthotropous 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). All the three types have been observed in all the three groups. Some families—*Trapaceae* (M. Ram, 1956), *Podostemaceae* (Mukkada & Chopra, 1973)—lack endosperm altogether. These families have, there-

fore, developed alternative strategies for the nourishment of the embryo, e.g. in *Podostemaceae*, pseudo-embryo sac, 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*, *Centrolpidaceae*, *Orchidaceae*, and others? We do not have any knowledge as to why some embryos have remained arrested? Their germination should be studied to throw light on their differentiation (see Johri *et al.*, 1992).

EMBRYOLOGICAL FEATURES IN MAGNOLIIFLORAE s.1. AND CERTAIN LILIIFLORAE

R. 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) (see Johri *et al.*, 1992). Some similarities are:

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

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

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

4. Monoaperturate (often sulcate) pollen are common in Monocots and some Magnoliiflorae, 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 are usually anatropous, bitegmic and crassinucellate in the Magnoliiferae; 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.

In some families, the initial development of endosperm is of the Cellular type, but free-nuclear divisions occur in each cell. Finally, the endosperm becomes completely cellular. This is described as the Cellular-Nuclear-Cellular type and is rare.

9. Ruminant endosperm, common in Annonaceae, Aristolochiaceae, Canellaceae, Degeneriaceae, Eupomatiaceae and Myristicaceae (Magnoliiflorae), is also known in *Avetia* 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 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. The seeds have copious starchy endosperm; starch is occasionally present in the Dioscoreales (*Croomia*, sometimes *Paris* and *Trillium*) and related Asparagales (*Ripogonum*, *Streptopus*). In the Magnoliiflorae, starchy endosperm is reported in several members of Annonaceae, Aristolochiaceae, Myristicaceae and others.

12. Polyembryony and apomixis are common to 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 superorders also have some common characters. It is quite

obvious that in many cases 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 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.

CONCLUSION

I wish to emphasise 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 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 taxa do have specific and distinctive features of their own. Whether the intriguing problem of primitive and advanced features in angiosperms can ever be solved, remains to be seen.

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