Links between embryology and evolutionary floral morphology

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The comparative embryological studies conducted in India over several decades (and similar studies from other countries) today represent a treasure trove of information on the diversity of plant structure for evolutionary studies. Such evolutionary studies have become possible using the results of molecular phylogenetic analyses, which provide an increasingly solid backbone for plant relationships. Molecular developmental genetic studies and new studies on the diversity of extant and fossil plants are complementary approaches to unravel evolutionary changes. However, despite spectacular novel insights of the new molecular fields, a comprehensive understanding of the diversity of plant structures is still far in the future. It is encouraged that a synthetic approach between these different disciplines be increasingly envisaged.

IT may at first seem odd to make a connection between evolutionary floral morphology and embryology, as there is a big developmental gap between an embryo and flowers. However, there is indeed a connection, especially via the ovules and the new fields of molecular systematics and evolutionary molecular developmental genetics (evo–devo).

Comparative embryology is largely dependent on microtome serial sections. Therefore, for practical reasons, classical studies conveniently included aspects of floral morphology, anatomy and histology. Embryo development was studied together with the area surrounding the embryo, the embryo sac and the ovule. Thus it included not only the young, embryonic, sporophyte, but also the gametophyte and the maternal sporophytic organ in which the embryo sac is formed. (Confocal techniques to circumvent sectioning used to be only feasible with thin ovules, which are restricted to evolutionarily derived angiosperm groups.) Likewise, comparative embryology includes pollen (microspores), male gametophyte and the paternal sporophytic organ in which the male gametophyte is formed, the anther and its microsporangia. Since the ovules and anthers (or microsporangia) are the evolutionarily oldest floral organs – the ovules even much older than the flowers, also the anthers, although in a different form – they are basic morphological units of the flowers.

In the studies by Panchanan Maheshwari and his long time collaborator and later successor, B. M. Johri, the standard embryological analysis of a plant always included development of ovule and anther, and contained meticulous drawings of longitudinal and transverse sections of various developmental stages. Both embryologists had a vast number of students who all used the same style of analysis (especially in the decades from 1930 to 1970)[1]. This style was the mark of quality of the embryological school by Maheshwari. Even if these studies were restricted to a single plant species in many cases, the fact that they were performed in such a great number, in hindsight significantly enhances the value of each single study, because it enabled the opening of an additional dimension, the dimension of diversity. What appeared somewhat uniform in scope, proves its value today, because all these studies taken together reveal a wealth of the diversity of ovules and other floral structures. Other embryologists and their students also made significant contributions[2–7]. Maheshwari's teacher, W. Dudgeon, was a former student of C. J. Chamberlain in Chicago, a pioneer in cycad embryology[8]. The Indian contribution is outstanding because it is the work of an especially large scientific community. Large comparative embryological studies cannot be done in a short time and by an only small number of scientists. It would be almost impossible, even with a sophisticated technology, to produce such a wealth of information throughout the flowering plants in the current organization of research.

Especially the detailed ink drawings of these publications are of the highest value, as they often convey even more information than the text. They show how the features were, before they were translated into a necessarily simplifying (and perhaps sometimes distorting) terminology. Classical works include the books by Maheshwari[9–11] and Johri[12,13]. The *Journal of the Indian Botanical Society*,

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Proceedings of the Indian Academy of Sciences, Proceedings of the National Institute of Science of India, Current Science and *Phytomorphology* are treasure troves of embryological publications, especially during the period of active research and research organization by Maheshwari and Johri, i.e. from about 1930 till the 1970s. The Department of Botany, Centre of Advanced Study (CAS) at the University of Delhi, was internationally leading in embryological research at that time. Never before, and never again afterwards has there been such a concentration of active embryologists anywhere in the world. It should be emphasized that notwithstanding the unique growth of knowledge in the diversity of embryological features during that time, our knowledge on basic embryological features in many angiosperm families is still almost zero and careful comparative studies are badly needed[14].

When I was a young plant systematist with interest in systematic embryology, I had the opportunity to spend several months at CAS, University of Delhi as a senior research fellow. I had all the support from Johri and H. Y. Mohan Ram, both former students of Maheshwari. Thus I was privileged to experience the congenial atmosphere at the department.

The subsequent radiations of embryological research into new fields, such as tissue culture, reproductive biology and applied technologies, by the schools of Maheshwari and Johri, have been observed, reported and evaluated by several botanists[15–18]. However, the connections between embryology and evolutionary flower biology were not emphasized in these accounts, probably because they are not so obvious at first sight.

Evolutionary floral morphology

The past fifteen years have brought an unprecedented development in our understanding of plant phylogeny and evolution in opening up new directions of research. Molecular phylogenetics has begun to reveal parts of the tree of life[19]. Only now that we have a growing backbone of the phylogeny of angiosperms[20–23], does it become possible to study the evolution of features based on a sound basis. Molecular developmental genetics has begun to show mechanisms of the origin of form[24–26]. Studies of exquisitely preserved floral fossils provide new glimpses on angiosperm history[27–31]. All these fields together provide a completely new basis for evolutionary studies. Numerous investigations have analysed character evolution of floral features in diverse groups of angiosperms based on phylogenetic studies[32–34]. Such studies need to be refined by more detailed character matrices and the use of better resolved phylogenetic trees.

Research on model organisms is at the centre of current biological research. Although the focus on model organisms is an extremely successful concept to study the complexity of life, a few model organisms cannot explain evolution.

To do this, a focus on diversity is equally necessary. Diversity and complexity are mutually dependent. Without diversity, complexity is not possible, and vice versa. It is difficult or almost impossible to focus on both at the same time. To overcome this dilemma is a difficult task. The field of evo–devo in plants is only beginning[35]. The Floral Genome Project[36–39] is an attempt to focus on an intermediate level in working with a number of semi-model plants that are chosen according to their potential evolutionary interest. This approach is expected to open a new perspective to understanding flower evolution.

Ovules

Ovules have become a central organ in plant developmental genetics[40–42]. Likewise, ovules and their evolutionary history in the spermatophytes continue to intrigue palaeobotanists[43]. Ovules are the oldest floral organs, as they can be traced back to the Devonian[44,45]. The emphasis of diversity of certain traits of ovules has shifted in the course of time. For instance, early ovules were all orthotropous, but were either radially symmetrical (radiospermic, i.e. round in TS) or disymmetrical (platyspermic, i.e. flat in TS); these two forms appear to have characterized major clades. In contrast, in angiosperms, the symmetry changed between radially symmetrical (orthotropous) and monosymmetric (anatropous), whereas the difference between round and flat is of minor importance, as it does not characterize larger groups.

Ovules are especially interesting in angiosperm systematics and evolution because their classical features are macrosystematically even more constant than previously assumed. For instance, it became clear that many groups that were traditionally classified in Rosidae are correctly placed in asterids, and most or all of those have tenuinucellate ovules. Thus they fit much better with asterids also in this structural feature. It had also been seen long ago that there is a diversity of forms within the classical categories of 'crassinucellate' and 'tenuinucellate' ovules, and there have been attempts to use a more differentiated terminology[7,46]. Although such attempts were based on the development of ovules of a large number of angiosperms, they were not carried out in a systematic context. It would be useful, to comparatively study a larger clade and seek constant features, at first independent of any terminology.

It appears that new patterns are present, which have not been discussed before and which characterize certain larger clades. The classical terminology should not be straitjacketed. We can now study these different forms and variants within many well-supported clades, and compare them with similar forms from other clades. Therefore, it will be possible to find clade-specific forms and variants. For instance, it appears that extremely tenuinucellate forms, in which the entire nucellus is filled with the meiocyte below the epidermis (or even the lower part of the meiocyte is

below the attachment level of the integument, and thus has an 'inferior' position) are characteristic of euasterids. It will be of interest to search whether and in which other clades such ovules are present. Likewise, it will be of interest to characterize variants of less extremely tenuinucellate forms in basal clades of asterids and in other angiosperms. Based on the the new phylogenetic results, it will be possible to trace the evolution of such forms. It can be expected that a new, more differentiated terminology can be devised, once this new information is available[47]. It should be emphasized that such a comparative study throughout the angiosperms is a vast task, which is still awaiting, and needs to rely on the information available in the literature, but also on new studies. The same is true for the understanding of ovule curvature. What are the developmental and evolutionary relationships between 'orthotropous', 'hemianatropous', 'anatropous', 'campylotropous', and 'amphitropous' ovules? Aspects of the specific development and function of campylotropous ovules were discussed[48] and this should be extended to other ovule forms.

What is the impact of ovary locule form and placenta position on the shape of ovules? As an example, the ovules of *Amborella* have been described as anatropous, hemianatropous or orthotropous[49–54]. This seeming discrepancy appears to be related to space constraints in the locule and also to an unprecise circumscription of the terms orthotropous and anatropous. For instance, an anatropous ovule is described as having an inverted body so that the micropyle and the hilum come to lie close to each other[9]; but it is not stated that the outer integument (or the only integument in unitegmic ovules) is extremly monosymmetric (i.e. short or even lacking on the hilar side). In the extreme case, this integument appears semiannular and hood-shaped. This asymmetry was addressed in several studies[54–57], where it was assumed that this difference in shape from the inner integument indicated the different evolutionary origin of the two integuments. It was interpreted that the hood shape of the outer integument was the basal character state in angiosperms. However, in broad comparative studies on basal angiosperm ovules[58], it was shown that annular and semiannular forms co-occur sometimes in closely related groups. It appears that minor developmental differences at integument inception may result in one or the other form.

Comparative floral studies in basal angiosperms and newly circumscribed orders of rosids (based on molecular phylogenetic studies by other authors) carried out in my laboratory showed that ovular features may exhibit shared tendencies in larger clades. In these studies, it was essential to have available the results of the many earlier embryological investigations as mentioned earlier, in addition to new ones.

Basal angiosperms

The ovules are commonly pronouncedly crassinucellate. The inner integument forms the micropyle in almost all groups.

The outer integument is thicker than the inner[51,59]. However, in Piperales (sensu APG)[22], the outer integument is thinner than the inner, and commonly only two cell layers thick[60]. There is a tendency to form pachychalazal or perichalazal ovules in Laurales[51]. Another tendency in basal eudicots (some Ranunculales) and in basal monocots (Acorales, Alismatales) is to form weakly crassinucellate or pseudocrassinucellate ovules, in some Alismatales also tenuinucellate ones[61,62]. Orthotropous ovules, which are characteristic of Piperaceae and some smaller groups of basal angiosperms, show a tendency to have a relatively thin outer integument[60]; the same tendency appears in Proteales among basal eudicots[61]. This tendency may be functionally correlated with the lacking curvature, as a well-developed outer integument appears to be necessary for ovule curvature. Ovules of *Arabidopsis* mutants in which the outer integument is not formed, fail to become anatropous[63]. In the unitegmic, anatropous ovules of asterids, the outer integument is not lacking, but both integuments appear to be congenitally united and form one thick structure[64].

Rosids

In Celastrales (Celastraceae and Parnassiaceae, but not Lepidobotryaceae), the ovules are almost always weakly crassinucellate or incompletely tenuinucellate with an endothelium on the inner epidermis of the inner integument, and the inner integument is thicker than the outer[65]. In Oxalidales, the nucelli also tend to be relatively thin and tend to dissolve at maturity, and an endothelium is present, however, they are commonly crassinucellate. The inner integument is thicker than the outer, except for Connaraceae and Oxalidaceae, in which they are about equally thick[66]. In Malpighiales, there is also a tendency to form relatively thin nucelli (crassinucellate or tenuinucellate) and an endothelium, as it appears from a literature survey. Thus, the three orders, Celastrales, Oxalidales and Malpighiales, which form a (weakly supported) clade in some molecular phylogenetic studies[20], appear to exhibit a general trend of having relatively thin nucelli, differentiation of an endothelium, and inner integuments thicker than the outer. In Cucurbitales and Crossosomatales, which are more distantly related with the three orders just discussed, the ovules are in most cases also crassinucellate. However, in contrast, there is no endothelium, and the inner integument is commonly thinner than the outer[67,68].

Embryo sac development

A monosporic, eight-nucleate, seven-celled embryo sac (Polygonum-type) and triploid endosperm are predominant in angiosperms and therefore have been long regarded as typical for the angiosperms; this condition also has served as a model in molecular developmental genetic studies[69].

However, surprisingly, new finds have challenged this view. Detailed analyses of embryo sac development and endosperm formation in some of the basalmost angiosperms ('ANITA grade')[70], including quantification of nuclear DNA contents, have revealed that the embryo sac is four-nucleate and four-celled, and the endosperm is diploid[71–75]. This was found in *Nuphar*, *Illicium* and *Kadsura*, which are representatives of Nymphaeales and Austrobaileyales. However, *Amborella* appears to have the Polygonum-type of embryo sac development[53]. *Piptocalyx* (Trimeniaceae, Austrobaileyales) was described as having a Polygonum-type embryo sac[76]; however, the depicted embryo sacs do not show antipodal cells. Some earlier classical studies also figured embryo sacs with only four cells in some of these basalmost angiosperms, but they did not discuss the potential significance of this result. The name 'Schisandra type' had even been coined earlier for this pattern[77], which had been found in *Schisandra*[78], but was regarded as an isolated occurrence at the time. These results are most significant and may have far-reaching consequences for evolutionary interpretations. Possibly, early angiosperms had a four-nucleate embryo sac and diploid endosperm. Thus the apparent ancestral pattern was more simple than in the majority of extant angiosperms. However, studies in additional basal angiosperms are required.

Gynoecium

Just as the ovules, the entire gynoecium also has become a focal point in developmental genetics, especially the establishment of polarity between adaxial and abaxial carpel side, the differentiation and function of the pollen tube transmitting tract, and histological differentiations leading to fruit dehiscence[79–81].

Studies of carpel and gynoecium structure through all families of the basal angiosperms[51,59,60], also including basal eudicots[61] and basal monocots[62], have revealed new features of evolutionary interest[32,58]. Angiosperm carpels enclose the ovules and are typically sealed; thus the carpels are angiospermous. Carpel sealing exhibits different types. The two extreme cases are sealing only by secretion (type 1), and sealing completely by postgenital fusion (type 4). Two intermediate types show a combination of sealing by secretion and postgenital fusion. In one, there is a continuous canal of secretion that merges with the outer world and postgenital fusion at the periphery (type 2). In the other, the canal of secretion does not reach the periphery, and the entire periphery is postgenitally fused (type 3). It has been shown that angiospermy type 1, sealing only by secretion, is predominant in the basalmost angiosperms. Type 4 and the intermediate types are more common in the other basal angiosperms. In other studies focusing on various orders of rosids, it has been shown that types 3 and 4 are predominant[65–68]. Another feature that is predominant in the basalmost angiosperms, is pronouncedly ascidiate (tubular) carpels[52,58,82–84]. Before the new molecular phylogenetic results were available, the significance of ascidiate carpels in basal angiosperms had been discussed by several authors[85].

Androecium

Stamens have a conservative organization, with an anther with two lateral thecae, each consisting of two collateral pollen sacs (microsporangia), and each theca opening by a longitudinal slit. The development of anthers has been closely studied in model species such as *Arabidopsis thaliana*[86] and *Nicotiana tabacum*[87]. As this pattern is so common in angiosperms, it has been assumed, similar to the case of the Polygonum-type embryo sac, that it is the basic pattern. However, a number of groups in basal angiosperms differ from this pattern in that their anthers are characterized by valvate dehiscence. In these, each theca does not open by a simple longitudinal slit, rather there are two kinds of variants. Either this slit bifurcates at both ends resulting in door-like valves (present in several Magnoliales, exceptional in Laurales, *Nuphar* of Nymphaeaceae)[88,89] or each pollen sac, has a separate opening line that follows the circumference of the pollen sac leaving a hinge either on top or at the side (present in many Laurales). The first type of valves also occurs in a few basal eudicots (Platanaceae, Trochodendraceae, rarely in Ranunculaceae) and in one family of (basal) core eudicots (Hamamelidaceae)[90,91]. Importantly, the first type is also present in a number of Cretaceous fossil stamens[92]. It appears now that anthers are prone to form valvate dehiscence when they have a thick (not broad) connective. This architecture makes it more difficult to open with simple slits than in anthers with a thin connective with bulging pollen sacs[91]. Thus valvate dehiscence per se is not necessarily basal. However, basal angiosperms tend to have thick connectives, and as a consequence, valvate dehiscence is prone to form, whereas in more derived angiosperms thin connectives predominate, which precludes the formation of valvate dehiscence. Except for this valvate dehiscence pattern in a number of basal angiosperms, the bisporangiate–bithecal anther structure is by far the most dominant type in all major angiosperm groups, and this is most probably also ancestral in angiosperms.

As in the case of the ovules, a more detailed grasp of the diversity of anther structure and development is evolving. Especially the tapetum as the adjacent tissue of the developing sporogeneous tissue and pollen has been a strong focal point[93,94]. In the study of pollen development, the structure and function of orbicules[95], and the diversity of modes of pollen coherence as dispersal units[96] were studied. An especially interesting topic from an evolutionary point of view is the aperture configuration and diversity of the pollen grains as a function of the symmetry of the pollen tetrad during meiosis[97–100].

Perianth

A double perianth with calyx and corolla is characteristic of core eudicots. However, it is still unclear when it originated. In basal eudicots, which have the phylogenetic structure of a grade, the basalmost clade, Ranunculales, appears to have evolved a double perianth several times[101]. This is reflected by several duplication events in the *APETALA* and *PISTILLATA* genes, which operate in the development of petals[102,103]. In contrast, surprisingly, in the other clades of basal eudicots, the perianth is either simple or weakly differentiated or lacking (Proteales[104–106]; Buxales[107–109]; Trochodendrales[90]). In Platanaceae, it is still unclear whether the perianth is simple or double[110]. In basal angiosperms, even if there are many groups with a perianth that has petaloid inner organs, these petaloid organs in most cases are different from typical petals in eudicots in some respects. An exception is *Saruma* (Aristolochiaceae, Piperales), in which the inner perianth organs show retardation that is typical of eudicot petals[111] and similar gene expression[112].

The problem of how to define sepals and petals is still unresolved, although it can now be stated better than before. There are different parameters that can be considered for a definition, such as position, function, development, shape, anatomy, histology, gene action, phylogenetic neighbourhood: (1) position in the first vs second series of the perianth, (2) primary function in protection vs optical attraction (or, in Ranunculales also attraction by nectar production), (3) continuous development vs retarded development after initiation, (4) broad shape at the base vs narrow shape, (5) anatomy with three vascular traces vs one vascular trace, (6) histology with chlorenchyma and smooth epidermis vs lack of chlorenchyma and parenchyma with large intercellular spaces and papillate epidermis, (7) gene activity by A class vs A plus B class genes, and (8) phylogenetic neighbourhood with close relatives potentially more easy to interpret. In many plant groups, not all these parameters are congruent. Should one or a few of them be given priority in an evaluation, and if so, which ones? Or should they all be considered equally? This is uncertain simply because most plant groups have never been studied in detail in all these aspects. Thus we are only at a beginning in our understanding of perianth homologies and evolutionary aspects of the perianth.

Outlook

The overwhelming new results with an impact on the understanding of reproductive structures, which come especially from the molecular fields of phylogenetic and developmental genetic research, as also from studies on new fossils and new comparative studies on extant plants, need to be synthesized for a reconstruction of the evolutionary history. As these fields proceed into very different directions; a synthesis requires interdisciplinary collaborations. The classical fields are not superseded by new ones. On the contrary, they are being freshly invigorated. They have to be envisaged in the new light and new questions have to be asked. A comprehensive evaluation of the diversity of plant structures is still far in the future. However, it can be hoped that with a synthetic approach, further advancement will be promoted.

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