

Character parallelism and reticulation in the origin of angiosperms

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SUMMARY

Angiosperms have appeared as assemblages of different life forms in association with the advanced gnetoid and other proangiosperms. Their origin was not a solitary event but rather a result of parallel evolution. Typical angiosperm characters, such as vessels, areolate venation, enclosed ovules, extraovular pollen germination, double fertilization, etc., appear scattered among different lineages of proangiospermous plants. Their assembly by horizontal gene transfer seems even more plausible due to the recently obtained direct evidence of interaction between proangiospermous plants and pollinivorous insects, with certain pollen characters, such as taeniate exine or columellate infrastructure, spreading across taxonomic boundaries. Insects might facilitate horizontal gene transfer in plants by transferring microorganisms capable of gene transduction. Major events in angiosperm evolution occurred during widespread environmental crises making plant populations more receptive to extraneous genetic material. Evolutionary significance of horizontal gene transfer is discussed.

31.1 INTRODUCTION

Angiosperm origin is still sometimes perceived as a single evolutionary event. However, a wealth of data drawn from different sources seems more reconcilable with the notion of a long and intricate angiospermization process in which a lateral spread of genes between lineages evolving in parallel might play a certain role as a mechanism of sharing a genetic

basis for the characters that appeared in a single or a few groups and then became, as it were, a common heritage (Krassilov, 1977; Syvanen, 1994). These might be characters under simple genetic control, as in pollen grains (haploid structures giving wonderful examples of translineage parallelisms) or the more complex characters arising from developmental accelerations or sequential changes caused by insertions of regulatory elements.

Morphological evidence of horizontal gene transfer is, by necessity, indirect. There are some points of interest, however, pertaining to angiosperm prehistory, angiosperm diversity and the ecology of angiosperm appearance, including the role played by insects.

31.2 SEED PLANT PHYLOGENY

Angiosperm evolution starts with protected ovules that appeared in the mid-Devonian time, about 400 million years ago. Currently, seed plants are thought to be rooted in progymnosperms of which both the heterosporous archaeopterids and homosporous aneurophytes are considered as potential ancestors (Rothwell and Erwin, 1987). Moreover, there were herbaceous plants of simpler axial anatomy but with elaborate cupule-like sporangial clusters, as in *Lenlogia* (Krassilov and Zakharova, 1995). Early seed plant diversity is insufficiently known for establishing progenitorial relations otherwise than in a very general form. The possibility of gymnosperm anatomy and seeds originating in different lineages and then being combined by horizontal gene transfer cannot be excluded.

Insofar as phylogeny primarily conveys our understanding of homology, it cannot be more objective than the latter. The objective elements in it are chronological relationships as well as morphological continuities furnished by intermediate forms that show character states midway in the morphocline, and by mosaic forms that combine typical characters of different taxonomic units, thus serving as phylogenetic links or stepping stones. Contemporaneous plant groups are likely to have independent origins or, if connected by intermediate forms, fraternal rather than progenitorial relationships. On the other hand, members of successive age groups, if connected by intermediate or mosaic forms, are likely to have progenitorial relationships. A phylogenetic tree based on the combined chronological information and intermediate/mosaic morphologies of the linking forms (Fig. 31.1) shows the following general tendencies.

1. The increase of the higher rank diversity that, for the non-angiosperm seed plants, peaked in the early Mesozoic, at the time of proangiosperm appearances. The subsequent decrease, at the expense of proangiospermous orders, might reflect the latter evolving into conventional angiosperms.

3. New groups of gymnosperms and proangiosperms appearing to occur in clusters rather than by a succession of dichotomies.
4. A widespread homoplasy of fundamental derived characters simultaneously appearing in fraternal lineages (a notable feature of the nodal arrangement). For example: phyllospermy in lagenostomaleans and trigonocarps; true pollen and platyspermic ovules replacing prepollen and radiospermic ovules in trigonocarps, callistophytes and cordaites; compound strobili in cordaites, walchians and conifers; radial synangiate and ovuliferous structures in pteridosperms, glossopterids, vojnovskyaleans and bennettites; taeniate pollen grains in glossopterids, peltasperms and conifers and their simultaneous transition to asaccate morphotypes; specialized laminar ovuliphores (seed-scales) in peltasperms, nilssonialeans, conifers, etc.; their fusion to subtending bracts assisting in seed dispersal in glossopterids, conifers and gnetaleans; peltate imbricate cone scales in peltasperms, cycads and several groups of conifers; destrobilation in *Ginkgo*, *Cycas*, Taxaceae and other conifers as well as Mesozoic gnetophytes; secondary cupules in caytonialeans, czezanowskias and other proangiosperms; asaccate anasulcate pollen morphologies in Mesozoic nilssonialeans, cycads, ginkgoaleans, etc.
5. The cyclicity of morphological evolution; in particular, the appearance of cupulate ovules in the Late Devonian–Early Carboniferous as the first round of angiospermization followed by gymnospermization in the late Paleozoic, in turn followed by a second round of angiospermization in the late Mesozoic. A morphological distance between cupulate structures of extinct seed plants and angiosperm gynoecia appears much shorter than between the latter and the scaly ovuliphores of extant gymnosperms.

31.3 PROANGIOSPERMS AS A MORPHOLOGICAL POOL

Seed plant evolution has proceeded through a series of successional hydrosperm, pteridosperm, cycadophyte and proangiosperm grades (Fig. 31.1) before reaching angiosperm level. The proangiosperm grade became apparent due to a series of paleobotanical findings (Krassilov, 1975, 1977, 1982, 1984, 1986; Krassilov and Bugdaeva, 1982) that brought to light seed plants chronologically preceding or contemporaneous with the earliest angiosperm records and showing some critical characters but lacking in other critical characters on which conventional recognition of angiosperms is based. Thus vessels appeared in gnetophytes and bennettites; paracytic stomata in bennettites; graminoid leaves in gnetophytes; compound-palmate to lobatopalmate leaves with reticulate venation in the *Sagenopteris–Scoresbya* group (Caytoniales and allies); 'dendroid' androclades anticipating fasciculate androecia in *Caytonanthus*; pollen

grains with protocolumellar infrastructure and zonal, as well as porous, protoapertures in *Classopollis* (Hirmerellaceae); cupular gynoecia in *Dirhopalostachys* of cycadophyte descent (with a solitary anatropous ovule) and *Basia* of bennettitalean descent (with a solitary orthotropous ovule); four-membered cupulate gynoecia with bracteate perianth in *Eoantha* (gnetophytes); ascidiform cupule with many ovules in *Caytonia*; syncupulate capsules with stigmatic crests in *Leptostrobus* (Czekanowskiales), etc. Thus proangiosperm groups are complementary in forming a morphological pool containing an almost complete set of typical angiosperm characters.

In angiosperms we find derived states of the characters that appeared in their prototypal states in proangiosperms, but no single proangiosperm lineage could conceivably have given rise to the basic angiosperm diversity evidenced by the mid-Cretaceous fossil record. Rather the diversity of angiosperm morphologies could have arisen by recombination of the diversity of proangiosperm morphologies. Angiosperms as a whole are 'pachyphyletic' in the sense that they descended from proangiosperms as a whole. At the same time, the basic dichotomy of seed plant morphoclines with receptacular orthotropous ovules versus appendicular anatropous ovules is traceable through the gymnosperm and proangiosperm grades to the early angiosperms, giving a clue to their progenitorial relations; for example, linking the gnetophyte-bennettite group of proangiosperms to graminoid monocots and the caytonialean-czekanowskialeen proangiosperms to ranunculids and related dicot and monocot orders.

31.4 ANGIOSPERM DIVERSITY

Traditional taxonomy represents angiosperms as a diverse but fairly integral group bound up by such critical characters as areolate leaf venation, vessels, flower, carpel, double fertilization, etc., the structures and the process lacking (at least nominally) in other seed plants, thus constituting a unique diagnostic complex that could arise only once in the history of the plant kingdom. The morphological diversity of angiosperms is then reducible to a single ancestral prototype.

The comparative morphology of angiosperms is governed by this creed. A drive for unity makes a taxonomist feel unsatisfied until all the items are brought to one end. In effect, monophyletic systems are much more popular than polyphyletic systems. Cladistics provide a seemingly objective approach to the problem by numerical estimates of intergroup versus outgroup similarities. In the case of angiosperms, the objectivity of results (invariably indicating monophyly) are doubtful for several reasons, notably the semantic. Strict morphological definitions are wanting for most of the characters used. Therefore their presence or absence

Table 31.1 Example of comparison of groups

	Gnetophytes	Monocotyledons	Dicotyledons
Flower	-	+	+
Stamen	-	+	+
Carpel	-	+	+
Cupule	+	-	-

depends on what we mean by them. Consider the example shown in Table 31.1 above.

This table is pointless unless we know that 'flower', 'carpel', etc. mean the same thing for all the compared groups. Incidentally, flowers, familiar by association with weddings and funerals, have escaped precise morphological definition. Historically 'flower' was scarcely considered as a discriminative feature: Linnaeus said that all plant species had flowers and fruits, even if concealed from our eyes (Linnaeus, 1751). While 'flower' is used discriminately at present as a special feature of angiosperms separating them from other seed plants, it seems logical to define 'flower' in relation to reproductive structures of non-angiospermous seed plants. In the majority of angiosperms, flowers consist of sporangiophores and/or ovuliphores formed of floral meristem that is similar to apical meristem of vegetative shoots but is mitotically more active and of a less distinct zonal structure. Gymnosperms also have specialized reproductive shoots, but their apices are not fully fertile, bearing sterile scales (in bennettites) or, in *Ginkgo*, fully developed leaves intermingled with ovuliphores. Although differing from typical flowers, these structures correspond to some anomalous 'flowers' with bracts in the gynoeceal zone, e.g. in *Eupomatia* where they form the 'inner corolla' between carpels and stamens. Such floral structures occur in a number of angiosperm families and are actually pre-flowers rather than typical flowers.

The situation with other typical structures is similarly biased semantically. Characters assigned to a certain morphological type are not necessarily homologous and, in fact, are rarely so. For example, follicles, often thought of as basic leaf-like gynoeceal structures, are either monomeric ascidiform (Rohweder, 1967) or pseudomonomeric (Vink, 1978). The unitegmic condition can result from fusion or reduction or integumental shifting (Bouman and Callis, 1977) while the bitegmic condition can result from splitting or modification of peripheral nucellar tissues with respect to the pollen-conducting function of the inner integument (Heslop-Harrison *et al.*, 1985). Even some characteristic biochemical compounds are end-products of dissimilar biosynthetic pathways (Kubitzki, 1973). Pseudohomology is a prolific source of phylogenetic misconceptions, such as morphological integrity of angiosperms.

Comparative morphological analysis shows that none of the critical characters is shared by all the species currently assigned to angiosperms: there are forms lacking distinct stratification of apical meristem, vessels, typical sieve element companion cells, with atypical double fertilization, as in *Onagraceae*, with embryogenesis nuclear up to 64–128 or even 256-nucleate stage, as in *Paeonia*, etc. On the other hand, such characters are not exclusively confined to angiosperms but occur, though less consistently, in seed plants that are not formally recognized as angiospermous; this includes not only pre-flowers and carpel-like cupules, but also double fertilization, as in *Ephedra*. The morphological boundary between angiosperms and gymnosperms is thus not absolute.

Notably the anomalous character states occur in angiosperm taxa that are generally considered primitive. An assembly of all such characters may be closer to an ancestral form than the paradygmatic angiosperm. This form may not be conventionally classified as angiosperm, thus making angiosperms cladistically paraphyletic with an implication that the typical angiosperm characters, not yet occurring in the common ancestor, appeared in parallel in the descendant lines and, therefore, are not uniquely derived.

Actually shared by all angiosperms is developmental acceleration resulting in highly condensed and/or chimeric structures of great morphological plasticity, but this is an evolutionary trend developing simultaneously in different seed plant groups.

31.5 COLLECTIVE BREAKTHROUGH

The angiosperm origin is here perceived as a process that does not have strictly definable starting points and deadlines. A semitectate pollen grain represents a step in morphological evolution towards angiospermy rather than the existence of angiosperms. Such records go back to the Triassic (Cornet, 1979) and even further. Assembled records of several angiosperm traits accumulate, after a period of single-trait appearances, in the Barremian/early Aptian, about 115–120 million years ago. Close to this date are the associated records of authentic angiosperms and various proangiosperms, notably the advanced gnetaleans, in central Asia, the Middle East, the Atlantic coasts and Australia. They not only testify to early angiosperm appearances in these areas, but also give evidence of the ongoing process of angiospermization.

Remarkably, the most important localities have yielded not only the first angiosperms and angiosperm-like fossils, but also the remains of advanced proangiosperms. In the Barremian Baisa locality in the upper reaches of the Vitim River, Transbaikalia, angiosperm leaves from *Dicotylophyllum pusillum* and pollen grains from *Asteropollis* and *Tricolpites* (Vakhrameev and Kotova, 1977) are accompanied by the abundant

achene-like disseminules of *Baisia*, a one-seeded cupule on persistent bristled receptacles (Krassilov and Bugdaeva, 1982). Recently, intact inflorescences of this plant were studied by Krassilov and Bugdaeva (in press), who confirmed the previously suspected bennettitalean derivation of this proangiospermous plant. From the same plant-bed came *Eoantha*, a bracteate preflower with a four-lobed gynoecium and with *Ephedripites* pollen grains in the pollen chambers of orthotropous ovules (Krassilov, 1986). A recently found attached flower (Fig. 31.2) enabled us to assign the associated graminoid leaves to this plant. New finds have added inflorescences with staminate pre-flowers of the gnetalean type (Fig. 31.2).

Even more diverse are angiospermoid and proangiosperm fossils in the roughly contemporaneous localities of Manlay, Gurvan-Eren and Bon-Tsagan in the western Gobi, Mongolia (Krassilov, 1982). Angiospermoid fruits from *Gurvanella* and *Erenia* are accompanied there by the monocot-like *Cyperacites*, *Graminophyllum* and unassigned *Sparganium*-like and *Potomageton*-like fruiting axes, as well as a pappose reed-mace-like *Typhaera*. Their preservation is unfavorable for detailed morphological studies, thereby making their angiospermous or proangiospermous status uncertain. Similar associations were recently found in northeastern China (Sun Ge and Dilcher, 1996).

Such situations are described in other parts of the world. In the Potomac flora of the Atlantic coast of North America, early angiosperms (Doyle and Hickey, 1972) appeared in association with *Drewria*, a herbaceous gnetalean plant (Crane and Upchurch, 1987). In the English Wealden, the entry of angiosperms in the pollen record was paralleled by the rise of gnetoid pollen (Hughes and McDougal, 1987). In Koonwarra, southern Australia, ceratophyllean fruits (Dilcher *et al.*, 1996) and racemose inflorescences (Taylor and Hickey, 1990) are joined by ephedroids (Douglas, 1969; Krassilov *et al.*, 1996) and perhaps some other gnetaleans represented by ovulate bracts and bracteate pollen cones (Drinnan and Chambers, 1986). In a small collection from the Aptian 'amphibian bed' of Makhtesh-Ramon, Israel, angiospermoid fruits are found together with *Sagenopteris*-type leaves of caytonialean proangiosperms (Krassilov and Dobruskina, 1995).

Thus the appearance of angiosperms was not a lonely breakthrough against a static background, pushing other plants aside, but, rather, was a collective breakthrough involving a number of parallel lineages that grew side by side as members of breakthrough plant communities.

31.6 INSECT ROLE

The communal association of proangiosperms makes horizontal gene transfer between them at least plausible. Sporangia of microscopic



Fig. 31.2 Proangiosperms of the Baisian assemblage, Early Cretaceous, Transbaikalia. (a) *Eoantha*, attached ovulate preflower, $\times 8$; (b) gnetalean inflorescence with pollen preflowers, $\times 8$; (c) single ovulifere with several sporangia from the same specimen, SEM, $\times 170$; (d) graminoid leaf of *Eoantha* plant, $\times 8$; (e) *Basia*, a cupule on persistent receptacle with bristles, $\times 12$.

endoparasitic fungi frequently found in fossil pollen grains (e.g. Krassilov, 1987) may indicate a potential transducing agent. Interactions with insects and other animal components of breakthrough communities might in turn mediate the transfer of such agents.

Direct evidence of plant-insect interaction in biotic communities of the geological past is provided by pollen preserved in the gut compressions of fossil insects first obtained from the Early Cretaceous Xyelidae

(Krassilov and Rasnitsyn, 1982) from the Baisa proangiosperm/early angiosperm locality (see above). Insects are known to transfer various gene-transducing microorganisms that can confer parallel genetic changes in the target plants. This mechanism might have already been in action in the Permian, as evidenced by the recently described striate pollen in the gut compressions of hypoperlid and grylloblattid insects of this age (Rasnitsyn and Krassilov, 1996).

Striate (taeniate) exinal structure gives one of the most spectacular examples of a single feature morphological parallelism appearing simultaneously in major gymnosperm groups, glossopterids, peltasperms and conifers, dominating late Paleozoic plant communities of Eurasia and Gondwanaland (Clement-Westerhof, 1974; Zavada, 1985). Our most recent finding of widespread angiospermoid *Classopollis* pollen grains in the intestines of Jurassic grasshopper-like katydid insects (Krassilov *et al.*, 1997) (Fig. 31.3) suggests a similar role of Mesozoic insects in the innovation of reproductive morphology occurring in proangiosperm lineages that evolved in parallel in the direction of angiospermy.

The katydid example shows that proangiosperms and, by implication, their succeeding early angiosperms with their small gregarious flowers

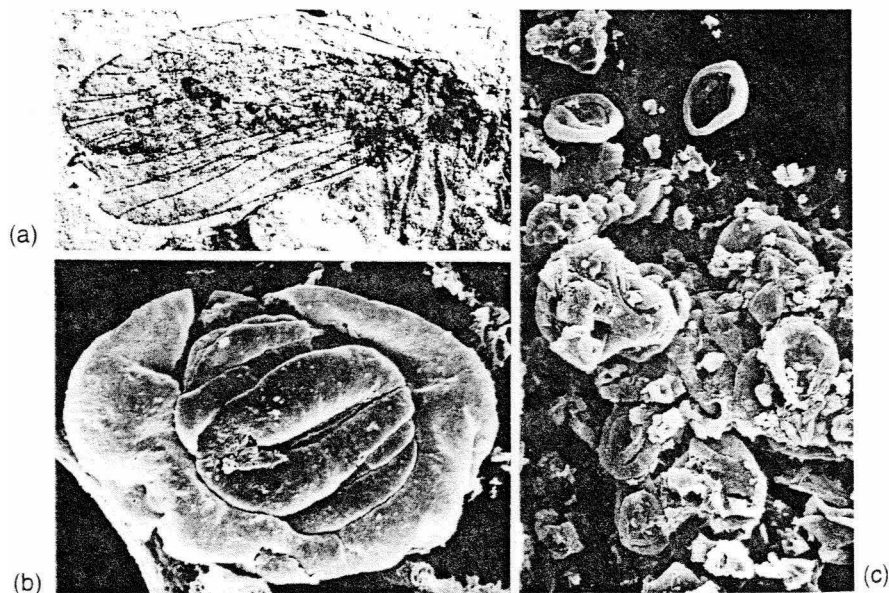


Fig. 31.3 Pollen in the gut compressions of fossil insects. (a) *Idelopsocus*, a Permian hypoperlid insect, $\times 9$; (b) taeniate pollen *Lunatisporites* from the intestine of the same specimen, SEM, $\times 1700$; (c) *Classopollis* from the gut of Jurassic katydid insect, SEM, $\times 700$.

could use unconventional pollinators, while beetles and other then existing anthophilous insects were engaged with more conspicuous bennettite pre-flowers (for the insects, they were flowers, irrespective of what plant morphologists might think of them). With the decline of bennettites at the end of Early Cretaceous, their insect retinue passed to the angiosperms, perhaps mediating horizontal gene transfer between these groups. In fact, solitary bennettite-like flowers of many parts (Dilcher and Crane, 1984) then first appeared in angiosperms.

31.7 ECOLOGICAL CRISES AS A GENE TRANSFER SITUATION

It follows from the above discussion that angiosperm origin was a communal event. The above-mentioned localities of early angiosperms and their accompanying proangiosperms reflect xeromorphic brachyphyllous communities widespread in the ecotonal zones of temperate summer-green and subtropical evergreen to winter-green vegetation, at about 50°N and 40°S. Angiospermization might conceivably have been going on throughout the extent of these zones but most of the actual records are confined to downfaulted grabens and semigrabens of the Early Cretaceous rift systems. Thus, the Transbaikalian and Mongolian basins are linear depressions of the extensive rift system striking north-east from Mongolia to the Sea of Okhotsk. The lacustrine facies of the rift zone are typical of stratified lakes, with thick, finely laminated black shale sequences interleaved with psammitic and carbonate interbeds, the latter abounding in fish and aquatic insect larvae remains. Large dragonfly, mayfly and beetle (coptocleidid) larvae pile up on the bedding planes, suggesting mass mortality, perhaps related to abrupt pH fluctuations caused by volcanogenic acid rains. The taphonomic data suggest stressful environments as a factor impelling the developmental acceleration and condensation of morphological structures characteristic of both proangiosperms and early angiosperms.

Major evolutionary novelties appear after major environmental crises for at least two reasons. The first is abbreviation of seral sequences (Krassilov, 1992). Successional species are, as a rule, more 'fine-grained' than climax species. Their relatively broad ecological niches are potentially splittable into narrower ecological niches. Elimination of climax phase thus leaves a community more open to entries by new species, either by invasion or by speciation. In addition, in perturbed communities, a decrease of stabilizing selection pressure provides opportunities for evolutionary experimentation. While species occupying well-defined ecological niches have to insulate their finely adapted genetic system from invading genes that are likely to decrease their fitness, the opposite is true for post-crisis species, which tend to be highly polymorphic. In the pioneer stage of ecological expansion, introgression of genetic material is

likely to be advantageous as a source of additional genetic variability. Therefore gene transfer, both vertical (by hybridization) and horizontal (by microorganisms), is promoted by ecological crises. Actually, new groups appearing after ecological crises show not only elaboration, but also recombination of characters occurring in their preceding groups. Thus recombination of proangiosperm characters in angiosperms can be taken as indirect evidence of interspecies gene transfer.

31.8 CONCLUDING REMARKS

The horizontal gene transfer concept is potentially of great importance for leading evolutionary thinking beyond the ossified tenets of 'synthetic' theory, first of all by introducing a long-sought mechanism – vigorously denied by traditionalists – by which macromutations can spread. The ubiquitous evolutionary parallels receive a new explanation and intra-communal interactions between coevolving organisms appear in a new light as not only competitive, but also cooperative, including at least episodic sharing of a communal gene pool, thus enforcing the idea of community as an evolutionary unit.

Although, at the first glance, horizontal gene transfer may seem accidental, the suggested association with ecological crises means that there could be method in its accidentality: it is effective when actually required as a mechanism of genetic enrichment promoting adaptive innovation and ecological expansion. At least, interpretation of the fossil record seems easier with horizontal gene transfer than without it, which can be taken as indirect evidence in favor of the mechanism.

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