
Origin of angiosperm characters

Valentin A. Krassilov

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Models of origin for the typical angiosperm leaf, flower, stamen, pistil and double fertilization are based on evolutionary trends in proangiosperms. It is suggested that angiosperm organs are of chimeric origin, acquired by aggregation and fusion of progenitorial structures. These morphological processes might involve different proangiosperm lineages in unstable (ecotonal, tectonically active) environments. An advantage of early angiosperms in such environments might be due to extended evolutionary potentials of their chimeric organs capable of acquiring new functions related to entomophily and zoochory.

Key-words—Angiosperm origin, Morphology, Evolution, Proangiosperms.

Valentin A. Krassilov, Palaeontological Institute, 123 Profsojuznaya, Moscow 117 647, Russia.

सारांश

आवृतबीजी लक्षणों की उत्पत्ति

वालॅनटिन ए. क्रसिलॉफ

सामान्य आवृतबीजी पत्तियों, पुष्पों, पुंकेसर, जायाँग एवं द्वि निषेचन के मॉडल आद्य-आवृतबीजी पौधों की विकासीय प्रवृत्तियों पर आधारित हैं। यह प्रस्तावित किया गया है कि आवृतबीजी अंग विभिन्न संरचनाओं के सम्मिश्रण आदि का प्रतिफल हैं। इन आकारिकीय प्रक्रियाओं से अस्थायी परिस्थितियों में विभिन्न आद्य-आवृतबीजी श्रंखलाओं का सम्भवतया विकास हुआ है। ऐसे पर्यावरण में प्रारम्भिक आवृतबीजीयों में नये कार्य करने हेतु नये-नये लक्षण ग्रहण करने की क्षमता आ गई थी।

ANGIOSPERMS are plants of considerable structural complexity including a number of characters, i.e., structural features essential for their description as a category of plant kingdom. There are characters they share as well as those they do not share (or if share then reluctantly) with other plant categories. Among the non-shared characters, some are present in all or the majority of the hitherto studied angiosperms, the other occur in a few species along. It is the former characters that are considered typical in taxonomic sense. Summarily, they give us an idea of what an angiosperm is or should be. Such an angiosperm is

ideal, or archetypal, rather than typical, for actually there could be none of the kind growing around. Even the expectations of finding archetypal angiosperm as a fossil are rapidly expiring with the progress of palaeobotanical research.

It is, thus, clear that the notion of angiosperm characters is meaningful only in comparison with another plant category showing a number of similar character states alongside with some dissimilar character states by the virtue of which this latter category is considered non-angiospermous. Our current notion of angiosperm characters has been formed when

PLATE 1

- 1, 2. Coherent pinnae of *Scytophyllum vulgare* (Prynada) Dobruskina, a Triassic peltasperm showing incipient areolation at the site of incorporated interstitial pinnule, x 7 (Krassilov, 1995).
3. Lateral branch of *Meeusella proteiclada* Krassilov et Budgaeva, an Early Cretaceous pollen organ showing a lateral branch apex with a pair of stalked sporangial heads, x 10 (Krassilov & Bugdaeva, 1988).
4. *Classopollis* pollen grain from the guts of a Jurassic katydid *Aboilus* shown in fig. 7, SEM x 330.
- 5, 6. Individual pollen grains of the same, x 20000.
8. *Baisia birsuta* Krassilov, an Early Cretaceous hairy cupule with a solitary orthotropous ovule, x 12 (Krassilov & Bugdaeva, 1982).
9. *Eoantha zherikhinii* Krassilov, a gnetalean proangiosperm flower, a new specimen recently found by E.V. Bugdaeva, x 10.



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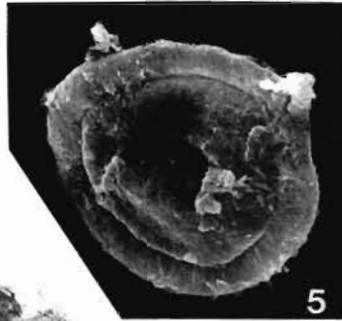
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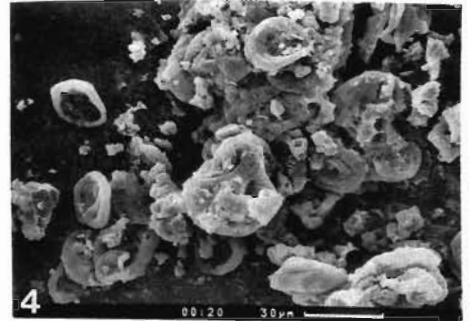
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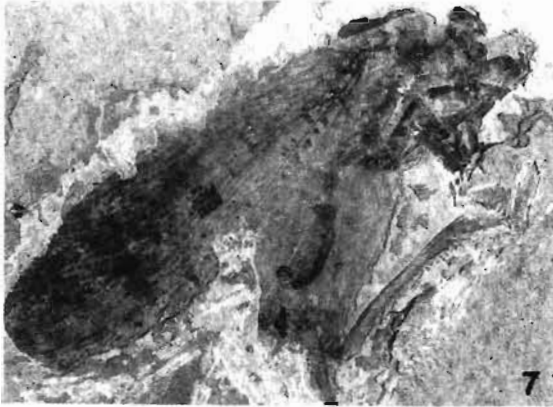
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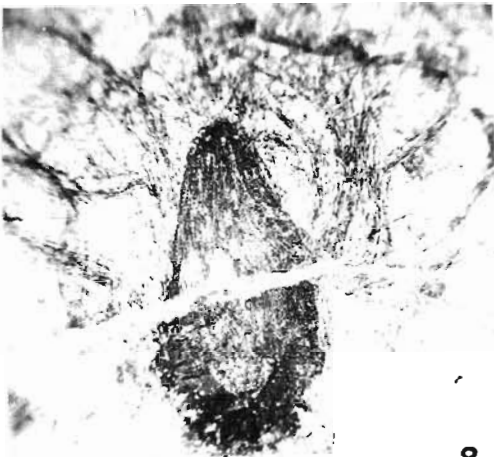
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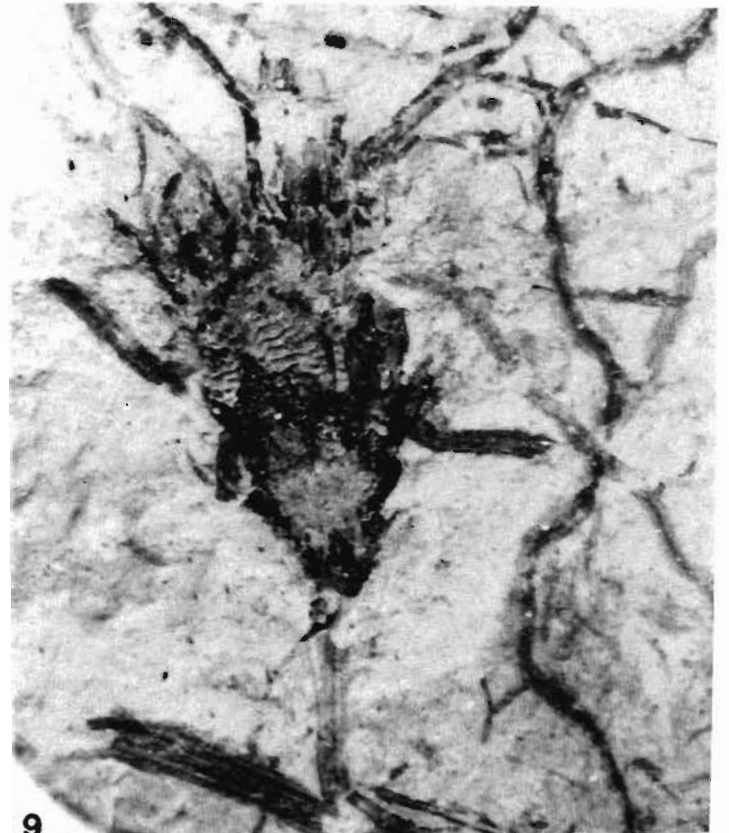
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PLATE 1

angiosperms were taxonomically separated from gymnosperms. The mid-XIX century system-makers have treated the both as divisions of Anthophyta, flowering plants, thus using the naked vs protected ovules, and not the flower, as a principal distinction.

As far as the extant plants are concerned (and there was nothing else to be concerned at the time) the distinction is clear cut. With addition of fossil plants, such as cupuliferous pteridosperms or caytonias, it is not. On the other hand, the much debated problem whether the conifer seed-scale complexes are flowers (of the same kind as the seed-scale complexes of grasses) or not seemed to have been resolved by Florins (1938-1945) work on fossil conifers showing that their seed-scales are ovuliferous shoots rather than ovuliferous leaves as the angiosperm carpels were then supposed to be. In effect flowers were rendered typical of angiosperms making them synonymous to flowering plants. Flower itself was, with admirable circularity, defined as a reproductive organ of flowering plants, although the bennettitalean flowers still posed some problems.

Generally, when fossil data infringe a taxonomic distinction the latter can nevertheless be sustained either by ignoring the fossil data or by claiming the fossil structures non-homologous - and therefore irrelevant - to morphologically similar extant structures, and both the methods have been vigorously exercised by plant morphologists. Even aberrant living plants, such as gnetaleans, were treated in the same way. The morphological proximity of caytonialeans and gnetaleans to angiosperms recently discovered by cladistic techniques, came as no surprise at all for it was evident to any plant morphologist since Wettstein (1907) and Thomas (1925). The problem lays not in the number of shared characters, but in their understanding. And the latter is achievable by factual analysis of evolutionary trends rather than by counting techniques.

Twenty years ago I defined proangiosperms as a group of parallel lineages showing evolutionary trends that led to character states typical for an-

giosperms, thus providing an angiosperm character pool (Krassilov, 1975). Whether they all or any of them actually gave rise to plants currently classified as angiosperms is another matter. More angiosperm characters are related to evolutionary trends in proangiosperms the more likely the angiosperm ancestry of the latter would seem. Here I briefly summarize the character origin models described in more details elsewhere (Krassilov, 1977, 1989, 1991) :

1. Proangiosperms including dirhopalostachians, leptostrobaleans (czekanowskialeans), caytonias, and extinct gnetaleans were represented by leptocaul trees with deciduous leafy spur shoots, shrubs and waterside - aquatic or semiaquatic - herbs (Baisia: Krassilov & Bugdaeva, 1981). All these life forms might occur in early angiosperms. Incidentally, *Caspiocarpus*, an early Albian angiosperm from Kazakhstan with pistillate panicles attached to leafy shoots (Vachrameev & Krassilov, 1979; Krassilov, 1991) was reconstructed as a herbaceous plant, and a quite similar form was then described from Koonwarra bed in Australia (Drinnan & Chambers, 1986).
2. The monocot-type parallel-veined leaves might have phyllode origin (Arber, 1918) as evidenced by histological studies (Kaplan, 1970) and similar tendency in czekanowskians, gnetaleans (*Welwitschia*) and bennettites. Some of the latter have phyllodial bracts still bearing miniature leaf blades (Harris, 1969; Krassilov, 1982a). Many Cretaceous angiosperm leaves with dichopodially branching segments (*Debeya*, *Halyserites*, *Proteophyllum*, etc.), as well as the caytonialean *Scoresbya-Sagenopteris* leaf forms show intermediate shoot/leaf (caulome/ phyllome) characters (Krassilov, 1989). The typical dicot-type leaf blade origin is modelled on the basis of segment fusion in compound leaves of peltasperms including such supposedly proangiospermous plants as *Furcula*. Segment fusion by marginal meristems initially has not affected the originally open venation pattern. However, the fusion

PLATE 2

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| <ol style="list-style-type: none"> 1. * Pistillate head from the Palaeocene of Kamchatka, x 20 (Maslova & Krassilov, in press). 2. Individual flower of the same, SEM, x 30. 3. Flower showing distinct staminodes (s) and interfloral phyllomes (i), SEM, x 30. | <ol style="list-style-type: none"> 4. Lemnoid fruit from the Maastrichtian of Mongolia, SEM, x 70 (Krassilov & Makulbekov, in press). 5. Ovule of the same showing funicle and embryo cap, SEM, x 70. 6. Funicle of the same, SEM, 660. |
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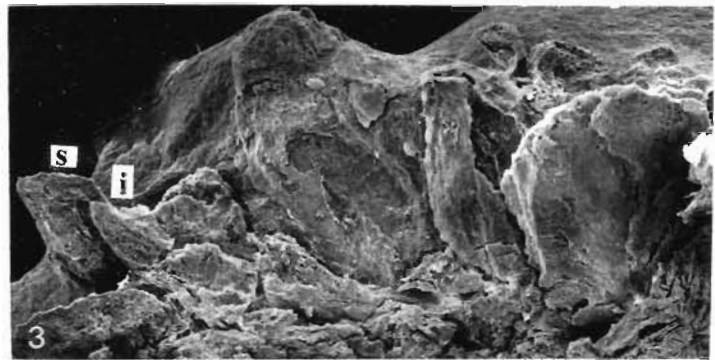
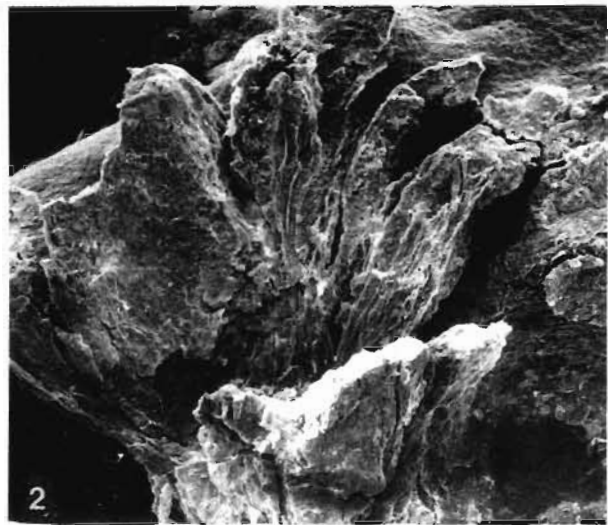
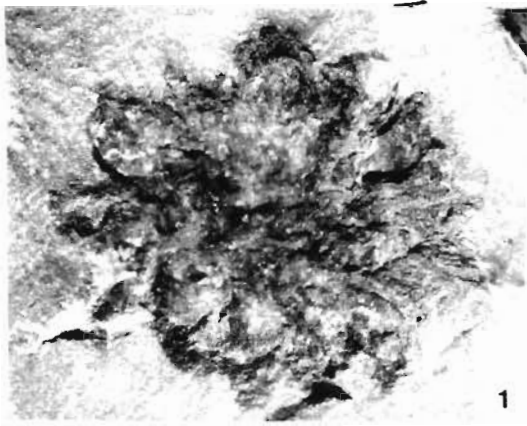
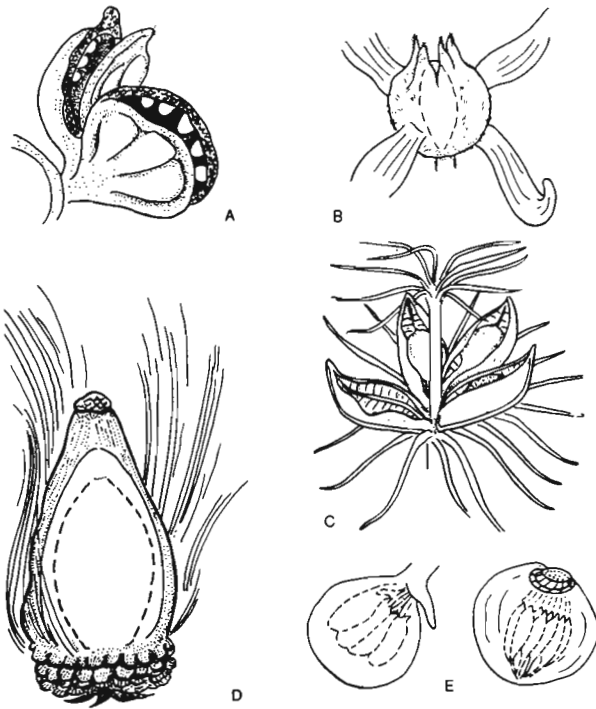


PLATE 2



Text-figure 1—Reconstruction of proangiosperm cupules: **A**- *Leptostrobus*, **B**-*Dinophyton*, **C**-*Eoantha*, **D**-*Baisia*, **E**-*Caytonia* and putative prototype with distinct subtending bract (after Krassilov, 1969).

meristem occurring within the aggregate leaf blade might give rise to plate meristem which mediated looping of the former midveins and, within the primary loops, of lateral veins and their branches, thus forming areolate venation of several orders (Krassilov, 1991, 1995; Plate 1).

3. The long debated homology of vessels in gnetaleans and angiosperms has been convincingly demonstrated by Muhammed and Sattler (1982). In addition, tracheid-like vessels with simple porous and scalariform perforation plates were found in bennettitalean leaf veins (Krassilov, 1982a) evidencing the occurrence of this character in more than one proangiosperm groups.
4. Anthocorm model of angiosperm flower (Meeuse, 1975) is supported by the occurrence of anthocorms—essentially short shoots with apical clusters of pistillate or staminate organs or both mixed with interfloral phyllomes (sterile leaves or cataphylls)—in several proangiosperm groups, such as *Irania*, bennettites, *czekanoskias* and possibly also caytonialeans and dir-

hopalostachians. Some early angiosperm flowers still retained a little modified anthocorm morphology (Dilcher, 1979). Moreover, distinct interfloral phyllomes were recently found in florets of Palaeocene hamamelid heads (Maslova & Krassilov, in press; Pl. 2, figs 1-3) indicating their primary rather than derived character in angiosperms.

5. Stamen origin is modelled on *Meeusella*, a staminate shoot with lateral branches bearing a pair of stalked sporangial heads (Krassilov & Bugdaeva, 1988; Pl. 1, fig. 3). Some lateral branches are sterile. The sporangial stalks—second order branches, are of variable length along the axis. In the case of their extreme reduction the paired sporangial heads are sessile, with the primary branch apex protruding between them as a connective of bithecate anther. The latter thus might derive from a pair of second order sporangiate branches while reduction of the main axis would give a fascicle of stamens. This model implies primary nature of fasciculate stamens (cf. Pauze & Sattler, 1978) as well as paired stamens, as in Saururaceae (Tucker, 1985) and possibly also stamens with sterile appendages (derived from sterile lateral branches of *Meeusella* prototype), as in Monimiaceae and Lauraceae.
6. The tricolpate and triporate pollen grains appearing rather early in the fossil record have no obvious precursors among proangiosperms. However, the monosulcate fossil pollen grains of *Eucommiidites* type have a zonal equatorial furrow (Hughes, 1994) or two additional furrows parallel to the sulcus. These furrows are scars of reduced sacci of monosaccate or bisaccate pollen grains occurring in caytonialeans and other proangiosperms. A polarity change along is required to transform *Eucommiidites* into tricolpate pollen grain of primitive angiosperms. Porate or pseudoporate apertures first appeared in *Classopollis*, fossil pollen traditionally assigned to conifers but referred to extinct gnetaleans by Krassilov (1982b). Recently clumps of *Classopollis* have been found in the guts of Jurassic insects (Pl. 1, figs 4-6) evidencing pollinivory and possibly entomophily. In these pollen grains the pore

area is surrounded by subequatorial rimula. They resemble tetrads of early angiosperms covered with common sexine layer and showing annulate pores (Walker *et al.*, 1983). Such tetrads might evolve in triporate pollen grains (one unit lost with the change of symmetry) which are then initially tetrasporic (Krassilov, 1989, 1991).

7. Reinterpretation of typical carpels as peltate or ascidiform structures (Rohweder, 1967; Endress, 1983; Erbar, 1986) make it easier to reconcile their morphology with their origin from proangiosperm cupules (Long, 1966; Krassilov, 1977; Heel, 1981). Among the Mesozoic cupules (Text-figure 1), the many-seeded bivalved *Leptostrobus* with submarginal anatropous ovules was formed by fusion of two open peltasperm-like cupules, the fusion meristem giving rise to stigmatic papillate crests (Krassilov, 1969, etc.). A similar origin was suggested for the paired Dirhopalostachys cupules (Krassilov, 1975). *Caytonia* had ascidiform cupules a slit-like exostome (mouth) of which was bordered by a lip-like appendage - a residual subtending bract. According to this interpretation (Krassilov, 1989) the ovules are anatropous while the mouth occurs in the fusion zone of cupule and its subtending bract. The cupule pairing and fusion, or syncupuly, occurred in different proangiosperms on their way to acquiring angiospermous carpels.

Another group of proangiosperms had orthotropous ovules borne in the four-lobed cupules with adnate bracts and tipped with tufts of hairs, as in *Dinophyton* (Krassilov & Ash, 1988) or with protruding axis crowned with bracts representing a reduced distal floral node, as in *Eoantha* (Krassilov, 1986) or utriculate with hairy corona of supposedly similar origin, as in *Baisia* (Krassilov & Bugdaeva, 1982). Among them, *Dinophyton* and *Eoantha* show definite gnetalean features (including ribbed pollen grains in the latter) on the virtue of which they are protognetalean as well as proangiospermous. These and perhaps others still undiscovered or misinterpreted cupules might give rise to different types of carpels while their bracteate or axial appendages might evolve in various stigmatic structures. Presently we have two rather

loosely defined proangiospermous groups, *Leptostrobus-Caytonia* and *Eoantha-Baisia* the cupules of which are comparable with pistils of ranalean dicots and monocots respectively. The recently found Late Cretaceous utriculate fruits with funnel-shaped stigmas (Pl. 1, fig. 4) contain a solitary orthotropous ovule the funicle of which appears as a direct continuation of the pedicel (Krassilov & Makulbekov, in press). The ovules show embryo cap and caruncle. These fruits are assigned to aquatic angiosperms related to Lemnaceae, a fairly advanced monocot family. However, they seem to retain a primitive cupule-like fruit structure and the ovule type common to a number of monocot families as well as for their protognetalean precursors.

8. Double fertilization in *Ephedra* involves the egg and ventral canal cell (Herzfeld, 1922; Khan, 1940). According to the gametophyte cell homology model proposed by Krassilov (1989) based on Cocucci (1973) the angiosperm embryo sac is formed of two or several archegonia, the eggs of which function as polar nuclei while the former ventral canal cell maintains its position close to the former neck cells (synergids) in the way of the entering sperm and is sexualized as a secondary egg (Text-figure 2).

The above models postulate chimeric origin of typical angiosperm characters acquired by aggregation and fusion of progenitorial structures. The latter morphological processes might reflect developmental acceleration and the ensuing condensation of developmental events. In my previous publications (Krassilov, 1977, etc.) the process of angiospermization was related to environmental crises. The earliest macrofossil angiosperm records occur in the Early Cretaceous ecotone between the summer-wet deciduous and summer-dry evergreen zones. Ecotonal environments are most sensitive to climatic and related vegetational changes. In addition, such important early angiosperm localities as, *Baisia* in the Lake Baikal region, Koonwarra in Australia and Makhtesh Ramon in Israel (Krassilov & Dobruskina, in press) are situated in the then active rift zones. Environmental instability generally promotes accelerated development and phenotypic plasticity. Therefore, parallel acceleration trends might involve

different proangiosperm lineages. An advantage of early angiosperms in such environments might be due to extended evolutionary potentials of their chimeric organs capable of acquiring new functions. New findings of proangiospermous pollen in the guts of Mesozoic insects support the idea of plant-insect interaction as a factor in the evolution of pollen selection on the basis of the password — response compatibility mechanism involving both stigmatic and exinal structures. Another factor leading proangiosperm cupules to typical angiospermy was endo- and exozoochory the role of which considerably increased with the rise of mammals. With some luck this scheme will be further tested by the fossil record.

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