FOSSIL RECORD OF ANGIOSPERM ORIGIN: NEW EVIDENCE AND INTERPRETATION

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Abstract

In this chapter, recent claims of pre-Albian angiosperm records are revised and
some re-interpreted. No clandestine period is found necessary for explaining the
mid-Cretaceous angiosperm diversity. Angiosperms evolved with development
of new type ecosystems, the "angiosperm cradle communities" with diverse
proangiosperms, in particular the recently discovered anthognetids. Both early
angiosperms and anthognetids were small herbaceous plants of neotenic
morphology characterized by prolific reproduction at a precocious stage of
vegetative growth. The typical angiosperm characters are related to accelerate
development and associated heterochronies conferring rapid morphological
changes. Neotenic transformation is a salient feature of angiosperm cradle
communities, involving non-angiosperm lineages as well, but in authentic
angiosperms typically followed by morphological reduction of ovules and the
uptake of pollen receptive function by extraovular structures. Through the
sequence of mid-Cretaceous (Aptian to Turonian) stages of climate change and
florogenesis, angiosperms evolved from rare morphotypes of proangiosperm
diversity to ecological dominants of major vegetation types. Prominent in the
basal angiosperm records are ranunculid forms giving rise to the dominant Late
Cretaceous groups of platanoid, cercidiphyllid and trochodendrocarpoid
angiosperms.

Introduction

In the spirit of misplaced Biblical symbolism, the problem of angiosperm origins is reduced to finding the first angiosperm preferably dated in millions of years, because such age assignments as "the Aptian" tells nothing to the public. Yet such a lucky find, like the dream of paleo-Eva, may never come true. This does not mean that the origin of angiosperms is in principle undecipherable from fossil record, a notorious imperfection of which creates such "abominable mysteries". Rather the mysteries are created by the chase of phantoms which, however dear to the public, has to be abolished in favor of an analytical approach based on understanding of morphological processes shaping seed plant evolution and coping with reality of the fossil record. Morphological trends are revealed by parallel developments across the lineages of seed plant evolution, while fossil record documents, albeit imperfectly, what actually happened rather than what might have had but did not happen.

This work elaborates upon (Krassilov, 1997) with evidence accumulated after this publication and bearing on evolutionary morphology of angiosperms, their cradle communities, as well as paleogeography, stratigraphy and paleoecology of proangiosperm and initial angiosperm occurrences, including the plant – arthropod interactions.

Acknowledgements

Institute of Evolution, University of Haifa and the German – Israeli Foundation of Scientific Research and Development.

Material and Methods

The material was obtained in the course of collecting, taxonomic description and analysis of Cretaceous fossil floras with early angiosperms or angiosperm-like (proangiospermous) plants from Primorye, Amur Province and Sakhalin Island in the Russian Far East, the Baikal Lake area (Transbaikalia), Gobi Desert in Mongolia, and Negev Desert in Israel, with additional data on selected plant fossils from the Triassic of Arizona U.S.A., Jurassic of Ust' Baley on the Angara River, East Siberia, Tchulym–Yenisey and Vilyuy basins in Siberia, western Kazakhstan, Spain, Lebanon, Libya, India and South Australia (Krassilov, 1967, 1972, 1979, 1982, 1986; Krassilov and Vakhrameev, 1979; Krassilov and Bugdaeva, 1982, 1999, 2000; Krassilov and Ash, 1989; Krassilov and Bacchia, 2000,; Krassilov and Golovneva, 2001, 2003; Krassilov and Volynets, 2009; Krassilov and Schrank, 2011; Srivastava and Krassilov, 2011; Krassilov et al., 1986; 2004, 2005).

The collections are deposited in the Institute of Biology and Soil Science, Vladivostok, Paleontological Institute, Moscow, and the Institute of Evolution, University of Haifa.

The laboratory techniques used through these studies are intended for obtaining macro- and micromorphological information the fossil material can yield under mechanical preparation, chemical treatment and microscopic studies with the stereo-, dissecting and scanning electron microscopes. Methods of cuticle and in situ pollen grain maceration were extensively applied. Plant macrofossil impressions were excavated with fine needles under stereomicroscope. Compressions were separated from the rock matrix mechanically or transferred to transparent films by dissolving the rock in hydrochloric and hydrofluoric acids. For separating and clearing the cuticles, fossil plant compressions were macerated with oxidizers and alkali. Maceration residues were screened for plant mesofossils. Transparent slides were prepared for light microscopy or the objects were mounted for SEM and covered with gold. The photographs were obtained under the stereomicroscope Leica MZ6 with camera Leica DEC320, dissecting microscope Nikon Eclipse 80i with camera Nikon DS-Fi1, and scanning electron microscope FEP Qantas 200.

Results and Discussion

Being an Angiosperm: Distinguishing Characters

When deciding that a plant is angiosperm rather gymnosperm, one immediately switches from one terminology to another, which creates the "abominable mystery", because of the chasm between the plants with flowers – carpels – stamens and those with strobili – cupules – microsporophylls.

In fact, the present day angiosperms seem well separated from the present day gymnosperms, but probably because the latter are a few small groups (*Ginkgo*, cycads and gnetaleans) and a single relatively large group of distinct growth form and wood characters widely used for commercial purposes (conifers or softwoods). On the other hand, angiosperms/flowering plants are an immensely diverse group defined by combinations of typical characters, such as the ovule enclosed at anthesis, semitectate pollen grains, extraovulate pollen germination, stigma as a special structure for this, flower, archegonia-less embryo sac, double fertilization, endosperm, vessels, hierarchical areolate venation (parallel venation with cross-veinlets in monocots) and others. Their classification principles are Adansonian, meaning that lacking one or another typical character may not entail exclusion from the group (conversely, the presence of one or few typical characters does not secure membership in the group).

It is well known that some plants considered to be angiospermous lack the typical (regular) flowers, double fertilization (the Podostemaceae), vessels in the secondary wood, etc., while having open venation. On the other hand, some gnetaleans have archegonia-less embryo sacs, double fertilization, vessels, and hierarchical areolate venation (reviewed in Krassilov, 1997). Extraovulate pollen capture structures seem to provide an unambiguous distinction, yet the ligule of *Araucaria* is just such structure. With discovery of diverse proangiosperms sharing more diagnostic features with angiosperms the demarcation problem has become even more acute.

The present day angiosperms are dominant in the majority of terrestrial biomes owing to their accelerate growth and development that entails ecological plasticity and co-evolutionary bonds with other organisms (discussed later in the paper). Parallel tendencies of morphological evolution have been recognized in the Mesozoic proangiosperms already, while the distinctions between proangiosperms and incipient angiosperms may reflect different degrees of evolutionary advancement.

Gametophyte Development

In the vascular branch of the archegoniates, structural degradation of gametophyte is a general tendency of morphological evolution going as far as the loss of morphologically distinct archegonia. In this the present day angiosperms are matched by *Welwitschia* and *Gnetum*, while *Ephedra* still retains archegonia. Yet double fertilization in *Ephedra* is the closest approach to this process in angiosperms with 8-nuclear gametophyte, in which the polar nuclei retain archegonial configuration and cytokines (reviewed in Krassilov, 1997), while in the multinuclear embryo sac of *Gnetum* the fusion of nuclei is more chaotic. On the other hand, a further reduction below the 8-nuclear state, as in the Podostemaceae, may disturb the typical double fertilization schedule (Murguía-Sánchez et al, 2002).
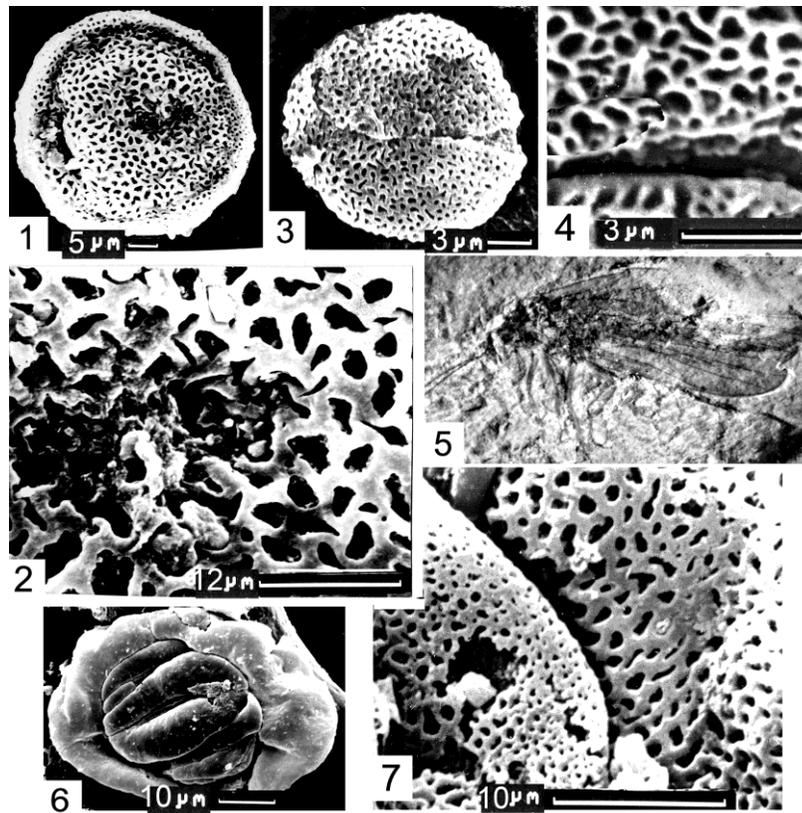
Figure 1. Angiospermoid features in a Permian pollen morphotype: 1, 2, *Reticulatina microreticulata* from the Lower Permian of Kungur, Cis-Urals, pollen grain and detail of reticulum (Zavialova and Gomankov, 2006); 3, 4. *Freyantha sibirica* Krasslov et Golovneva Cenomanian, Chulymo – Yeniseysk Basin, *in situ* pollen grain and detail of reticulum (Krassilov and Golovneva, 2001); 5 – 7, taeniate pollen grain with infratectal reticulum exposed from the gut contents of an insect *Idelopsocus diradiatus*, Kungur (Krassilov and Rasnitsyn, 1997).

Pollen characters in angiosperms are commonly attributed to germination on stigma and the ensuing sperm competition, although syphonogamy have led to the loss of motility and morphological reduction of sperm in angiosperms and higher gymnosperms alike. Surface reticulum is commonly believed to be a typical character of angiosperm pollen grains, releasing signal substances stored in the columellate layer, thus granting recognition of the pollen by the stigma. However, reticulate pollen grains occasionally occur in the gymnosperm-dominated Permian and Triassic assemblages. Moreover, the reticulate Permian pollen (Zavialova and

Gomankov, 2009) resemble the partly digested taeniate grains found in the guts of Permian insects (Krassilov and Rasnitsyn, 1997) thus relating reticulation to either abrasion or underdevelopment of the tectum (Fig. 1), an acceleration phenomenon appearing much before germination on stigma that conferred a new function on the reticulum.

Similarly, an incipient clavate - columellate infrastructural layer has appeared before angiospermy in *Classopollis*, *Eucommiidites* and other pollen morphotypes produced by the Triassic to Early Cretaceous gnetophytes, which makes probable parallel development of *Clavatipollenites* morphology in both angiospermous and gymnospermous lineages. On the other hand, the tricolpate – triporate pollen morphologies are not so far registered in gymnosperms, thus providing evidence of angiosperms in the fossil record. Their supposedly multiple origins in the mid-Cretaceous angiosperms was ascribed (Krassilov, 1997) to abolished meiotic division with the radial symmetry acquired by exclusion of one monad and transformation of distal sulci into equatorial colpi or pores.

Leaf

Leaves of dicotyledonous angiosperms are typically cladodic, that is developed from leafy shoots, the original leaves being transformed into leaflets, lobes, marginal teeth or altogether abolished. Such leaves occasionally occur in monocotyledonous angiosperms as well, but more typical of the latter are phyllodic leaves derived from leaf petioles. Veins forming areolas of 3 – 5 orders filled with a finer reticulum or free-ending veinlets are characteristic of dicotyledonous angiosperms occasionally occurring in monocots as well (Trivett and Pigg, 1996).

The Palaeozoic *Cordaites*-type leaves of various taxonomic alliances as well as the Mesozoic czekanowskialean and ginkgoalean leaves may have a phyllodic origin that is most obvious in the so called *Miroviaceae*, a morphological group with tubular "leaves" terminated by a vestigial leaf blade.

Cladodic leaves or phylloclades appear in the Permian gymnosperms (Karasev and Krassilov, 2007) and are occasionally recognized in their descendent forms when segment fusion is re-iterated in the leaf blade ontogeny, otherwise remaining undetected. In the Permian – Triassic gigantopterids and peltasperms with "coherent" leaf blades formed of coalescent pinnules, the original vein pattern is still discernible as dendrites of free-ending branchlets bound by the vein-less stripes of fusion meristem (Fig. 2). An incipient areolate venation of Triassic *Lepidopteris* (*Scythophyllym*) might have developed with transformation of intraplate fusion meristem into the vein-producing plate

meristem (Krassilov, 1997), the fairly advanced stages of which are found in the Trassic *Furcula*, *Scoresbya* Harris, 1932a) and *Pannaulika* already (Cornet, 1993). However, the Early Cretaceous angiosperm leaf remains show a much simpler venation pattern that can be open as in the present day relict forms (the Kingdoniaceae and Circaeastraceae) betraying a more recent round of segment fusion and areolation.
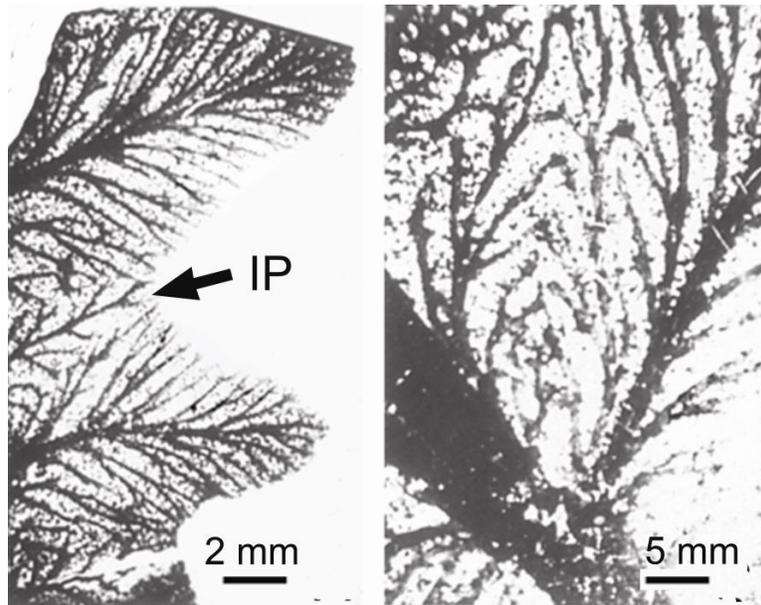

Figure 2. The appearance of areolate venation in fused pinnules of a Triassic pteridosperms *Scytophullum vulgare*: 1, basal fusion involving an interstitial pinnules (IP); 2, areolate configuration of veins overarching the interstitial pinnule (Krassilov, 1997).

Widespread among the early dicotyledons of ranunculid grade were digitate asymmetrically lobed leaves, often with acroscopically laminaless lobes as in *Suifunophyllum* and *Baikalophyllum* (Fig. 3). As our data on *Ternaricarpites* (Krassilov and Volynets, 2009) suggests, these ware basal leaves growing from a stem base and forming prostrate rosettes. A perennial herb with basal leaf rosettes and morphologically distinct or abolished cauline leaves seem to have been widespread among early angiosperms thus ranking among their distinguishing characters. However, the *Scoresbya*-type leaves known since the Permian (Holmes et al., 2010) represent essentially the same morphotype and are

considered as evidence of basal leaf rosettes in peltasperms (Srivastava et al., 2011).
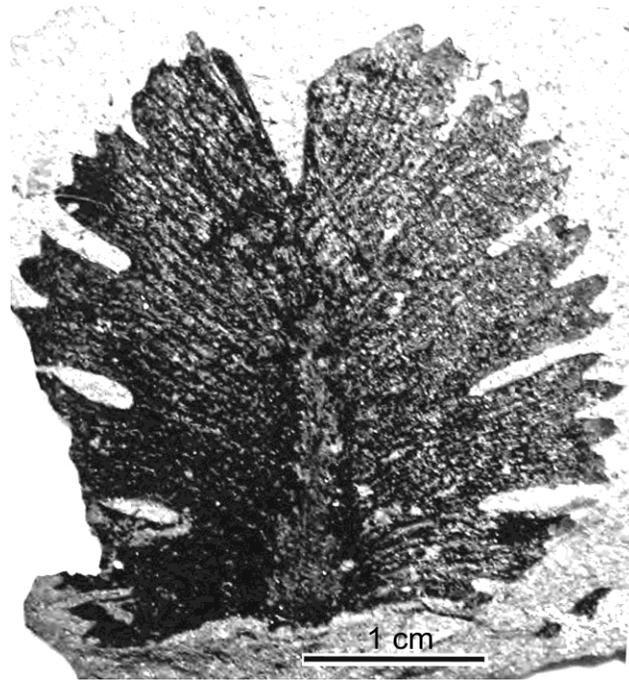

Figure 3. Basal leaf morphology in early angiosperms or angeospermoid plants: *Baikalophyllum* from the Early Cretaceous (Aptian to Early Albian) Semen Locality, Transbaikalia (courtesy of Eugenia Bugdaeva).

Flower

Typical flower is a sequence of a few co-axial whorls of sterile and fertile organs. It differs from inflorescence and cone or strobilus (which is inflorescence of a kind) mainly in termination of apical growth after the distal fertile organs are formed. A delayed termination of apical growth results in atypical flowers with protruding floral axis, spiral arrangement of floral parts and with intrafloral sterile appendages that are characteristic of a few extant angiosperms. Such transitional structures can be primary (*preflowers or anthostrobili:* Krassilov, 2010), whereas the flower-like structures derived from congested inflorescences are designated as pseudanthia. An archaic angiosperm *Cercidiphyllum* represents a situation, in which the flower-like structure of intermediate flower – inflorescence

characteristics might have never been a gathering of true flowers. Instead, it may represent an ancestral condition of a flower in making (Krassilov, 2010).

Experimental work on flower development (the "evo–devo" studies) traces the inflorescence/flower conversions to mutant genes expressions of the ABC system of sterile, staminate and carpellate whorls (Weigel & Meyerowitz, 1994; Theissen & Saedler, 2001; Theissen & Melzer, 2007) invoked by a system of transcription factors (Lohmann & Weigel, 2002; Bomblie et al., 2003; Blazques et al., 2006; Hamés et al., 2008). This machinery is needed, in the first place, to prevent leaves from growing among floral organs and on top of them and, in the second place, to secure an orderly arrangement of floral parts into successive whorls rather than being chaotically scattered over the floral axis. Under certain intrinsic, environmental or experimental impacts, the machinery can be confused into misplaced (ectopic) production of certain characters.

In particular, an ectopic expression of *LEAFY*, a gene responsible for initiation of floral meristems, invading the inflorescence apex in the *TERMINAL FLOWER1* mutant transforms indeterminate inflorescence into determinate floral structure (Schultz and Haughn, 1991; Souer et al., 1998). In contrast, a mutation of *SEPALLATA* genes expressed in the inner whorls confers indeterminate growth and produces a sequence of coaxial flowers (Pelaz et al., 2000). These experiments explain the occurrence of transitional flower/inflorescence morphologies in angiosperms and their precursors, revealing a general trend toward determination and complete fertilization of floral apex. The process involves transformation of spiral into verticillate phyllotaxy and elimination of foliar appendages (pherophylls) from the inner whorls.

Among extant gymnosperms, *Ginkgo* produces clusters of biovulate stalks terminal on reproductive short shoots inside a whorl of bracts .However, in such flower-like structures, fertile organs are interspersed with leaves. Similarly, the bennettitalean "flowers" are short shoots producing the sequential whorls of perianth bracts, pinnate sporangiophores and stalked ovules interspersed with sterile scales. Preflower stage is more typically represented in *Eoantha*, an extinct genus of Early Cretaceous anthognetids (Krassilov, 1986, 2010), with the floral axis protruding over the gynoecium of ovulate cupules and topped with a residual whorl of linear bracts representing a reduced floral node (see under gnetophytes below). A reduction of sterile apical protrusions seems to have occurred at the anthognetid level already (Krassilov, 1910). Yet the processes is not fully accomplished in the modern archaic angiosperms having sterile bracts in the floral zone as in *Cercidiphyllum* (Fig. 4).
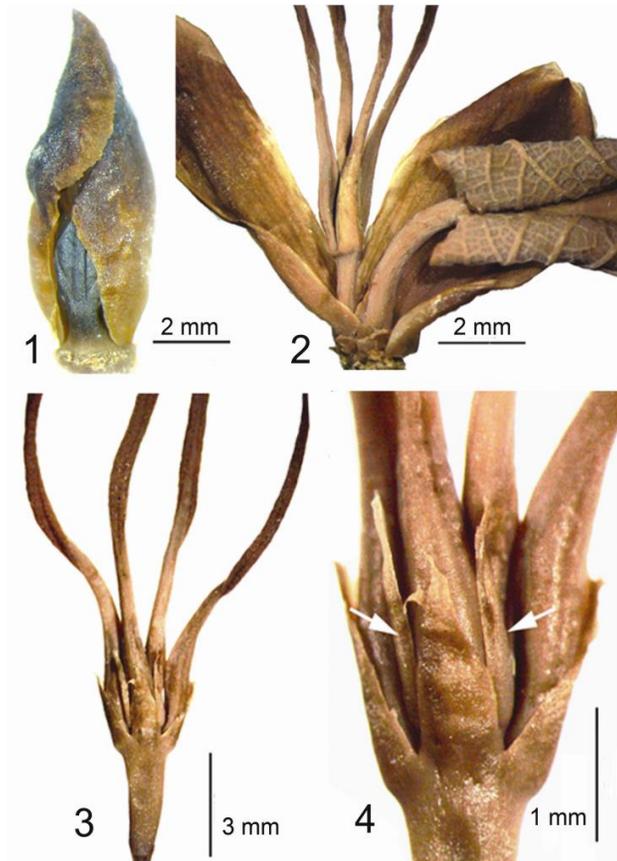
Figure 4. Preflower features in pistillate flower of *Cercidiphyllum japonicum*: 1, floral axis with prophyll enclosed in calyptrate cataphyll; 2, flower and prophyll emerging at anthesis; 3, 4, flower with additional bracts between the carpels (arrows) corresponding to preflower of proangiospermous plants (Krassilov, 2010).

Carpel

Carpel is an ovule investing structure giving the flowering plants their alternative designation, the angiosperms. Having carpels gives them a radical distinction from gymnosperms in the present day situation when most of the latter have their ovules fully or partly exposed. Yet in the past many gymnosperms had their ovules enclosed in cupules. Were carpels derived from cupules? Few plant morphologists would answer in affirmative (Long, 1966), while the majority would argue that cupules and carpels are non-homologous. Carpel is commonly

considered to be a modified (involute, conduplicate or ascidiate) leaf, while cupule basically derives from a whorl of branchlets surrounding the ovule.

Yet morphological diversity of carpels seems somewhat excessive for a single developmental model being universally applied to all of them. Even the most elaborate peltate model by Troll (1932) developed by Eber (1934), Baum (1952), Weberling (1955). Leinfellner (1950), Rohweder (1967), Guédés (1971) and other researchers, leaves a considerable diversity of carpels, the most "primitive" among them, as "epeltate". A peltate carpel consists, as the model requires, of a fertile cross-zone overtopped by a sterile abaxial bulge primordial to the style and stigma. What was then the function of such a bulge in the progenitorial ascidiate leaf? Leaves become peltate on other reasons than forming stigmas. As an alternative, the sterile prominence may represent a vestigial floral axis that in such anthognetid forms as *Eoantha* rises above the ovulate cupules and bears a rudimentary bract whorl of the terminal floral node, which explains the branched apical stigmas.

In the apparently primitive carpel of *Cercidiphyllum*, the ovules appear being borne on the closure ridge of a horse shoe shaped carpel primordium, that is plicate or ascoplicate (Taylor and Kirchner, 1996). Yet the placenta, readily detachable from the carpel wall, is a lobed laminar structure with a midrib and lateral veins supplying the ovules that are borne at the base of the marginal lobes forming the outer integument (Fig. 5). Reminiscent of the gonophyll model (Melville, 1965), such placentas may suggest a complex basal structure of a simple follicular carpel.

Plant evolution is a problem solving that inevitably creates further problems. For protecting ovules at anthesis stigma is a solution, but stigmas have also be protected. In some "primitive" angiosperms, the whole flower is enclosed in a calyptrate cataphyll to be delivered shortly before anthesis (Fig. 4 above). With a flower or preflower committed to cryptic development in the calyptra or cupule, the whole gynoecium or a part of it might have been transformed into a placental structure. This explains the amazing morphological diversity of placentas.

Notwithstanding morphological relationships, the distinctions between carpel and cupule are functional in the first place. With few exceptions, cupules are protective through the early ovule development, but not at anthesis when pollen is grunted accesses to the ovule. In distinction, carpels not only protect the ovules, but also facilitate an extraovular pollen capture and germination making an exposure of micropyle unnecessary. Just this justifies being an angiosperm.
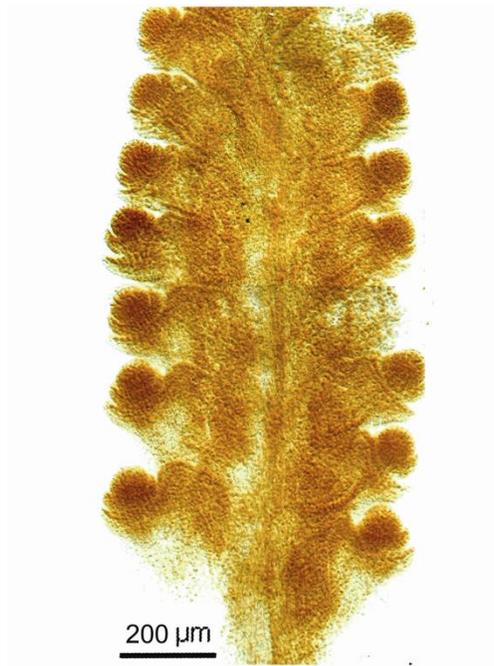
Figure 5. Leaf-like placenta of *Cercidiphyllum japonicum* with juvenile ovules shortly before anthesis (Krassilov, 2010).

Organ Conversion

Plant phylogeny was based on the XVIII century naturphilosophical idea of metamorphosis or transmutation producing a diversity of forms from a primordial element, such as leaf in the historically famous foliar theory of Goethe (1790). Developed into a comprehensive plant morphological concept by De Candolle (1927), Goethe's foliar theory dominated the field until the advent of telome theory in the mid -1900s, but even now a homomorphism of foliar and floral organs is interpreted as evidence of homology.   Recently, the molecular developmental ("evo–devo") studies lent support to the foliar theory (Pelaz et al., 2000).   In particular, the homomorphism of leaves and carpels may seem compelling, but the foliose carpels and fruits (ranunculid follicles) betray leaf features of the same species rather than of a theoretical ascidiate prototype.

The molecular level developmental experiments confer conversion of floral organs onto leaves by a modified expression of *LEAFY* and homologs that control transition from vegetative development to florogenesis.   Similar effect is

achievable through ectopic (out of a destined location) expressions of the ABC genes defining the identity of floral meristems. At the same time, the ectopic expressions of the inner whorl genes may induce a conversion tendency toward floral organs in cauline leaves. Even the basal rosette leaves of the model plant *Arabidopsis thaliana* can be transformed into petals (Mizukami and Ma, 1992; Krizek and Meyerovits, 1996; Pelaz et al., 2001). These experiments and the naturally occurring conversions of the kind (Krassilov, 2010) suggest that foliose floral organs result from ectopic gene expressions becoming constitutional in the course of evolutionary development.

Modifications arising from ectopic gene expressions do not have a long evolutionary history of minor changes and selection, as required by the Darwinian theory. Rather they are saltational events reminiscent of metamorphoses postulated by the old school of natural philosophy. But, notwithstanding their significance for morphological evolution, the foliar –floral organ conversions are not evidence in favor of Goethe's foliar theory (Pelaz et al. 2000, 2001), because floral organs originated before leaves.

Both vegetative and reproductive laminar organs (foliage leaves, sporophylls of spore plants and spermophylls of seed plants) have appeared in the leafless early land plants by planation and webbing of the original thelomic branching systems in response to decreasing light availability under the canopy of primeval progymnosperm forests. Later in the history, morphological segregation of vegetative and reproductive organs occurred in response to the spread of leaf-eating (folivorous) organisms. Through the Mesozoic, the laminar spermophyll production was abolished in the descendants of Paleozoic pteridosperms, but reappeared as a constitutional ectopy in *Ginkgo* and *Cycas*. Floral organs of early angiosperms were scarcely more foliar, often less so, than in their extant descendants. The tiny mid-Cretaceous plants of the anthognetid–angiosperm grade have produced ovulate cupules not unlike in the Devonian progymnosperms, a striking evidence of retroconvergence (Krassilov, 2010).

Before considering foliar origin of floral organs in angiosperms, it has to be reminded that early representatives of the group were herbaceous plants with a few or no cauline leaves. With increase in size and foliation, leaves might have been produced by conversion of floral primordia rather than the other way round. Partial conversions toward the leaves might have conferred foliar features on the floral organs (hence, "foliose" carpels). Thus, in *Cercidiphyllum*, the leafy shoots are shown to be produced by the naturally occurring conversion of floral axis toward leafy axis (Fig. 6), while the older parts of the branching system are foliated by the floral prophylls alone. These peculiar branching/foliation mode was interpreted (Krassilov, 2010) as being inherited from a neotenic ancestral

plant (such as the Albian *Ternaricarpites*, below) With increase in size, foliation became a problem and was solved by conversion of reproductive organs (their prophylls) toward foliage leaves.
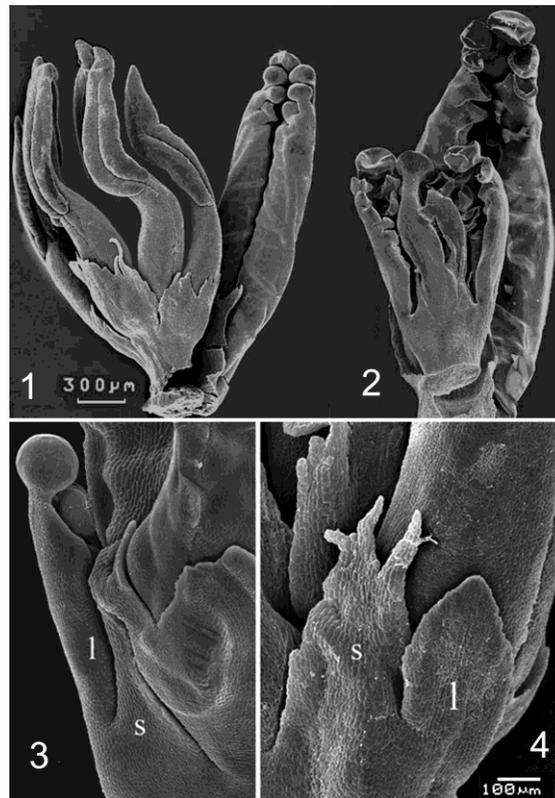
Figure 6. Floral organ conversions in *Cercidiphyllum magnificum*: 1, pistillate floral structure in bud; 2, leafy shoot replacing pistillate structure in bud, 3, 4, miniature leaves with apical glands and stipules replacing floral bracts, l – leaf blade, s, stipule (Krassilov, 2010).

Becoming Angiospermous: Parallelism, Developmental Acceleration and Heterochrony

Parallel Developments

In the cladistic analysis, only holophyletic groups are recognized as natural, while parallel developments (homoplasies) are seen as a hindrance to

phylogenetic reconstruction. However, a unique event is not analyzable and can only be described as occasional, whereas parallel developments give us the idea of general evolutionary trend involving a number of lineages responding to environmental forcing they shared.

As Norman Hughes (1976), I see the choice between monophyletic and polyphyletic modes of angiosperm origins as premature, although many researchers made it already. Among extant gymnosperms, the gnetaleans hold most of angiosperm characters ascribed to parallel developments. By the end of XIX century, many botanists supported the phylogenetic theory of Wettstein (1907), who used modern *Ephedra* as outgroup for angiosperm phylogeny implying the basal position of plants with small inconspicuous flowers. Later, the ranalean theory of angiosperm origins took over asserting the opposite polarity of floral characters.

What paleobotany has told us so far is a much higher than now diversity of Mesozoic gymnosperms some of which were more angiosperm-like than any of extant representatives. Irrespective of our opinions on their genealogy, early authentic angiosperm fossils were preceded or accompanied by angiosperm-like, but admittedly non-angiospermous or dubious fossils having flower-like (bennettites, anthogentides), anther-like (*Caytonia*), stigma-like (*Leptostrobu*s) reproductive structures, trisulcate, cingulated, reticulate and otherwise angiospermoid pollen grains (*Eucommiidites*, *Classopollis, Clavatipollenites*), enclosed ovules (*Caytonia, Leptostrobus, Dirhopalostachys*), areolate leaf venation (peltasperms) and other typical angiospermous characters. Such plants constitute the grade of *proangiosperms* that are angiosperm-like in a set of characters diagnostic for the group that are combined with those more typical of gymnosperms.

The Mesozoic gnetophytes are a recently discovered morphologically heterogeneous group of proangiospermous plants that first appeared in the Permian (Wang, 2004) and developed a considerable diversity of both vegetative and reproductive structures through the Triassic (Krassilov and Ash, 1988; Cornet, 1989, 1993, 1998; Anderson and Anderson, 2003; Anderson et al. 2007). Their second round morphological diversification coincided with the appearance of early angiosperms (Krassilov, 1986, Crane and Upchurch, 1987; Krassilov and Bugdaeva, 1999, 2000; Dilcher et al., 2005).

Fossil gnetophytes are recognized primarily on the basis of their ovulate organs that in both extant and extinct forms seem to represent the same basic structural type of a bracteolate cupule containing a solitary, occasionally two, erect ovules and supported by a bract which is typically included in the

disseminule ("fruit"). The sporangiophores of extant gnetophytes are also distinctive, cupulate with synangiate anther-like sporangia. Such structures are found in some fossil gnetophytes, such as *Dinophyton* and *Baisianthus* (Krassilov and Ash, 1988; Krassilov and Bugdaeva, 1999), yet in the others they are of a generalized gymnospermous type.
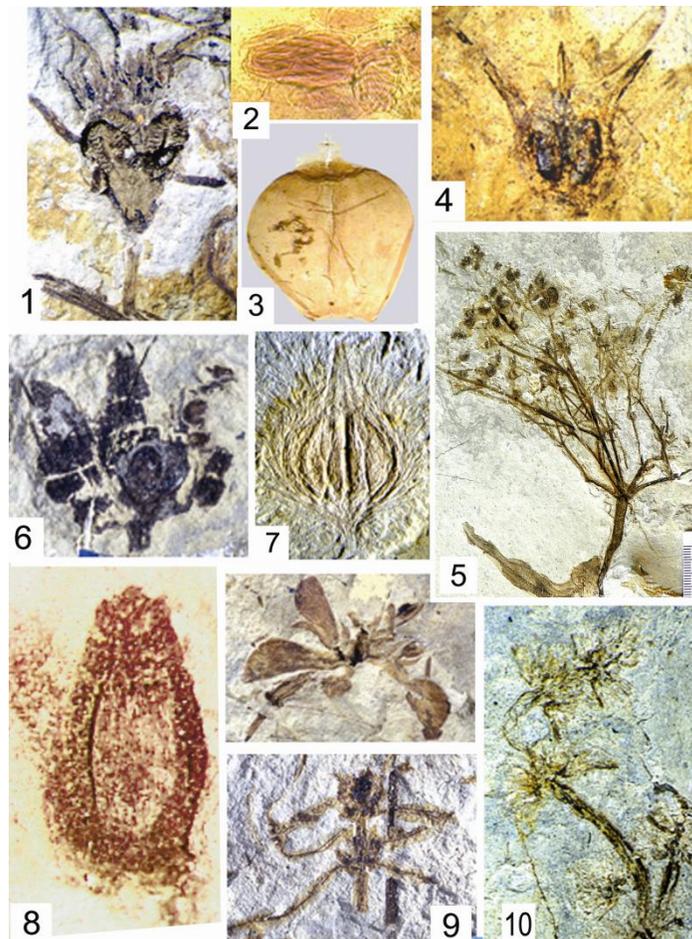
Figure 7. Diversity of gnetophytes from the Early Cretaceous (Aptian to early Albian) of Baisa, Transbaikalia and Yixian, China: ovulate (1 – 9) and pollinate (10) structures (not to scale):1 – 3, *Eoantha zherikhinii*, with pollen grains preserved in the pollen chamber, Baisa; 4, *Eoantha rostrata*, Baisa; 5, *Eoantha rostrata*, whole plant, Yixian (courtesy of Sun Ge), 6, *Preflosella nathani*a, Baisa, 7, *Gurvanella dictyoptera*, Yixian; 8 – 10, *Baisia*

hirsuta, Vitimantha crypta, *Prognetella minuta*, and *Baisianthus*, Baisa, (Krassilov, 1986; Krassilov and Bugdaeva, 1999, 2000; Akhmetiev and Krassilov, 2000).

Several morphotypes of pollen grains are assigned or related to gnetophytes on the basis of their *in situ* or nucellar chamber occurrences in the sporangiate or ovulate organs of gnetophytic morphology or else on account of their intrinsic morphological complexity. Thus, *Classopollis*, traditionally assigned to conifers, represents a higher, essentially angiospermous, level of morphological complexity, perhaps related to pollinivory and entomophily (Krasslov et al., 1997). Yet no clear-cut demarcation lines can be drawn between gnetophytic pollen morphologies and those of conventional gymnosperms on the one hand and angiosperms on the other, with parallel tendencies of saccate to asaccate, mono- to polyaperturate, granulate to columellate and possibly also alveolate to columellate transformations.
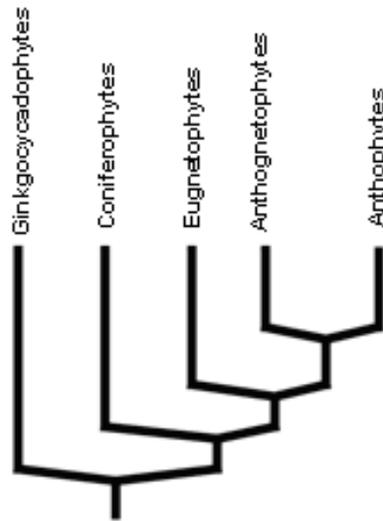
Figure 8. Morphological similarities between angiosperms, anthognetids, eugnetids and the ginkgophyte – cycadophyte level gymnosperms.

Mesozoic gnetophytes show combinations of modern and supposedly archaic non-gnetophytic characters that betray their affinities with such extinct groups as peltasperms and bennettites (with *Baisia* as a link to the latter). The known morphological diversity of Mesozoic gnetophytes (Fig. 7) suggests several orders that can be grouped in two clusters of subclass rank: the Eugnetidae and Anthognetidae (Krassilov, 2009). The eugnetids embrace all

forms with ovulate and pollinate strobili (the orders Gnetales, Ephedrales, Welwitschiales. Fredlindiales, Heerales, and Cheirolepidiales), whereas, in the anthognetids, ovulate structures are flower-like with a tendency toward verticillate arrangement of the floral parts and perianth (the orders Dinophytales, Axelrodiales, Euanthales and Baisiales). Insofar as destrobilation is a crucial feature of angiosperm reproductive morphology as well, the extinct anthognetids are closer to angiosperms than the eugnetids that comprise all extant gnetophytes (Fig. 8). In discussing the gnetophyte/angiosperm relationships, it must be taken into consideration that both traditional cladistic analysis and molecular phylogeny involve extant eugnetids that are less angiosperm-like and not an adequate phylogenetic substitute for extinct anthognetids. As in the case of the avian dinosaurs, without extinct forms no realistic phylogeny of angiosperms can be constructed, because the nearest morphological allies are not there.

Meanwhile the proangiosperm grade can be seen as a pool of characters essential for becoming an angiosperm and shaping their incipient morphological diversity. Proangiosperms coexisted with early angiosperms and might have contributed to the initial diversity of the group. "Contribution" means membership in angiosperm cradle communities, sharing the retinue of parasitic/symbiotic fungi, nematodes and arthropods, horizontal gene transfer through hybridization, transduction, allelopathic interaction, growth rate alteration by secondary metabolites, and the processes to be learned (Krassilov, 2002). A new character state first appearing in a single or a few lineages can be conferred on coexisting forms by interaction with pollination/dissemination vectors (e.g., seemingly recent insect pollination in cycads involving pollinators from angiosperm retinue or the large pulpy seeds in *Ginkgo*, a post-Cretaceous phenomenon). Moreover, a new feature enhances further parallelisms by being involved in organ conversions by ectopic gene expression (see above).

But the most general cause of parallel developments is involvement of co-occurring plant lineages into general trends of morphological evolution, such as accelerate development, governed by environmental change.

Neoteny

When evidence, however imperfect, does not fit a theory, it may be expedient to look for alternative theory. An alternative to the higher taxa origin through gradual accumulation of minute changes by natural selection is the origin of evolutionary novelties through developmental heterochronies, in particular the neoteny or precocious sexual maturation. The role of neoteny as a mechanism of macroevolutionary change has been advanced by Garstang (1922) and

substantiated by De Beer (1940), Severtsov (1935), and for angiosperms by Takhtajan (1976), but was rejected as typological and largely superfluous by the proponents of the Neo-Darwinian paradigm. In seed plants, neoteny refers in the first place to the sexual generation (gametophyte) that in angiosperms is typically reduced to the eight-nuclear embryo sac and a few cell divisions in the pollen grains before fertilization takes place, thus extremely neotenic. In a broader sense, neoteny occurs in the sporophyte generation as well, signifying accelerate reproductive maturity in advance of the vegetative body that remains underdeveloped.

Accelerate development is accompanied by shortening of internodes, verticillation and fusion of metameric organs. Fusion is a byproduct of overlapped (telescoped) sequential developmental events, giving rise to hybrid fusion meristems of great morphogenic potentials. The phenomenon is of a very general significance in angiosperms, extending from the composite leaves of phylloclade origin, with a new type of plate meristem arising from the fusion meristems of original leaves or leaflets, to synflorescences, synandria, syncarpia, etc.

Flowers are assemblages of foliar and floral organs integrated by accelerate development, organ fusion, conversion and convergence over the separate, but interrelated homeodomains. As such, flowers require a more elaborate network of developmental regulators than gymnosperm cones. In the process of their evolutionary origin, a top controlling element, like *LFY* must have been recruited among developmental genes, providing a short cut to expressions of a greater number of homeotic genes than in any other group of higher plants (see under flower development above).

Neoteny, a developmental regulation phenomenon accelerating reproduction relative to vegetative growth, might have disrupted a developmental regulation system of gymnospermous predecessors, giving rise to a new more flexible system of interconvertible foliar – floral meristems. A dosage dependent determination of meristem identity, as in the case of *LFY,* promoted a developmental integration of the foliar and floral structures, involving leaves in accessory reproductive functions.

The origin of angiosperms from small herbaceous plants was postulated on the basis of comparative extant angiosperm morphology by Tsvelev (1977) and Taylor and Hickey (1996). In fact, the early angiosperm records more frequently provides the whole or nearly whole plant specimens than the subsequent stages of evolutionary development. These include the Middle Albian herbaceous angiosperms from western Kazakhstan (Vakhrameev, 1952; Vakhrameev and Krassilov, 1979; Krassilov et al., 1983), of which the relatively complete

Caspiocarpus was an herbaceous plant with a few deeply dissected cauline leaves and a large tripartite inflorescence/infructescence of many congested minute follicles (Fig. 9). In particular, the ovules were extremely neotenic, of microscopic dimensions and with slender integuments. It was accompanied by *Hyrcantha* and *Sarysua* of a similar habit (Krassilov et al., 1983).
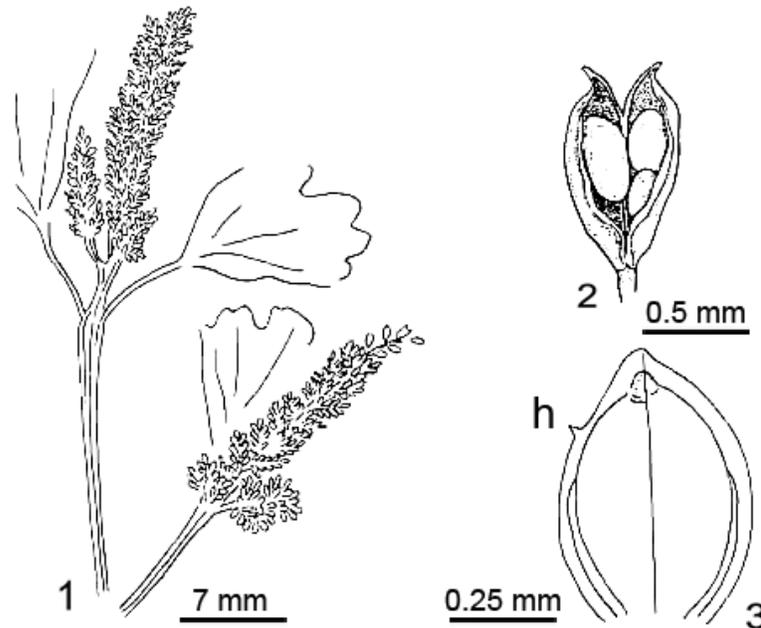
Figure 9. Neotenic early angiosperms: *Caspiocarpus paniculiger*, Middle Albian of Kazakhstan: 1, stem with two *Cissites*-type cauline leaves and a relatively massive terminal inflorescence of minute carpels in crowded racemes; 2, open follicle; 3, bitegmic anatropous ovule with slender integuments, h – hilum (Vakhrameev and Krassilov, 1979).

The whole plant specimens from the Middle Albian of Primorye, Russian Far East (Krassilov and Volynets, 2008) were 5 to 10 mm high, with a solitary basal leaf (*Ternaricarpites*) or with a pair of cauline leaves and with a relatively massive head of small achenes (*Achaenocarpites*). In their reproductive morphology these neotenic plants are related to the arboreal cercidiphyllids and platanoids respectively, appearing at the next stage of angiosperm evolution (see under phylogenetic relationships below).

The fossil record and morphological analysis of archaic extant angiosperms thus give evidence of neoteny in the evolutionary history of early angiosperms.

Irrespective of their mono- or polyphyletic origins, accelerate development and neotenic transformation might have determined such basic angiosperm features as the herbaceous growth habit, phyllocladic leaves with areolate venation derived from leafy shoots by planation and fusion of leaf primordia, phyllodic parallelodromous leaves derived from petioles with reduction of the leaf blade, shortening of floral axis, aggregation of staminate and carpellate organs into the androecial and gynoecial whorls, tricolporate or triporate pollen grain morphologies supposedly derived from permanent tetrads by shifting the meiotic division one step before the gymnosperm schedule, and stunting of ovules that enhanced the structural reduction of female gametophyte.

More than one angiosperm lineage might have passed through neotenic transformations before the basic diversity of flowering plants has emerged. The process is evident at the anthognetid level already represented by small herbaceous plants with phyllodic leaves or leafless and with relatively massive preflowers (Krassilov, 2009). Functional differentiation of successive floral whorls in the anthognetids suggests parallel development of an ABC type regulation system, although less effective in elimination of foliar appendages (pherophylls) from the inner whorls than in the majority of authentic angiosperms.

Such neotenically transformed proangiospermous plants as *Basia* and *Eoantha* (Fig. 7) are not here admitted being angiospermous because their ovules were fully developed at anthesis overgrowing the cupule, whereas the reverse relationships are typical for authentic angiosperms. Although *Baisia* lacks a gymnospermous pollen chamber near the top of the nucellus, the nucellar apex itself was evidently transformed into receptive surface of a kind, whereas in archaic angiosperms the ovule is still juvenile and unready for reception of pollen at anthesis (see Fig. 5 above). This function is transferred to the external coat that in effect develops into conventional carpel.

Irrespective of how far neotenic transformation might have advanced in the other morphological domains, it is the ovule that is the key feature. Ovule is the most conservative organ of seed plants and the last being neotenically transformed over the gymnosperm – angiosperm transition, delegating an essential part of its functions to the carpel. The gametophyte reduction, although being in line with the general trend of seed plants evolution, might have been enhanced in angiosperms by the sporophyte neoteny, approaching the lower limit of complexity at which sexual reproduction is still effective.

Geology of Early Angiosperm Occurrences

The geographic coverage of angiosperm advent by macrofossil records is so far sporadic, coming mostly from the late Early Cretaceous of the central trans-Atlantic coastal areas, Mediterranean, and central – eastern Asia. Local finds in the Lower Cretaceous of Siberia, Patagonia and Australia indicate that early angiosperms were there (Romero and Archangelsky, 1986; Archangelsky and Taylor, 1993; Cantrill and Nichols, 1996; Passalia et al., 2003; Archangelsky et al. 2009), but vast areas of northern Asia and Gondwana lack reliable early angiosperm macrofossils. Palynological records are more evenly distributed. However, angiospermoid pollen grains of dubious, but most probably non-angiospermous affinities are known since the Early Permian and through the early Mesozoic (Zavialova and Gomankov, 2009; Tripathi, 1997; Cornet, 1999). For many Cretaceous pollen morphotypes of the kind, their conventional assignment to angiosperms is yet to be confirmed by reliable *in situ* records (or rejected on the basis of *ex situ* nucellar pollen chamber records, documenting a gymnospermous pollination mode). Taxonomic position of many Early Cretaceous pollen morphotypes is uncertain and some of the earliest, such as *Afropolles* and *Clavatipollenites*, seem to have included both angiospermous and non-angiospermous pollen grains.

Yet in many cases the macrofossil evidence proves to be no less problematic. It is considered highly prestigious to find a pre-Cretaceous angiosperm and a number of candidates have appeared, such as *Furcula, Sanmiguelia* or *Pannaulika*, seemingly confirming a long period of clandestine evolution. However, despite a close similarity in venation pattern, their affinities are more probably with gigantopterids, peltasperms or gnetophytes rather than angiosperms (e.g., Cornet, 1986).

Geological age determination is also a problem, in particular for lacustrine carbonates that are the major source of supposedly pre-Albian angiosperm-like fossils. Their associated faunistic assemblages are extremely rich and of high preservation quality, but poorly correlated with the chronostratigraphic scale. In eastern Asia, their age assignments wander between Late Jurassic and Barremian, although palynological correlation suggests younger ages up to the Albian (Nichols et al., 2000). This problem is here illustrated with two examples of the early angiosperm stratigraphic occurrences in the northeastern Asia and Mediterranean.

Northeastern Asia

I studied the chronology of angiosperm advent in paralic sequences with marine intercalations providing precise geochronological markers. In eastern Asia, such sequences are known from the Primorye Region, Russian Far East, where the coal-bearing and volcanomictic deposits accumulated in the back-arc basins of the rising Sikhote Alin Ranges. The fossil plant-bearing Berriasian and Valanginian deposits are marginal marine with ammonites and bivalves. The Hauterivian is poorly represented because of the regional unconformity. The overlying coal-bearing sequence is assigned to the Barremian – Aptian by its stratigraphic position mainly, being truncated by the marine early Albian *Trigonia* horizon merging with lagoonal and lacustrine black shale facies inland. The middle – upper Albian sequence is tuffaceous, with a few marine intercalations in the northern Sikhote Alin Ranges.

The coal measure flora of Primorye ranks among the richest in the world, representing the diverse fern marsh assemblages, peat bog bennettite assemblages with *Nilssoniopteris*, taxodiaceous wetlands with *Elatides* and other conifers, as well as dryland xeromorphic cycadophyte – conifer shrub assemblages and the upslope ginkgophyte – conifer forest. Their succeeding Albian assemblages differ in a considerable reduction of peat bog elements and a near proportionate increase in dryland contribution.

Through many years of sampling, no evidence of angiosperms has been found in either macrophossil or palynological assemblages of the Neocomian – Aptian age (Krassilov, 1967; Bugdaeva et al., 2006). However, some poorly studied plant groups are perspective for detecting proangiospermous grade morphologies. Krassilov (1967) described as *Paracmopyle* a few fragmentary foliar fossils with a single lateral stomatal band interpreted as bilaterally flattened linear leaves comparable to those of extant *Acmopyle*, the Podocarpaceae (in such leaves, the median ridge represents leaf margin rather than midrib as in the far more common dorsiventrally flattened needle leaves). Similar leaves from the Jurassic of Poland were assigned to a supposedly ginkgophytic genus *Mirovia* (Reymanówna,1969). Subsequent finds in the European Wealden-type floras have been erroneously assigned to the Sciadopityaceae, Coniferales, later being transferred to the "Miroviaceae" (Bose and Manum, 1990). Their overlooked similarity with *Paracmopyle* suggests a widespread and probably heterogeneous group. The foliar organs are here interpreted as phyllodic, consisting of a tubular part with one or more vascular strands, corresponding to the leaf petiole, and a minute apical scale representing the reduced leaf blade. Phyllodic foliar organs are common in angiosperms, but virtually unknown in gymnosperms except in the gnetophytes.

The recently found abundant accumulation of phyllodic plants is here interpreted as representing an expansion of proangiospermous plant community just before the advent of angiosperms.

The early to middle Albian angiosperm assemblages are found in several localities of the marine *Trigonia* horizon, including the black shales and tuffaceous equivalents, in which they associate with *Anemia* ("*Asplenium*") type ferns and fragmentary confer remains. The *Suifunophyllum* type digitate rosette-forming leaves is common in all of them. The whole plant fossils of rhizomatic *Achaenocarpites* and *Ternaricarpites* came from a single locality of the tuffaceous horizon, supposedly representing a pioneer (weedy) plant growth on a fresh ash fall substrate (Fig. 10).

Figure 10. Neotenic early angiosperms: *Ternariocarpites floribundus* from the Middle Albian of Primorye, Russian Far East: fruiting plant with a solitary basal leaf (L).

More diverse angiosperm communities with platanoids and trochodendroids as dominant groups come from the higher horizons of the volcanomictic sequence assigned to the late Albian and Cenomanian. By this time a dynamic system of volcanic island arcs, coastal ranges, intermountain depressions and back arc

basins have extended over the eastern Sakhalin, Kuril Islands, Sikhote Alin, and Zeya – Bureya depressions of the Amur region. Fossil plant localities occur in each of the structural zones providing ample evidence of angiosperm evolution at the continental margin.

Different ecological and taphonomic environments are represented in the non-marine Cretaceous deposits of the Mongolo–Okhotsk intracontinental fault belt, stretching over the Lake Baikal area (Transbaikalia), Gobi Desert and northern China to junction with the coastal fold belts of Primorye and North Korea. Rich floristic and faunistic localities are confined to the laminated shales and lacustrine carbonates of the rift lake facies widespread over the fault belt. An outlier of black shale facies in the junction basins of South Primorye is assigned to the early Albian on marine fossil evidence, yielding the earliest regional macrofossil and palynological angiosperm records (see above). These provide the regional chronostratigraphic markers, but axial depressions of the belt may contain geologically older angiosperm records.

Initially given a Jurassic age, the lacustrine deposits, or part of them, have been then re-assigned to the Cretaceous. Their age assignments are based on the ostracod and conchostracan assemblages that are highly endemic, but reveal certain evolutionary trends thought to be of stratigraphic significance. Both aquatic and terrestrial insect assemblages are fairly diverse, but no chronostratigraphic markers have been singled out so far and their Jurassic or Cretaceous age is still debated by the experts.

An angiospermoid pollen morphotype *Asteropollis*, mainly Albian on the Atlantic coast of North America, has been found in the upper horizons of the lacustrine shale sequences of Transbaikalia (Vakhrameev and Kotova, 1967), Khurendukh horizon of Mongolia and Yixian Formation of western Liaoning, China (Nichols et al., 2006). Yet the possibility of its wider stratigraphic ranges in eastern Asia cannot be excluded. *Asteropollis* is reported from the well-known Baisa Locality on the Vitim River dated as the Aptian on compromise of the plant macrofossil and palynological evidence (Vakhrameev and Kotova, 1967). Bugdaeva confirmed this age assignment by climatostratigraphic correlation, recognizing an Aptian climate worming followed by a cooling in the Albian (after Krassilov, 1973).

Neither the well-studied Baisa Locality, nor the stratigraphically equivalent Semen Locality yielded unequivocal angiosperm macrofossils. A small entire leaf described form Baisa by Vakhrameev (Vakhrameev and Kotova, 1967) appears to be a cataphyll rather than foliage leaf. However, *Baikalophyllum* from Semen Locality shows an asymmetric leaf blade segmentation (Fig. 3) characteristic of the basal leaves of early angiosperms. The diverse angiosperm-like reproductive

structures include *Baisia* and *Eoantha* (Krassilov and Bugdaeva, 1982; Krassilov, 1986). Fortunately, both are preserved with pollen grains in the pollen chambers, therefore being immediately recognized as non-angiospermous. These were the first findings of fossil gnetophytes since Heer (1876) has described "*Ephedrites*" in his pioneer work on the Mesozoic flora of Siberia.

With more such finds it has been realized that we are dealing with a peculiar Cretaceous assemblage representing a weedy gnetophyte-dominated community, in which morphological distinctions between gnetophytes and angiosperms might have been less clear-cut than in the extant flora. It became clear that angiosperm-like plants from the stratigraphically equivalent deposits of Mongolia (Krassilov, 1982) may, partly at least, belong to gnetophytes, although no evidence but circumstantial was obtained.

In Mongolia, the angiosperm-like fossils described by Krassilov (1982) came from Manlay Locality of southern Gobi and Gurvan-Eren locality of the Gobi Altay in the northwestern part of the country. Both localities were assigned to the Neocomian as the basal Cretaceous deposits of the area. Yet my subsequent visit to Manlay in 2009 has shown that, although onlapping the Paleozoic basement, the plant-bearing deposits are actually younger than those of the central part of the basin and are stratigraphically equivalent to the Khurendukh Formation, Choyr Basin, containing *Asteropollis* (Nichols et al., 2006; Ito et al., 2006), therefore Albian or no older than Aptian and the most probable stratigraphic correlate of the Baisa Locality of Transbaikalia.

At least some of the supposed angiosperm genera, *Gurvanella* from Gurvan-Eren, was recognized in the Jehol flora of Liaoning, China and revised by Sun et al. (2001). It was interpreted by Krassilov (in Akhmetiev and Krassilov, 2000) as a variation of the same theme as *Eoantha* and therefore gnetophytic. Common in the Jehol flora is also an another Baisian gnetophytic species *Eoantha rostrata* (*Beipiaoa spinosa*). *Archaefructus*, a peculiar angiosperm with fern-like foliage (Sun et al., 2001) was found in association with the Baisa-type gnetophytes, whereas *Leefructus* coming from a higher horizon of the Yixian Formation, is comparable with the relatively well-dated Middle Albian angiosperms of western Kazakhstan (Vakhrameev, 1952; Krassilov et al., 1983) suggesting a wider stratigraphic range of the Jehol biota.

Mediterranean

Thick non-marine to marginal marine deposits occur in the rift basins on the northern flank of the submeridional African fault system and their transcurrent fault belts traversing the Negev Desert. In the central–northern Negev, Israel, the

clastic Lower Cretaceous Hatira Formation exposed in erosion windows ("craters") from under the uniform cover of thick limestones is a sandstone/shale sequence unconformable on the mid-Jurassic deposits. The Zuweira Marine Tongue in the lower part of the sequence contains a littoral assemblage of bivalves, gastropods, *Lingula*, and crustaceans, as well as plant remains. It is correlated with the marginal marine deposits of Abu Ballas Formation in southern Egypt, as well as the gastropod shales ("Couches à Gasteropodes") of Lebanon dated as the Barremian - Aptian (Gvirtzman et al., 1996). Angiospermoid pollen appeared at about this level (Schrank, 1992; Brenner, 1996), but plant macrofossils are mostly ferns *Weichselia*, cycadophytes, and cheirolepids. The fruit-like *Afrasita*, first described as *Leguminocarpon* from the Abu Ballas Formation of Dakhla Basin, southern Egypt (Lejal-Nicol, 1981) was re-interpreted as proangiospermous of gnetophytic affinities, representing the same evolutionary grade as the gnetophyte records from the Lower Cretaceous (Aptian) of Central Asia (Krassilov et al., 2004). The lower Hatira sequence is topped by the Ramon basalts radiometrically dated as the Aptian – early Albian (Segev et al., 2005). The macroflora from interbasaltic shales is non-angiospermous, except a poorly preserved *Ramonicarya* (Krassilov and Dobruskina, 1995), a dubious angiosperm record.

In the Upper Hatira sequence above, two fossil plant bearing shale horizons are bracketed between the argillaceous limestones with ammonites *Knemiceras* sp. probably representing the *Knemiceras gracile* assemblage, Early Albian (Abu-Zied, 2008) and the carbonate unit with *Knemiceras dubertreti* Basse, a member of the Late Albian assemblage widespread in the Tethys realm (Robaszynski et al., 2008). Variegated sandstones and shales separate this marine intercalation from the uppermost Albian – Cenomanian Hevyon limestones with abundant marine fossils. The diverse flora of ferns, ginkgophytes and conifers contains both narrow-leafed and broad-leafed morphotypes, as well as aquatic forms with floating leaves (Silantieva and Krassilov, 2006a). Plant assemblages of tidal flat deposits are dominated by *Weichselia negevensis* represented by roots, stems, sterile and fertile leaves, as well as dispersed spore-bearing structures and interpreted as an ecological precursor of mangrove ferns (Silantieva and Krassilov, 2006b). The narrow-leafed *Acaciaephyllum* with compound intramarginal veins and irregular areolation suggesting a gnetophytic rather than angiosperm affinities is found with *Weichselia* as a member of the same or adjacent coastal marsh community. The ranunculid *Cisites – Vitiphyllum* and *Sapindopsis* morphotypes are comparable with the early – middle Albian herbaceous angiosperms of Primorye and Kazakhstan (above), being represented in the Potomac flora of Atlantic coast as well (Hickey and Doyle, 1977). The broad-leaved platanoid remains came from sandy facies and are

interpreted as allochthonous on the preservation quality criterion (Silantieva and Krassilov, 2006a).

In Makhtesh Qatan to northeast, the plant-bearing horizons are stratigraphically equivalent to those of Makhtesh Ramon, but the fossil plant assemblages from shaly and sandy facies are markedly different (Krassilov and Schrank, 2011). The shaly plant-bearing facies contain abundant fusainized plant debris, pyrite nodules and scattered pieces of amber. The presence of *Botryococcus* and dinoflagellate cysts indicates a meromictic lake with an input of organic-rich water from surrounding wetlands. The plant assemblage is dominated by a gymnosperm genus *Qataniaria* of supposed gnetophytic affinities. Its leaves are resiniferous, suggesting a source plant for amber. Likewise common are the osmundaceous ferns, while *Weichselia* is represented by transported debris. The conifer and angiosperm remains are fragmentary, except a few leaflets of *Parvileguminophyllum*. The angiosperm and angiosperm-like pollen is a scarce element of the palynological assemblage (0.5% or less), including *Clavatipollenites*, *Pennipollis*, *Retimonocolpites*, *Afropollis*, *Tricolpites*, *Rousea* and the winteraceous pollen tetrad *Walkeripollis*. Yet *Clavatipollenites* is occasionally preserved in dense masses from dispersed sporangia.
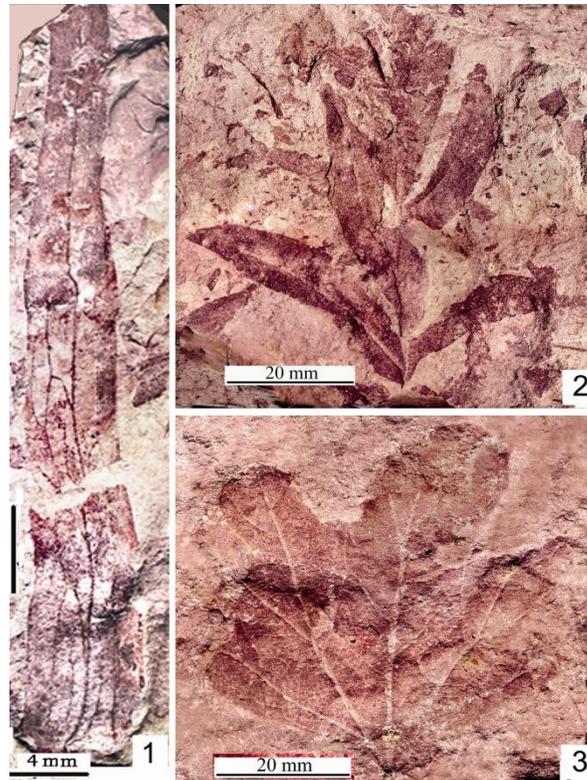
Figure 11. Angeospermoid and angiosperm leaf morphotypes from the Middle Albian of Negev, Israel: 1, *Acaciaephyllum* from tidal flat deposits of Makhtesh Ramon; 2, pinnatifid *Sapindopsis* and 3, platanoid leaf from fluvial deposits of Makhtesh Qatan (Silantieva and Krassilov, 2006a; Krassilov and Schrank, 2011).

The shales are overlain by a silty sandstone of quartz grains coated with iron oxides. The plant remains are coarsely preserved as ferric impressions. Absolutely dominant among them are the large ribbon-shaped leaves, forming mat-like accumulations on the bedding planes, with articulate stems occasionally preserved as three-dimensional moulds. The occasional finds of fruit-like *Afrasita* may belong to the same plant. A reed-like growth in the iron-rich shallow ox-bow water seems the most plausible interpretation for the mats. *Araucaria* is numerically dominant in the fluvial deposits and is found as an allochthonous component elsewhere, suggesting a coniferous forest, with *Brachyphyllum* and *Nageiopsis* as subdominants, on the benches and slopes of the river valley. Angiosperms, next in abundance to conifers, are represented by a polymorphic

Sapindopsis and platanoids (Fig. 11). The other angiosperms, including *Ranunculaecarpus* and *Nelumbites*, are the single-specimen records.

Thus, the Negev localities show dramatic changes in composition of fossil plant assemblages and angiosperm representation in respect to different depositional environments. The tidal flat *Weichselia – Acaciaephyllum* assemblage of Makhtesh Ramon contains rare ranunculid and platanoid angiosperms as allochthonous element. Out of stratigraphic context, the *Qataniaria* – fern bog assemblage with inconspicuous angiosperm macrofossils and the riparian conifer assemblage with co-dominant angiosperms appear as different stages of early angiosperm evolution, the former being more archaic also in respect to the palynological records. The idea of an early, supposedly Neocomian stage of small monosulcate (*Clavatipollenites*) and inaperturate pollen grains (Brenner, 1996) is probably based on diachronous occurrences of such pollen in this type facies domain. On the other hand, the fluvial sandstone assemblage is fairly close to the Potomac flora of North America, with abundant *Araucaria (Arucarites), Athrotaxopsis*, *Nageiopsis* and *Sapindopsis* represented by the same or closely related morphotaxa, such as the Potomacian *Araucairtes aquinensis* Fontaine, *Athrotaxopsis expansa* Fontaine, *Brachyphyllum crassicaule* Fontaine, and *Sapindopsis magnifolia/variabilis* Fontaine. The most closely comparable assemblages are assigned to the Subzone II-B, early – early late Albian of the Potomac Group (reviewed in Upchurch et al., 1994), while the pinnatifid *Sapindopsis* morphotype is confined to the upper, Late Albian part of the same subzone, where it is associated with broadleaved platanoids as in the fluvial sandstone locality of Makhtesh Qatan.

The above examples suggest a roughly synchronous angiosperm first appearance in the fossil records of such distant regions as northeastern Asia and Mediterranean when based on well dated stratigraphic sequences. When not so well dated sequences are added, the chronology of the first angiosperm appearances may seem widely discrepant. The facies differences are very prominent and of a so far underrated significance for stratigraphic correlation.

The trans-Atlantic angiosperm records may suggest an earlier angiosperm first appearance than in the other regions. Yet in this case the regional evolution rates must have been slower there than in the Mediterranean, because the Late Albian angiosperm assemblages are at the same level of evolutionary advancement. Having a long history of paleobotanical research, the Atlantic coast localities of North America and their European counterparts rank among the richest in the world and a major source of inference on early angiosperm evolution. Parallel evolutionary sequences are reconstructed for the foliar and pollen records (Doyle and Hickey, 1976; Hickey and Doyle, 1977). The

taxonomic diversity of macrofossil and palynological remains is recently augmented by mesofossil studies (e.g., Friis et al., 1992, 1994, 1995, 1997 and elsewhere). Yet the age assignments are less rigidly controlled than in the case of the fairly similar Albian plant-bearing sequences of the Negev Desert intervened and truncated by four marine horizons in the Hatira and the overlying Hevyon formations. The abovementioned similarities suggest roughly coeval stages of angiosperm evolution in the trans-Atlantic and Mediterranean regions. A recent revision of stratigraphic correlation implies that angiosperm macro- and mesofossils are scarcely older than Early Albian on both sides of the Atlantic (Heimhofer et al., 2005, 2007; Hochuli et al., 2006). Hitherto no attempt has been made to differentiate between authentic angiosperm and proangiosperm remains in the mesofossil Atlantic coast assemblages, while the differences in taxonomic assignments are interpretational (reviewed in Crepet et al., 2004 and below). Both the trans-Atlantic and Mediterranean early angiosperm macrofossil records are preceded by the first appearances of sulcate columellate pollen grains coincident with pre-Albian proangiosperm assemblages.

As in eastern Asia, the most significant proangiosperm – early angiosperm European occurrences are confined to intersections of the marginal Atlantic troughs and the rift basins of their transcurrent fault systems. The marginal basins contain the non-marine to marginal marine Wealden facies of a long disputed geological age. Their correlation on the basis of non-marine faunistic assemblages gave incongruous results and was largely replaced by marine intercalation markers, indicating the age range from Berriasian to Albian (Allen and Wimbledon, 1991). However such markers are lacking in the rift lake sequences of the Pyrenean and Iberian basins with lithographic limestones yielding the angiosperm-like *Montsechia* and *Montsechites* ("*Ranunculus*") widely publicized as highly specialized aquatic angiosperms of Neocomian age, attesting to a long period of clandestine angiosperm evolution (Daviero-Gomez et al., 2006; Gomez et al., 2006). The lithographic limestones of the Montsec Range, once considered to be Late Jurassic (Kimmeridgian), were later re-assigned to the early Neocomian (Barale et al., 1984). At the famous Las Hoyas locality of Cuenca Province their geological age was given as the Late Hauterivian based on charophyte and gastropod assemblages (Sanz et al., 1988) to be re-assigned to the Late Barremian (Gomez et al., 2006; Soriano and Declos, 2006; Fregenal-Martínez et al., 2007; Buscalioni and Fregenal-Martinez, 2010). However, the recently found leaf fragments with areolate venation typical of dicotyledonous angiosperms (Barral-Cuesta and Gomez, 2009) suggests the possibility of a still younger age.
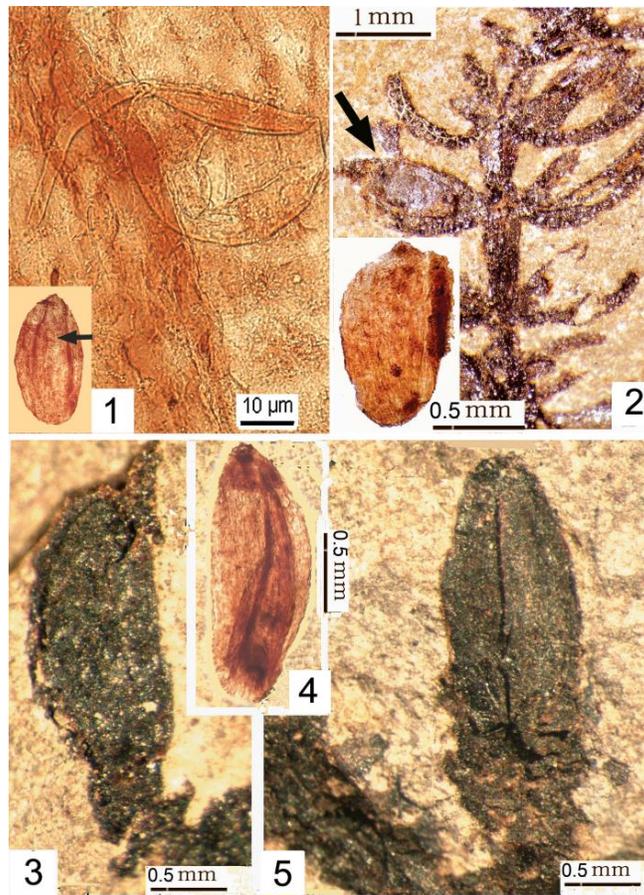
Figure 12. Angeospermoid plant *Montsechia vidalii*, Las Hoyas, Spain: 1, germinate pollen grain on the nucellus (insertion, arrow indicates position of the pollen grain); 2, long shoot bearing leafy short shoots, one (arrow) with a cupule; macerated nucellus shown on insertion; 3, 5, reproductive short shoots with scale leaves and a terminal cupules; 4, nucellus macerated form (3).
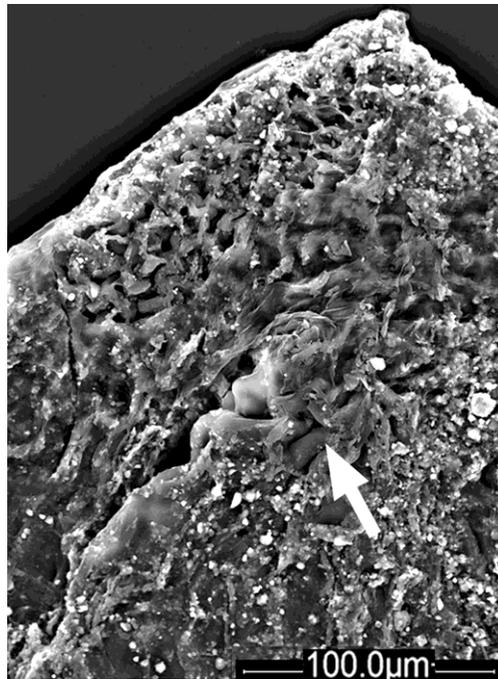
Figure 13. Angeospermoid plant *Montsechia vidalii*, Las Hoyas, Spain: nematode larva (arrow) emerging from a seed-like body.

My revision of shoot morphology in *Montsechia vidalii* indicates a heloxeromorphic growth habit characterized by the shoot dimorphism and heterophylly. Slender shoots with decussate leaves produced knobby axillar short shoots bearing both scaly and elongate leaves as well as intermediate varieties. The long leaves are thick and fibrous, although feebly cutinized. In the "scaly" form, both long and short shoots are bearing scale leaves that are trichomate with well protected stomatal pits.

These features of growth habit are scarcely typical of angiosperms, but rather suggest derivation from a scale-leaved gnetophytic group such as cheirolepids. The ovulate organs are cupules terminal on bracteates short shoots and containing a solitary epitropous or sometimes apotropous ovule. The nucellar apex is densely papillate and germinate pollen grains are occasionally found stuck to it (Fig. 15). On account of these features *Montsechia* is comparable with *Baisia* rather than angiosperms.

I found that the "scaly" variety of *Montsechia* was heavily infested with seed-like nematode galls (Fig. 16) probably responsible for its morphological

distinctions from the "leafy" variety. The habitat of *Montsechia*, in particular its "scaly" form must have been favorable for nematode reproduction that requires warm moist soil with turf roots. Conceivably, the nematodes and associated parasitic organisms might have contributed to acquisition of a stunted feebly foliated growth habit characteristic of the Early Cretaceous proangiosperm assemblages and, indirectly, to evolutionary development of angiosperm morphology by accelerate reproduction.

Thus, in the case of *Montsechia* at least, there is no ground for asserting a long-time angiosperm evolution in a local isolated area. Neither is there evidence for diachronous first appearances of angiosperms over the globe. A revision of supposed Rajmahal angiosperm macrofossils from India (Srivastava and Krassilov, 2011) casts doubts on their pre-Albian occurrences in Gondwana. The Koonwarra assemblage containing the earliest angiosperm macrofossilsin Victoria, South Australia is conventionally assigned to the Aptian. However, the thermophilic bennettites decrease in Koonwarra relative to their diversity in the preceding Early Cretaceous assemblages, while the temperate ginkgophytes increase, suggesting a cooling trend that globally commenced in the Early Albian. The authentic Koonwarra angiosperms (Taylor and Hickey, 1990) are similar to *Caspiocarpus* and belong to the same grade as the mid-Albian ranunculids of Kazakhstan and Far East. They are likewise accompanied by gnetophytic plants (Krassilov et al., 1998).

Rise to Dominance: Stages of Early Angiosperm Evolution

Although roughly coeval on global scale, the early stages of angiosperm evolution show regional and facial differences in their numerical representation, diversity and evolution, being highly dependent on composition of their cradle communities, climatic differentiation and topography of their habitats (see Makhtesh Qatan example above).

Cradle Communities

Before the advent of authentic angiosperms, characters thought to be typical of the group appeared in various gymnosperm lineages that advanced in the direction of angiosperm level of morphological evolution (Krassilov, 1997). These developments culminated in the Aptian –Albian angiospermoid communities that included angiosperm-like gymnosperms (proangiosperms) and occasional authentic angiosperms. Proangiosperms evolved in parallel with, and

probably contributed to the origins of conventional angiosperms that rapidly increased through the subsequent Cenomanian to Turonian stages, giving rise to the basal stalks of the modern angiosperm diversity.

Proangiosperm communities were discovered in the Aptian (age discussed above) of Baisa Locality, Transbaikalia, including several genera of putative bennettitalean – gnetophytic affinities, such as *Baisia, Eoantha, Vitimantha, Prognetella, Preflossela, Baisianthus*, and others (Krassilov, 1986; Krassilov and Bugdaeva, 1982, 1999, 2000, reviewed in Krassilov, 1997, 2010). Later on, similar assemblages were found in Mongolia and eastern China (Krassilov, 1982; Sun et al., 2001) Their dominant plants are herbaceous, sometimes rhizomatous of monocot aspect, mostly diclinous, but occasionally monoclinous (*Preflosella*), with cupulate gynoecia and variously developed perianth bracts. Those having a flower-like structure of perinth and gynoecial whorls are classified as anthognetids (Krassilov, 2010). The Jehol biota of the Yixian Formation, eastern China comprises the richest gnetophyte communities and (Sun et al., 2001), also containing abundant *Leptostrobus*, a proangiosperm with papillose (stigmatic) marginal flanges of carpel-like cupules. This grade communities thus betrays parallel developments toward angiosperm morphology. Rare fossils are identified as authentic angiosperms (Vakhrameev and Kotova, 1967; Krassilov, 1982; Sun et al., 2001, 2011).

Perhaps equally rich, but insufficiently studied gnetophyte assemblage is represented in the Santana plant and insect locality of the Crato Formation, Brazil (Mohr and Friis, 2000; Rydin et al., 2003; Dilcher et al., 2005). Both Yixian and Santana assemblages attest to increase of gnetophyte participation in the tropics. Yet a considerable participation of gnetophytes is documented for the extratropical Aptian – Albian Koonwarra Locality of Victoria, Australia (Krassilov et al., 1998), as well as the coeval Atlantic coast localities of North America and Portugal (Crane and Upchurch, 1987; Rydin et al., 2006).

A different type of proangiosperm assemblages with less diverse, but numerically prominent plants of gnetophytic grade, such as *Afrasita*, *Qataniaria*, and *Montsechia* are known from the Lower Cretaceous of the Middle East and Pyrenees. They represent different variants of wetland to semiaquatic vegetation. Their age assignments are controversial, but when based on marine fossils range from the Aptian to the early – middle Albian. *Afrasita* from the marginal marine late Aptian deposits of Egypt and Israel (Krassilov et al., 2004) is a fruit-like fossil compared to the gnetophytic *Gurvanella* (Krassilov in Akhmetiev and Krassilov, 2000), as well as the bennettitalean *Vardekloeftia* (Harris, 1932b; Pedersen et al., 1989).

Qataniaria is numerically dominant in at least two Albian assemblages of the Negev, both representing coastal wetlands. Leaf shedding is suggested by the taphonomy of abundant accumulations of its detached leaves and cataphylls (Fig. 14). The foliar features find their close analogues among the gnetaleans with sheathing leaves. The ovulate organs consist of a four-lobed bracteate perianth and a ribbed cupule as in the ephedroid gnetophytes.
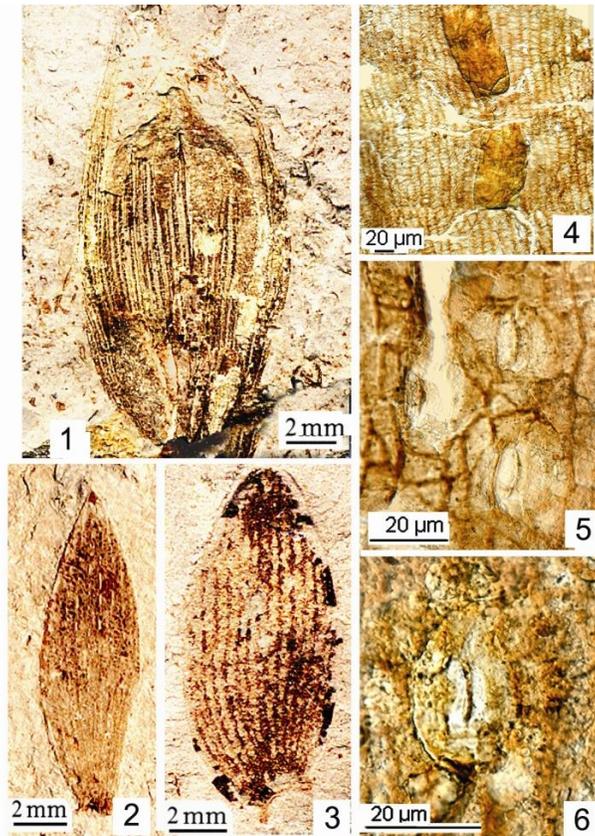
Figure 14. Gnetophyte domination in the Albian fossil plant assemblages: *Qataniaria noae*, Middle Albian, Makhtesh Qatan, Negev, Israel: 1, cupulate ovule invested in calyptrate cataphylls, 2, 3, detached cataphylls, 4, leaf cuticle with a massive resin duct, 5, 6, leaf cuticles showing stomata.

Montsechia, a supposed earliest aquatic angiosperm, is re-interpreted (Krassilov, 2011) as an herbaceous, probably rhizomatic marsh plant with dimorphic shoots and heteromorphic leaves. Its angiospermoid aspect is partly

conferred by nematode infestation (Fig. 13). On account of cupulate ovules and nucellar features its putative taxonomic affinities are with gnetophytes rather than angiosperms. Pure Montsechia of Las Hoyas representing a semiaquatic variant of monodominant gnetophyte vegetation and comparable to the marshy *Baisia* of Asiatic lacustrine assemblages and the *Gerofitia – Gerocladus* group from the ecologically equivalent Turonian assemblages of the Dead Sea area (Krassilov et al., 2005).

Prominent in the Albian to Turonian wetlands were leaf morphotypes of uncertain gnetophytic or angiosperm affinities such as *Acaciaephyllum* from the Albian of Makhtesh Ramon Notably all proangiosperm localities yield angiospermoid pollen of *Clavatipollenites* grade, although angiosperm macrofossils are lacking or exceedingly rare and a matter of interpretation.

The *Pentoxylon* flora of southern continents, typically represented in the intertrappean Early Cretaceous of Rajmahal Basin, India, represents a woody herb community, for which some evidence of underground storage organs is reported (Srivastava and Krassilov, 2011) suggesting a geophytic habit that predominantly occurs in perennial herbs of seasonally dry climates. *Pentoxylon* plant produced pulpy cupulate seeds, betraying zoochorous adaptations atypical of Mesozoic gymnosperms. Authentic angiosperm macrofossils are lacking from the typical *Pentoxylon* assemblages (Srivastava and Krassilov, 2011), yet they contain angiospermoid pollen grains (Tiwari and Tripathi, 1995; Tripathi, 2008).

The Late Albian – Turonian Early Angiosperm Communities

The Negev Desert Aptian to Turonian succession of macrofossil plant assemblages documents the most significant stages of early angiosperm evolution starting with gnetophytic proangiosperms with occasional macrofossil and palynological fossils classifiable as angiospermous in the Aptian, proceeding through the sequence of progressively increasing angiosperm representation in the Albian and Cenomanian, and culminating with complete angiosperm dominance over a wide range of habitats in the mid-Turonian, which is the end of the early angiosperm evolution. Certain stages of this evolutionary sequence are represented in the widely scattered mid-Cretaceous localities of the Middle East, northern Africa and southern Europe (Bender and Madler, 1969; Lejal-Nicol and Dominik, 1990; El Chair et al., 1995; Barale et al., 2003; Barale and Ouaja, 2001, 2002; Schrank and Rüffle, 2003). The first appearing angiosperm fossils, such as *Acaciaephyllum* and *Sapindopis* are of hypothetic alliances or not at all assignable to any families or orders of modern angiosperm classifications. Their diversity scarcely exceeded 3 – 4 species per a bedding plate plant assemblage. They were

members of wetland plant communities reconstructed as coastal marshes (Silantieva and Krassilov, 2006a). At the end of the early evolution sequencce, the bedding plant assemblages might have ap to 20 species, most of them of a definite modern alliance, and a number of recognizable angiosperm plant communities nearly proportionally increased (Krassilov et al., 2005).

At the same time, the appearance of such archaic communities as *Qataniaria* bogs with inconspicuous angiosperm participation and, simultaneously, the burst of conifer diversity in the middle Albian indicate that the process was not one-directional, being regulated by the forces of a very general significance for plant life. Climate change is such a force affecting both plant distribution and morphological adaptations. The effect of climate change is most prominent near the boundaries of latitudinal and altitudinal vegetation zones. The Cretaceous plant localities of the Middle East are presently situated, and apparently were situated through the Cretaceous, near the boundary of xeric and humid zones of subtropical vegetation where the climatically induced shifts of the boundary brought about alternation of xeric and mesic plant assemblages, reflected in the fossil record.

Two large cycles of climate change and plant evolution are inferred from the regional successions of mid-Cretaceous plant assemblages, with xeric phases in the Aptian and Cenomanian alternating with humid phases in the mid-Albian and mid-Turonian. Angiosperms increased through the cycles from a subordinate to dominant status in both the wetland and dryland communities. The role of climatic cyclicity for angiosperm evolution is still to be learned, but they roughly correspond to the first appearance – diversification phases of the early angiosperm lineages.

The Aptian flora is sparsely represented in the marginal marine deposits and intertrappean redbeds, reflecting a species poor xeromorphic vegetation. In contrast, the exceptionally high diversity of conifers in the inland Makhtesh Qatan assemblages, as well as the appreciable contribution of the fern bogs runoff to lacustrine sediments attest to a relatively humid phase of climatic evolution, followed by a drier climatic conditions in the Cenomanian of Ein Yabrud, Judean Mountains, Nammoura of Lebanon, Batn al Ghul of southwestern Jordan and Atjoula of Libya (Dilcher and Basson, 1990; Krassilov and Bacchia, 2000 and unpublished), with xeromorphic practically leafless *Frenelopsis* and phyllodic Miroviaceae. The angiosperms are predominantly *Sapindopsis* (Fig. 15) with an appreciable representation of the xeromorphic narrow serrate morphotypes and small-leaved aquatic forms. Floras of this stage are essentially uniform across the Tethys.

0.5 cm

Figure 15. Xeromorphic Sapindopsis, Cenomanian, Nammoura, Lebanon (Krassilov and Bacchia, 2000).

In distinction form the temperate zone of northern Asia, the role of conifers decreased through the Cenomanian dry phase. With recovery of riparian vegetation in the Turonian, conifers were replaced by broadleaved angiosperms in the canopy of mesic lowland forests. This latter stage is represented by the Gerofit assemblages of the Dead Sea – Arava rift basin. Their mid-Turonian age is based on ammonite records from the underlying and overlying marine deposits (Bartov et al., 1972; Lewy, 1989; Krassilov et al., 2005). The Gerofit flora is presently the most representative for Mediterranean realm. It comprises about 50 species of angiosperms of extant orders in particular the Nymphaeales, Cercidiphyllales, Hamamelidales, Myrtales, and Arecales, as well as extinct groups. The Gerofit assemblage of arthropod feeding and habitation traces constitute one of the most diverse regional phyllostigm assemblages (Krassilov,

2007; Krassilov and Shuklina, 2008; Krassilov and Rasnitsyn, 2008). Taphonomic analysis of the mid-Turonian assemblages revealed a catenic sequence of plant communities including the *Dewalquea* mangroves, *Gerofitia* marshes, *Nelumbites* – *Brasipelta* aquatic vegetation, and *Eucercidiphylites* broadleaved forest.
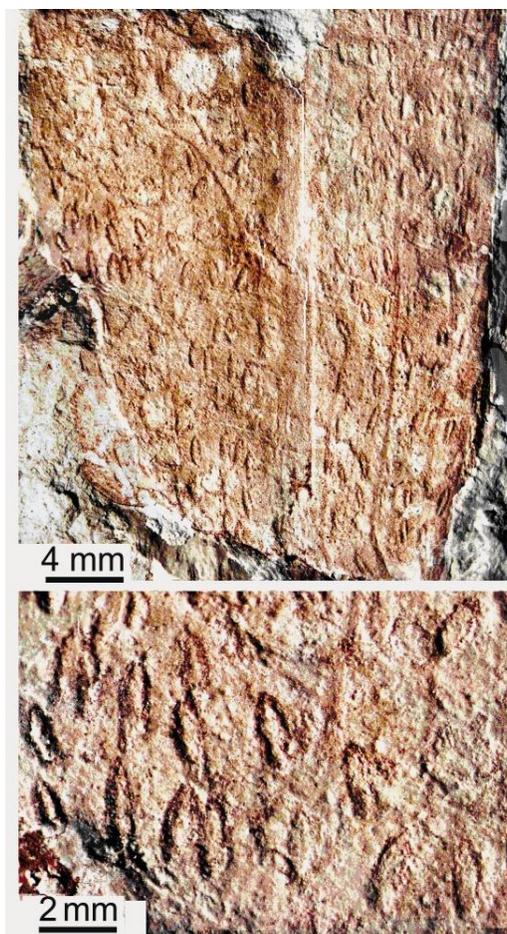
Figure 16. Odonata egg set on *Acaciaephyllum* leaf from the middle Albianof Makhtesh Ramon, Negev Desert and the egg scars enlarged.

Unlike the Albian pre-mangroves, the Turonian *Dewalquea* assemblage represents the typical mangrove adaptations, including the knee roots and cyptoviviparous seedlings (Krassilov et al., 2005). The Turonian aquatic community gives evidence of a considerable advancement since the Albian both

in terms of morphological evolution and diversity of both dicots and monocots. The appearance of the broadleaved dryland vegetation of diverse arboreal angiosperms can be considered as a major evolutionary innovation since the Albian.

Our regional data provide a spectacular example of ecogenesis and morphogenesis going hand by hand. The bursts of morphological diversification accompanied the build-up of new plant communities, such as mangroves or broadleaved forests, and were enhanced by new types of biotic interactions, their complexity increasing with angiosperm diversity and having the increasingly powerful feedbacks. In particular, the significance of plant – arthropod interactions can be deduced from diversity of leaf damages. Thus traces of arthropod feeding/habitation are rather scanty through the late Early Cretaceous becoming much more diverse in the Cenomanian and exceptionally abundant in the Turonian.

Of the Early Cretaceous phyllostigmas, the Odonata egg sets on angiospermoid *Acaciaephyllum* type leaves (Fig. 16) represent an evolutionary innovation of insect habits. They are evidence of a waterside habitat, because the larvae of damsel flies must fall into water or they perish. Feeding traces are infrequent, while the marginal and apical cutouts, the most severe leaf damages are more probably related to a cocoon construction activities. In contrast, the diverse Turonian phillostigm assemblage includes egg scars, procecidia, diverse mine types, somewhat less diverse gall types, larval cases, and marks of leaf surface feeding, as well as punctures left by mine and gall predators suggesting correlation between abundance and specificity of arthropod damages on the one hand and complexity of angiosperm host communities on the other (Krassilov in Krassilov and Rasnitsyn, 2008).

The plant – parasite interaction is a two-level trophic system superimposed by the third level of mine predators and parasitoids. The system is regulated from bottom up, by plant responses, and from top down, by predation (Faeth, 1985). In the putative mangrove foliage of *Eudebeya – Dewalquea* group, each parasitized leaf bears more than one, and not infrequently up to five different types of phyllostigmas (Fig. 17), suggesting that plant resistance decreased, with an increasing impact of leaf parasites (the "weakness parasitism"). Traces of mine predation are relatively rare attesting to insignificant role of top–down regulation, becoming more numerous in a more stable broadleaved assemblage (Krassilov, 2008a).

A general evolutionary tendency in the Cretaceous plant-arthropod interaction system is a concomitant increase in parasite diversity and host specificity impelling diversification of host plants. This tendency is reiterated with

appearance of new plant communities, such as angiosperm mangroves vulnerable to weakness parasitism at their early evolutionary stages. Plant morphological effects of arthropod damages tend to evolve from severe to benign with increase of ecological complexity, including temporal mining and the gall/mine predation (Krassilov, 2008 a, b).
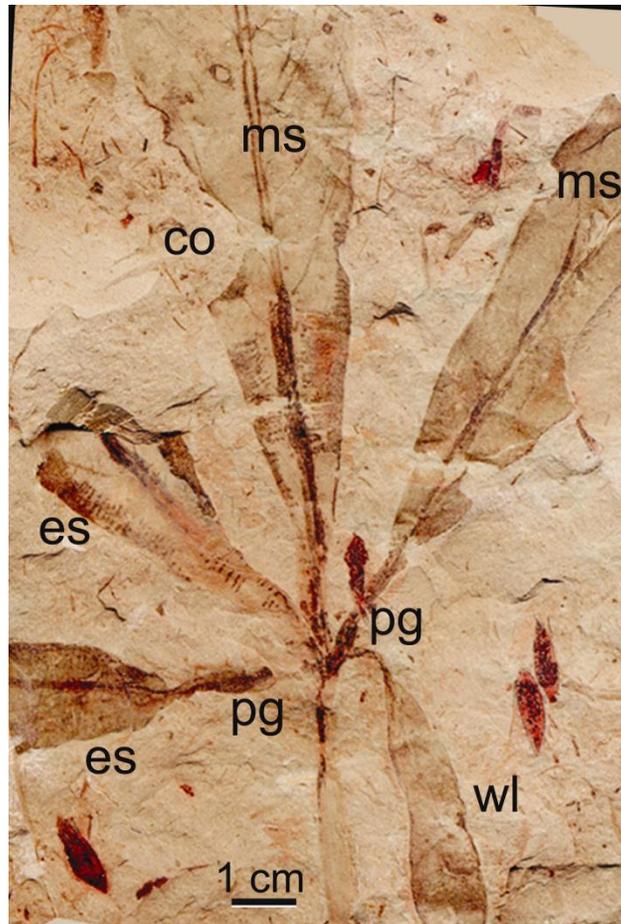

Figure 17. Weakness parasitism in the Turonian mangrove plants from Gerofit South Israel: on-leaf association of marginal cutouts (co) transverse rows of egg scars (es), midrib splitting gall (ms), petiole gall (pg), and welting leaflets (wl).

Phylogenetic Relationships among Early Angiosperm

Rather than being assumed from mechanistically derived "phylogenies", the phylogenetic relationships of early angiosperms can be inferred from their chronology and intrinsic evolutionary tendencies. The following is a step in this direction.

Ranunculids

Angiosperm families occurring at the base of a morphological system (e.g., Takhtajan, 2000) are supposed to be the end members of angiosperm lineages appearing in the first round of adaptive radiation to remain conservative through further developments. Paleobotanical findings suggest that herbaceous growth habit appeared early in the evolutionary history and was perhaps primary for the group. It is well known that herbaceous plants are underrepresented in the fossil record. However, in the mid-Cretaceous they were more common than afterwards and were represented by a number of morphotaxa suggesting a considerable diversity and morphological disparity. Most of these plants are assignable to ranunculids s. l., showing phylogenetically meaningful similarities with the modern Ranunculaceae, as well as Menispermaceae, Berberidaceae and isolated genera *Sargentodoxa*, *Glaucidium, Circaeaster and Kingdonia* of the same morphological plexus.

Among them, *Caspiocarpus* from the Middle Albian of Kazakhstan, the first early angiosperm for which microscopic information was obtained (Vakhrameev and Krassilov, 1979), represents a herbaceous plant with a slender stem bearing a pair of palmate deeply dissected cauline leaves as in extant *Ranunculus acris* (the "*Cissites* type" of the paleobotanical leaf classification) subtending a large tripartite head of numerous small follicles with minute bitegmic anatropous ovules. It is assigned to ranunculids on account of its general habit, leaf morphology, dorsiventricidal follicles and the structure of ovules with extremely reduced one cell thick integuments as in the modern Ranunculaceae and Circaeasteraceae.

Hyrcantha from the same locality (Krassilov et al., 1983) is represented by slender branched axes bearing biternate cauline leaves (as in the Isopyroideae, Ranunculaceae) and regular flowers with floral parts persistent in fruits. The fruits are basically ternate, although occasionally pentamerous, of urn-shaped ventricidal follicles, truncate at the broad sessile stigmas as in *Paeonia*, a controversial genus linked to the Ranunculales or Dilleniales (Cronquist, 1981).

Achaenocarpites, the whole-plant angiosperm fossil from the early – middle Albian of Primorye, Far East, represents small rhizomatic plants with tubers (Fig. 18). Their foliar architecture is basically ternate, with additional leaflets or lobes appearing on the larger leaves. As ontogenetic studies suggest (Kürbs, 1973; Tamura, 1993), in the Ranunculaceae the leaves, although morphologically diverse, are invariably tripartite in early development. The terminal actinomorphous flowers with a gynoecium of free uniovulate carpels developing into a head of achenes are of a rather common type among the modern Ranunculoideae, as well as Thalictroideae. The anatropous ovules pendulous from near the apex of achene occur in the tribes Anemoneae and Ranunculeae (taxonomy after Tamura, 1993).
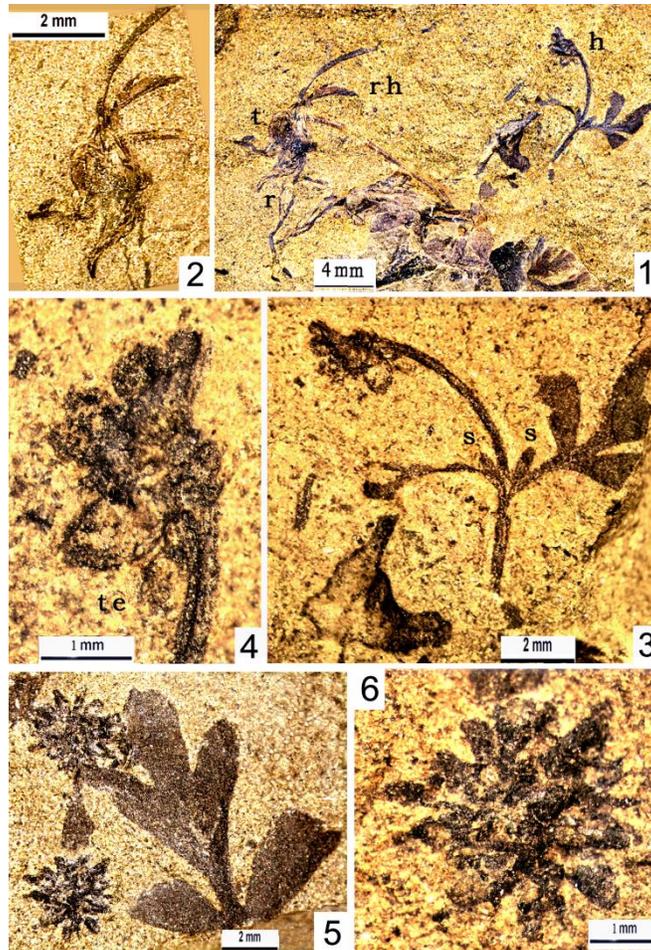
Figure 18. Ranunculid stage of early angiosperm evolution: *Achaenocarpites capitullatus* fom the Middle Albian of Primorye, Russian Far East: 1, whole plant, 2, rhizome with tubers and adventitious roots, 3, stem with two cauline leaves and a terminal flower, 4, flower, 5, 6, detached leaf and the heads of achenes (Krassilov and Volynets, 2008).
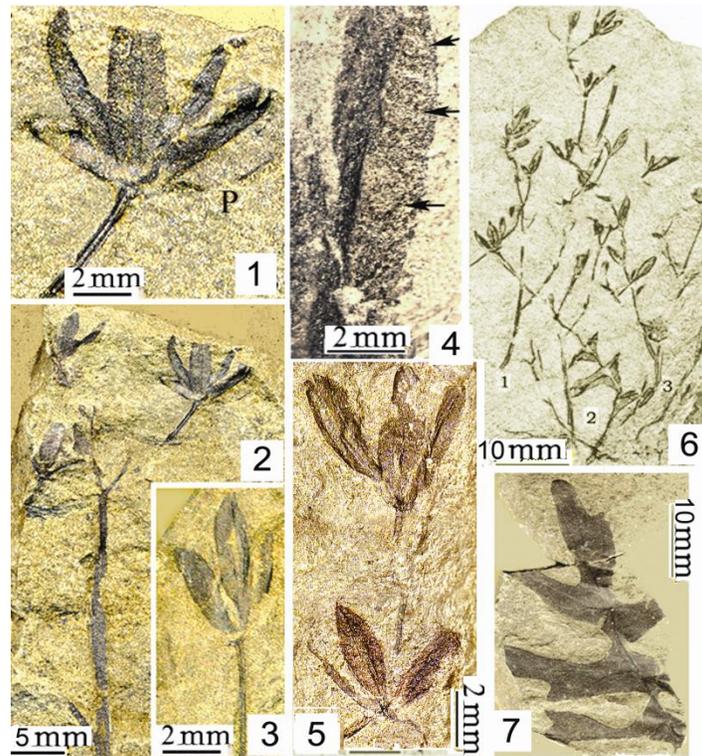
Figure 19. Ranunculid stage of early angiosperm evolution: *Ternaricarpites floribundus* from the Middle Albian of Primorye, Russian Far East: 1, flower with a prophyll (P), 2, reproductive shoot, 3, ternate follicles showing adaxial suture, 4, dehiscent follicle with seed impressions (arrows), 5, two fruits of ternate follicles, 6, whole plant drawing from photograph (Fig. 10), 7, pinnatisect *Suifunophyllum* type (Krassilov and Volynets, 2008).

Ternaricarpites from the same locality is a rhizomatous plant producing a solitary pinnatisect basal leaf with open venation (Fig. 19). The flowers are somewhat zygomorphous with 5 sepals. The fruits are ternate many-seeded follicles. Similar foliar and floral features occur in modern *Trollius Delphinium*, *Caltha*, *Aquilegia*, *Kingdonia*, and some other helleborid and isopyrid genera. As in the Isopyroideae, transverse fibres are lacking in the follicles of *Ternericarpites*. Both terminal and axillary position of flowers on a branching axis also find its analogy in the floral organography of Isopyreae (Tucker and Hodges, 2005). Moreover, the monochlamydeous perianth of five unequal tepals, with the larger one in a median abaxial position may result from organogenesis typical of this tribe, with a successive helical initiation of sepals reflected in their

size differences. The adult floral structures of a Cretaceous ranunculid developmentally recapitulated in the modern taxa suggest phylogenetic relationships. Open venation is a rare feature in angiosperms known in *Kingdonia* and *Circaeaster* (Foster, 1961).

Closely similar herbaceous angiosperms with cauline leaves and fruiting heads intact are reported from early angiosperm localities worldwide (although they are not unanimously recognized as ranunculids). Among them, *Leefructus* from the upper Yixian, Liaoning (Sun et al., 2011) is similar to the Albian ranunculids of Kazakhstan and Primorye in the "*Cissites*" type cauline leaf morphology. In the Mediterranean realm, *Sagaria* rom the middle Albian of Italy (Bravi, 2010) is a recognized member of the group.

On the Atlantic coast of North America, the ranunculid *Cissites – Vitiphyllum* group is common among the leaf morphotypes (Hickey and Doyle, 1977). Representation of ranunculids in mesofossil assemblages is seldom recognized (Von Balthazar et al., 2005). However, a possibility of Circaeasteracean affinity is mentioned for *Appomattoxia* (Friis et al., 1995). An apparently ranunculid cone-like receptacle with spirally arranged follicles was repeatedly found with the supposedly chloranthaceous *Anacostia* in the Albian of North America and Portugal (Friis et al., 1997)

In *Araripia* from the Aptian – Albian Crato Formation, Brazil (Mohr and Eklund, 2003), the leaves compared to extant *Sassafras*, Lauraceae are practically indistinguishable from the ternate leaflets of *Achaenocarptes*. The pedicellate ovate bodies interpreted as floral buds betray spiral arrangement of numerous elongate appendages with a prominent apical beak, more likely representing fruit heads of small follicles or achenes.

The supposedly chloranthoid angiosperm from Koonwarra, Australia, is similar to *Caspiocarpus* form the middle Albian of Kazakhstan in both leaf and inflorescence morphology (Taylor and Hickey, 1990).

The Cenomanian representatives of the group spread far beyond the ancestral ranges penetrating the temperate realms. Among them, *Callicrypta* from the Lower Cenomanian of Siberia is an actinomorphic flower less than 2 mm wide, functionally pistillate, although found with sticking pollen grains probably produced by a staminode (Krassilov and Golovneva, 2003) The perianth is 3-seriate of a relatively massive calyx and a corolla of dimorphous inner and outer petals (Fig. 20). The gynoecium is apocarpous of small ascidiform carpels. Our analysis points to the Menispermaceae and Arborellaceae as possible extant affinities, at the same time revealing a significant similarity between the two. Occupying a basal position in the molecular phylogeny, *Amborella*, traditionally assigned to the Monimiaceae, is now placed in the vicinity of Nymphaeaceae

(Mathews & Donoghue 1999; Endress, 2001) at the expense of neglected ranunculid similarities. *Freyantha* from the stratigraphically equivalent horizon in West Siberia (Krassilov and Golovneva, 2001) is a racemose staminate inflorescence, terminal on the axis with minute prophylls. The flowers consist of fasciculate stamens subtended by calyptrate bracts. Features shared with Menispermaceae and Sargenthodoxaceae make *Callicrypta* and *Freyantha* assignable to ranunculid plexus, but they are morphologically advanced far beyond the Albian level and no longer an ecologically dominant group.
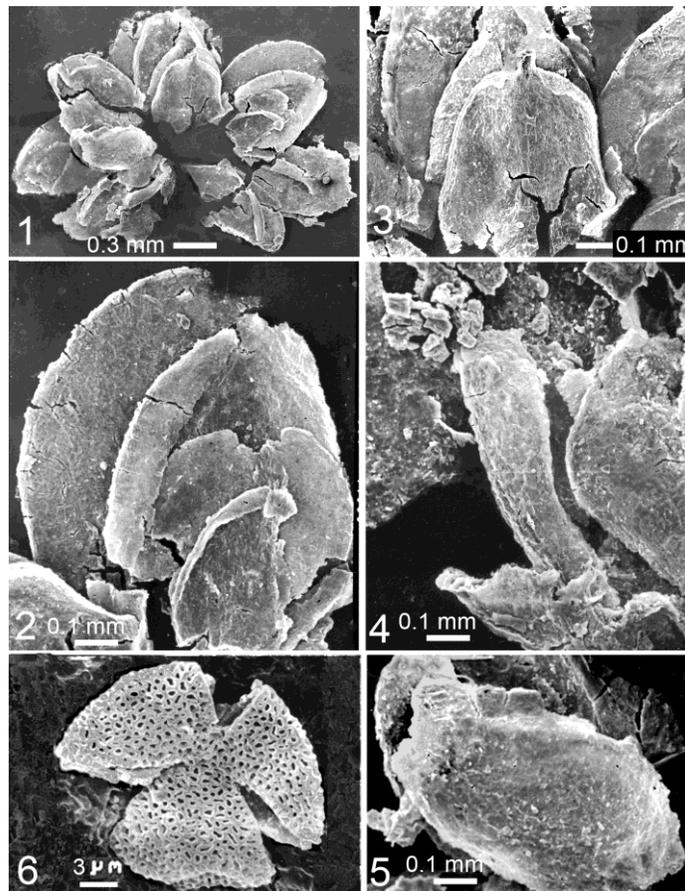

Figure 20. Ranunculid stage of early angiosperm evolution*: Callicrypta chlamydea* from the Cenomanian of Vilyuy Basin, East Siberia: 1, pistillate flower with calyx, biseriate corolla, and apocarpous gynoecium, 2, radial sequence of sepal, outer petal, inner petal, and carpel, 3,

carpel with a short style, abaxial aspect; 4, staminode (?) clasped at base by an inner petal; 5, carpel, lateral view, style missing, 6, pollen grain.

Joint occurrences of *Caspiocarpus* and *Hyrcantha*, as well as *Achaenocarpite*s and *Ternaricarpites* is evidence of ranunculid communities in which the initial diversification of the group took place. On taphonomic evidence, these plants grew on ash falls as a pioneer rhizomatous fern – angiosperm community. Their Albian occurrences are confined to the tropical/subtropical zone of the most advanced proangiosperm communities here considered to be the cradle angiosperm communities.

In their growth habits, the Early Cretaceous ranunculids are similar to the preceding and coeval anthognetids of the Aptian – Albian proangiosperm communities (above). Certain reproductive features, such as an extended apical growth producing elongate receptacles can be inherited from anthognetid ancestors. The *Cissites – Vitiphyllum* leaf morphotype might have appeared in early ranunculids by cladodic transformation of proangiosperm foliage (whereas the phyllodic tendency gave rise to parallelodromous monocot leaves). A differentiation of monospermous and polyspermous ranunculid stalks is evident at the Albian level already as are the features linking the ranunculids to the later appearing cercidiphyllids, platanoids and trochodendrocarpoids.

Cercidiphyllids

Cercidiphyllum, a relict genus of archaic angiosperms, grouped with Trochodendrales or Saxifragales or assigned to an isolated monotypic order Cercidiphyllales (Takhtajan, 2008) is similar to modern and fossil ranunculids in the dimorphic leaf morphology with conspicuous stipules, extended apical growth of floral receptacle responsible for its inflorescence characters, triporate pollen grains, "peltate" carpel development with a tubular fertile zone, and follicular fruits (Krassilov, 2010). Peculiar for the genus are the embedded renovation buds, sympodial branching, calyptrate cataphylls enclosing the floral parts before anthesis, and precocious fertility of ovules that are morphologically primordial at anthesis (Fig. 5).

Unlike in the other gymnospermous and angiospermous trees with dimorphic long and short shoots, in *Cercidiphyllum* reproductive structures are naturally converted into leafy shoots, while the short-shoot leaves (floral prophylls) foliate most of the branching system. This means that vegetative body of this plant is partly or mostly produced in the reproductive line of a neotenic ancestral form of vegetative parts much reduced relative to reproductive sphere. The Albian

Ternaricarpites, a tiny herbaceous plant with a solitary basal leaf, sympodial branching of fertile axes, and relatively large both terminal and axillary produced flowers is just such form (Krassilov and Volynets, 2008; Krassilov, 2010).
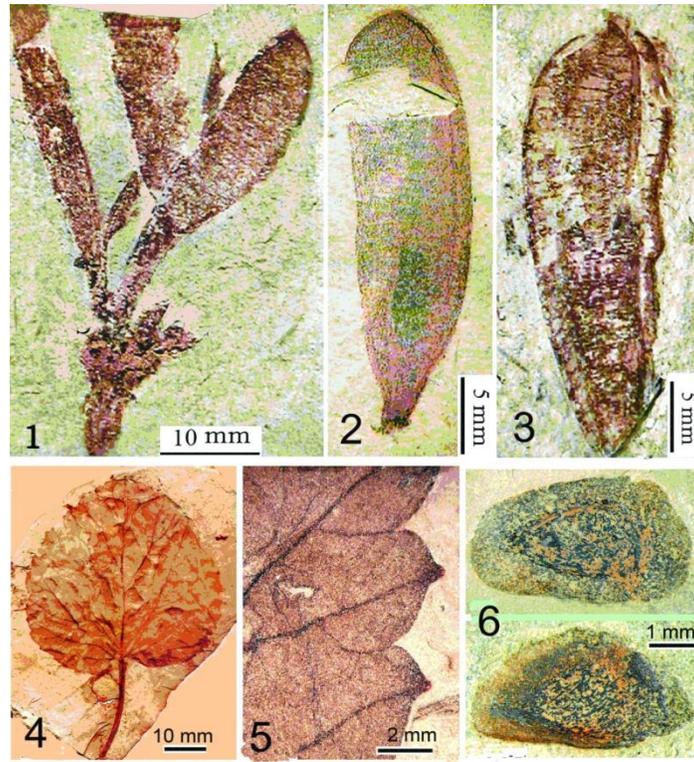

Figure 21. Cercidiphyllid angiosperms from the Turonian of Gerofit, South Israel: 1, pistillate flower of four carpels with subtending bracts, 2, 3, follicles, 4, leaf, 5, marginal glands, 6, seeds (Krassilov et al., 2005).

A recently found cercidiphyll from the mid-Turonian of Gerofit, southern Israel (Fig. 21) attests to a great antiquity of the group ranking among the first arboreal derivatives of the ranunculid stalk rising to dominance in the mid-Cretaceous broadleaved forests. The fossil leaves show prominent marginal glands as their most constant distinguishing character, whereas in the modern species glands excessively develop in juvenile leaves, decreasing with maturity. Moreover, the occasionally preserved juvenile leaves of the fossil form are strikingly similar to adult leaves of extant *Cercidiphyllum* in their palmato-pinnate venation with a strongly developed basal pair, as well as in the irregular serrate

and sometimes doubly serrate marginal prominences, thus giving evidence of recapitulation, or persistence of an adult ancestral feature as a juvenile feature in descendent forms. The seeds are essentially like in *Cercidiphyllum*, but with orbicular wing and a relatively stronger developed micropylar lobe (that in modern species is overgrown by chalazal lobe) and the straight course of vascular bundle occasionally observed as an anomalous paedomorphic feature in extant *Cercidiphyllum japonicum*.

The post-Cretaceous history of the lineage is an example of evolutionary conservatism, with a few innovations, such as long stigmas, abaxial dehiscence, and papery free-flowing seeds being related to anemophily and anemochory, the effectiveness of which might have increased with plant size. However, the pistillate floral structures were fixed at the pre-flower stage of incomplete elimination of sterile appendages from the fertile zone and a flexible balance of floral and foliar meristem production, enabling interconversions of fertile and sterile structures.

Platanoids

In the Late Albian and through the Late Cretaceous, angiosperms with platanoid leaf morphology are recognized all over the temperate northern realm as subdominants of coniferous forests or local dominants of riparian vegetation preserved as leaf mats in the fluvial deposits. They were less conspicuous in the Mediterranean realm, subordinate to cercidiphyllids in the Turonian Gerofit assemblage. For a long time erroneously attributed to the extant genus *Platanus,* the plants with platanoid leaves are presently re-assigned to a number of morphological genera, indicating a considerable diversity of the group the larger part of which was lost through the end-Cretaceous and Paleogene extinctions.

The platanoid leaves are an inflated version of the ternate foliage typical of the early and modern ranunculids, sometimes retaining a trifoliate morphotype (Kvaček et al., 2001). The constant presence of stipules and the occasional compound leaves among the Cretaceous platanoidss are additional evidence in favor of such relationships. Small heads of platanoid aspect occur in *Achaenocarpites* and are attributed by association to *Sapindopsis* (Crane et al., 1993), a possible link between platanoids and the early ranunculoid stalk. The stomatal structures of *Sapindopsis* are of an unspecialized anomocytic types as in the ranunculids rather than *Platanus* (Krassilov and Bacchia 2000; Carpenter et al., 2005).

Platanus and *Cercidiphyllum* share such developmental features as renovation buds embedded in the leaf petioles, sheathing leaf stipules and calyptrate

cataphylls of floral axis. Intrafloral foliar appendages occasionally occur in extinct platanoids and in modern cercidiphyllids. These are here considered as sister groups rooted in the mid-Cretaceous ranuncolid assemblage and, at a deeper level, in the proangiosperm grade with anthostrobili of bristled achenoid cupules (*Baisia*).

While the strobilar features in pistillate flowers of ranunculids and cercidiphyllids are related to an excessive apical growth of their receptacles, in the platanoids, the carpels are basally sunken in the radially expanded receptacles, a feature shared with *Nelumbo* and fossil nelumbonoids, the aquatic – semiaquatic rhizomatic forms apparently retaining the ancestral rhizomatic habit with a sympodial arrangement of foliage leaves, prophylls and ochreic stipules (Esau and Kosakai, 1975). Appearing in the Middle Albian, the nelumbonoids are here considered as a branch of the initial radiation at the ranunculid level of morphological evolution.

Trochodendrocarpoids

Dominant in the middle – high latitude fossil plant assemblages of eastern Asia and western North America in the Late Cretaceous and over the Cretaceous – Paleocene transition were the deciduous broadleaved plants with dimorphic leafy shoots bearing reniform to elliptic leaves commonly, assigned to *Trochodendroides*, but also to other morphological and natural genera (Krassilov, 1976). The leaf shapes, leaf margin morphology and venation patterns are highly polymorphic, while the species level classification can be based on variation ranges rather than typology.

The associated reproductive structures might have been more instructive if having been less problematically interpreted. The commonly found infructescences are the racemes or panicles of partly paired follicular fruits described as *Nyssidium, Trochodendrocarpus* or *Joffrea* (Fig. 22). Such a configuration is totally unlike in *Cercidiphyllum,* the reproductive short shoots of which produce a sympodially branched floral axis and a solitary prophyll (functioning as a foliage leaf later in development), with the growing point enclosed in a pit at the base of petiole. The trochodendroid seeds have a one sided rather than orbicular wing lacking a pin-shaped vascular loop characteristic of *Cercidiphyllum*. Moreover, the recently found Turonian and Coniacian inflorescences (Krassilov et al., 2005) are much more *Cercidiphyllum*-like than the geologically younger *Trochodendrocarpus – Joffrea* group. The associated leaves are readily recognizable by prominent marginal glands recapitulated in

juvenile leaves of extant *Cercidiphyllum*, but lacking or inconspicuous in *Trochodendroides*.
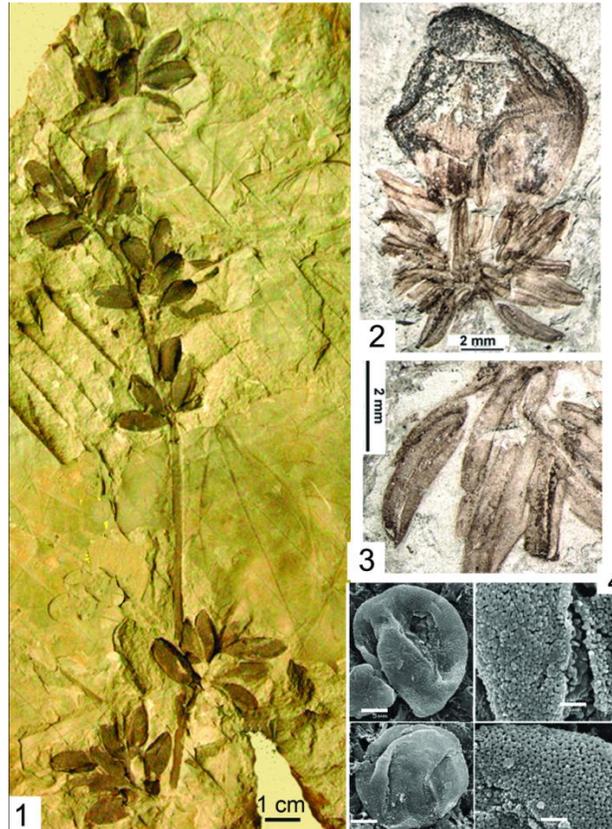

Figure 22. Trochodendrocarpoids from the Late Cretaceous – Paleocene of the Amur Basin, Russian Far East: 1, *Trocohdendrocarpus arctica*, paniculate infructescence, 2, 3, Alasia, staminate flower and anthers enlarged, 4*, in situ* pollen grains and their surface sculpture, scale bars 1 and 5 μm. (Krasislov, 1976; Golovneva, 2006; Krassilov and Kodrul, 2008).

The staminate organs *Alasia* (Golovneva, 2006) are inflorescences of helically arranged bracts subtending flowers of numerous stamens, whereas in *Cercidiphyllum* staminate flowers develop opposite a solitary prophyll and are subtended by a lateral pair (or sometimes also a median pair) of small bracts. In *Alasia*, the stamens at anthesis have short filaments (long filaments in *Cercidiphyllum*). The massive anthers were dorsifixed (basifixed in

Cercidiphyllum), introrse (latrorse in *Cercidiphyllum*), and lacking a prominently protruding connective. The pollen grains were tricolpate with long colpi (Krassilov and Kodrul, 2008), whereas in *Cercidiphyllum* the apertural type, although sometimes described as tricolpate with short colpi, is actually triporate (Krassilov, 2010).

Both foliar and floral features of trochodendrocarpoids find their analogues in the Ranunculaceae suggesting derivation from early ranunculids, but as a separate line of their phylogenetic radiation.

Myrtoids

After the apparently cosmopolitan incipient stages, geographic differentiation of Cretaceous angiosperms has become for the first time evident in the Turonian, when the temporally dominant angiosperm groups have been split into the Laurasian and Gondwanan stalks. The Turonian plant assemblage of Gerofit, southern Negev, contains floral structures not known from the Late Cretaceous of Laurasian realm, although probably related to some geologically younger fossils from northern continents (Berry, 1913, 1934; Friis et al., 1992; Takahashi et al., 1999). Five types of hypanthial flowers are recognized (Krassilov, 2004), all with a fully inferior ovary and with the floral tube exserted well above it. The bracteoles are variously developed, occasionally forming a bipartite cup (*Shelemonasca*). The upper cupuliform hypanthium is persistent in fruit. The sepals are connate with short free lobes or reduced to bristles, whereas the corolla is relatively massive, with the petals interlocked in bud, their marginal hairs interlacing. The petals are relatively thick, valvate (*Desertiflosca*) or slender and deciduous (*Shelomonasca*) or the corolla is lacking (*Zeevlewya*). The stamens, when present, are well, but unequally exserted. In *Minevronia,* the flowers of the same basic type are clustered in capitate inflorescences, dichasial and bracteate in bud. The dispersed fruits (*Seraphocarpus*) are ribbed with narrow wings and a crown of hypanthial appendages. It was possible to trace development from flowers to fruits with persistent floral parts and occasionally further to seedlings (Fig. 23). The associated leaves are compound, of pedate architecture, with dichopodial basal segments and with narrow elliptical to elongate entire or serrate leaflets (Krassilov et al., 2005).

The closest affinities of these floral structures are with the myrtalean families Combretaceae and Rhizophoraceae (in the modern morphological systems, the latter is separated in a monotypic order Rhizophorales placed next to the Myrtales: Cronquist, 1981). Not only the general morphology of epigynous flowers, but also such structural details as the bipartite bracteolate cup, unequally developed

hypanthial lobes and interlocked petals find their equivalents in the extant combretaceous or rhizophoraceous genera. However, the Cretaceous floral structures combine characters of various myrtalean families perhaps not yet recognizable at the Turonian level of morphological evolution.
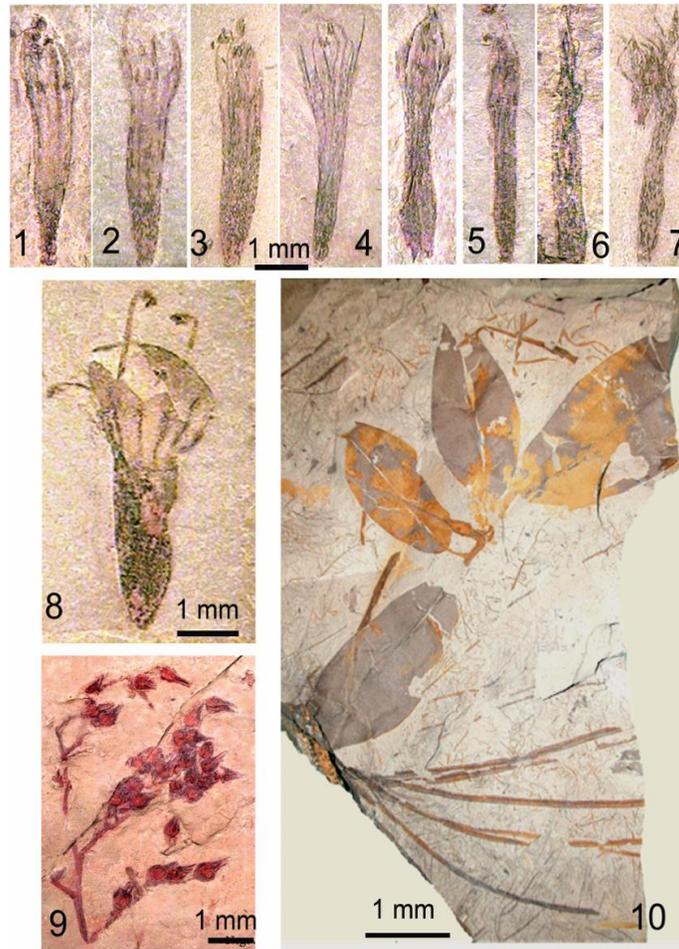
Figure 23. Myricoids from the Turonian of Gerofit, South Israel: *Zeevlewya gracilis*, a developmental series of floral buds (2, 3), hypanthial flowers with exserted stamens (4 – 6), fruit (6), and cryptoviviparous seedling (7); 8, *Desertiflosca perfecta*, flower with connate sepals, inflate petals and variously exserted stamens; 9, Negevirea paniculata, infructescence; 10, associated roots and leaf (Krassilov et al., 2005).

Although fully deserving generic status upon the classification criteria applied to the extant myrtoids (Briggs and Johnson, 1979), the Turonian floral morphotypes of the group are basically similar as variations of the same theme, suggesting a recent diversification, supposedly related to incipient development of angiosperm mangrove communities.

Such features as synflorescence of capitate heads and tetramerous flowers are shared with the Cretaceous platanoids. Remarkably, the endocingulate pollen grains, characteristic of the Rhizophoraceae, first appeared in some platanoids (Krassilov and Shilin, 1995; Krassilov, 1997.

Conclusion

What does it mean being an angiosperm must be clarified prior to the quest of initial angiosperm. The characters supposed to be typical of the group result from neotenic transformation and associated heterochronies responsible for the scapose or scantily foliated herbaceous habit, cladodic leaves, whorled floral parts, elimination of foliar appendages from fertile whorls that make flowers, underdevelopment of ovules at anthesis that requires extraovular pollen germination for which carpels with stigmas are developed, and the ensuing reduction of female gametophyte. In angiosperms these processes are parallel to, but further advanced than in the diverse angiospermoid (proangiospermous) gymnosperms forming their cradle communities.

Taking into account the ubiquity of parallel developments and convergence of morphological structures, an occasional appearance of a morphotype that can be recognized as angiosperm is not a miracle. Yet the evolutionary meaningful appearance of angiosperms implies their further persistence over times and geography in the context of plant community evolution. The rather popular idea of angiosperms entering the Mesozoic plant communities after a long period of clandestine evolution leaving no traces in the fossil record takes angiosperms out of evolutionary context. This is how abominable mysteries are created.

Angiospermoid plants first appeared in the Aptian gnetophyte dominated plant assemblages as rare aberrant morphotypes of the pre-existing proangiosperm variation. The diversity of the group steadily increased through the succession of the Albian – early Cenomanian "mixed" assemblages. At this stage, the numerical angiosperm representation was strikingly different in the fluvial and marshland facies. As in the Middle Albian of Makhtesh Qatan, northern Negev, the angiosperms are scanty in the marshland runoff conferring an archaic pre-Albian aspect on the lacustrine shale assemblages. Fully angiospermous floras first

appeared in the mid-Turonian, with angiosperms forming new types of wetlands (the incipient mangroves of Gerofit, South Israel) and the broadleaved dryland forests. This was the end of early angiosperm evolution. New types of floral structures witness a burst of morphological innovation that accompanied these ecological developments.

Our regional data provide a spectacular example of ecogenesis and morphogenesis going hand by hand. Angiosperms have appeared with advent of new plant communities with restructuring of Mesozoic vegetation associated with continental rifting, basaltic magmatism and rapid sea-level fluctuations. The prevailing adaptive strategy in thus appearing plant communities is accelerate development and precocious reproduction. Two climatic/florogenetic mid-Cretaceous cycles are recognized, with xeric phases in the Aptian and Cenomanian alternating with humid phases in the mid-Albian and mid-Turonian. Through these cycles, angiosperms increased in numerical representation, diversity and disparity rising from a subordinate to dominant status in both wetland and dryland communities. Significant for early angiosperm evolution were plant – arthropod interactions. A correlation is found between abundance and diversity of arthropod damages and composition of angiosperm communities, involving the on-leaf associations, severe/benign plant morphological effects, and host specificity of parasitic arthropods. A directional change in one or more such variables affected the whole interaction system.

Neotenic features in archaic extant angiosperms such as *Cercidiphyllum* with floral prophylls functioning as foliage leaves, ectopic foliation of floral receptacles, and precocious fertility of ovules still primordial at anthesis, suggest an ancestral form, in which a drastic reduction of vegetative growth took place. Such forms can be found among the Albian ranunculids that are here considered to be a stem group for the cercidiphyllid, platanoid, trochodendrocarpoid and myrtoid lineages forming the bulk of the Late Cretaceous angiosperm floras.

Having a theory of angiosperm origins means that our understanding of the process would no longer depend on occasional finds. If the gnetophytic Baisa-type assemblages actually represent angiosperm cradle communities, then angiosperms scarcely appeared before such communities and the chances of finding authentic angiosperm remains in pre-Cretaceous deposits are near zero. The neotenic transformation part of the theory suggests that at the early stages the evolution rates should have been high enough to produce a saltation effect documented by the fossil record. A clandestine period of million year scale is unlikely, while rapid changes need not be systematically interpreted as representing gaps in the fossil record. At their first appearance, early angiosperms were but slightly different from their contemporaneous anthognetids and the other proangiosperms

advancing to the modern grade through a succession of mid-Cretaceous stages taking about 20 million years. This resolves the Darwinian "abominable mystery".

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