

Diversity of Mesozoic Gnetophytes and the First Angiosperms

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Abstract—A provisional system of gnetophytes is proposed, including recently discovered Mesozoic members. The following principal characters are used, in descending order of significance: strobilar structure of ovulate organs (eugnetophytes) as opposed to flowerlike cupules and their aggregates (anthognetophytes), radial vs. bilateral symmetry of seed cupules, and morphological distinctions in the pollen organs, pollen micromorphology and exine ultrastructure. The fossil members show mosaic associations of morphological traits, which attests to different evolution rates of their ovulate and pollinate structures. The system includes two superorders and eight orders, several of which are new. A dichotomous key is provided to differentiate between genera of fossil gnetophytes based on ovulate structures. Two stages in evolution of gnetophyte morphological diversity are recognized: first in the Triassic and then in the Early Cretaceous, the latter was associated with the origin of new type herbaceous wetland communities. Angiosperms or some of them might have originated as elements of gnetophyte diversity in such communities.

Key words: gnetophytes, Mesozoic plants, plant morphology and taxonomy, origin of angiosperms.

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INTRODUCTION

Although only three far diverged genera of Gnetopsida, *Gnetum*, *Ephedra*, and *Welwitschia*, persist in the modern flora, this group is charismatic owing to its transitional character states between gymnosperms and angiosperms. By the end of 19th–beginning of 20th century, most botanists supported the phylogenetic theory of Wettstein (1907), who used modern *Ephedra* as a model for angiosperm ancestor implying a basal position of extant angiosperms with small inconspicuous flowers. Later, the so-called ranalean theory of angiosperm origins came over asserting the opposite polarity of floral characters. In the second half of the 20th century, the *Ephedra* theory was nearly abandoned.

In the last few decades, the situation has dramatically changed due to (1) rapid accumulation of data on floral morphology of Cretaceous angiosperms, among which forms with small flowers arranged in many-flow-

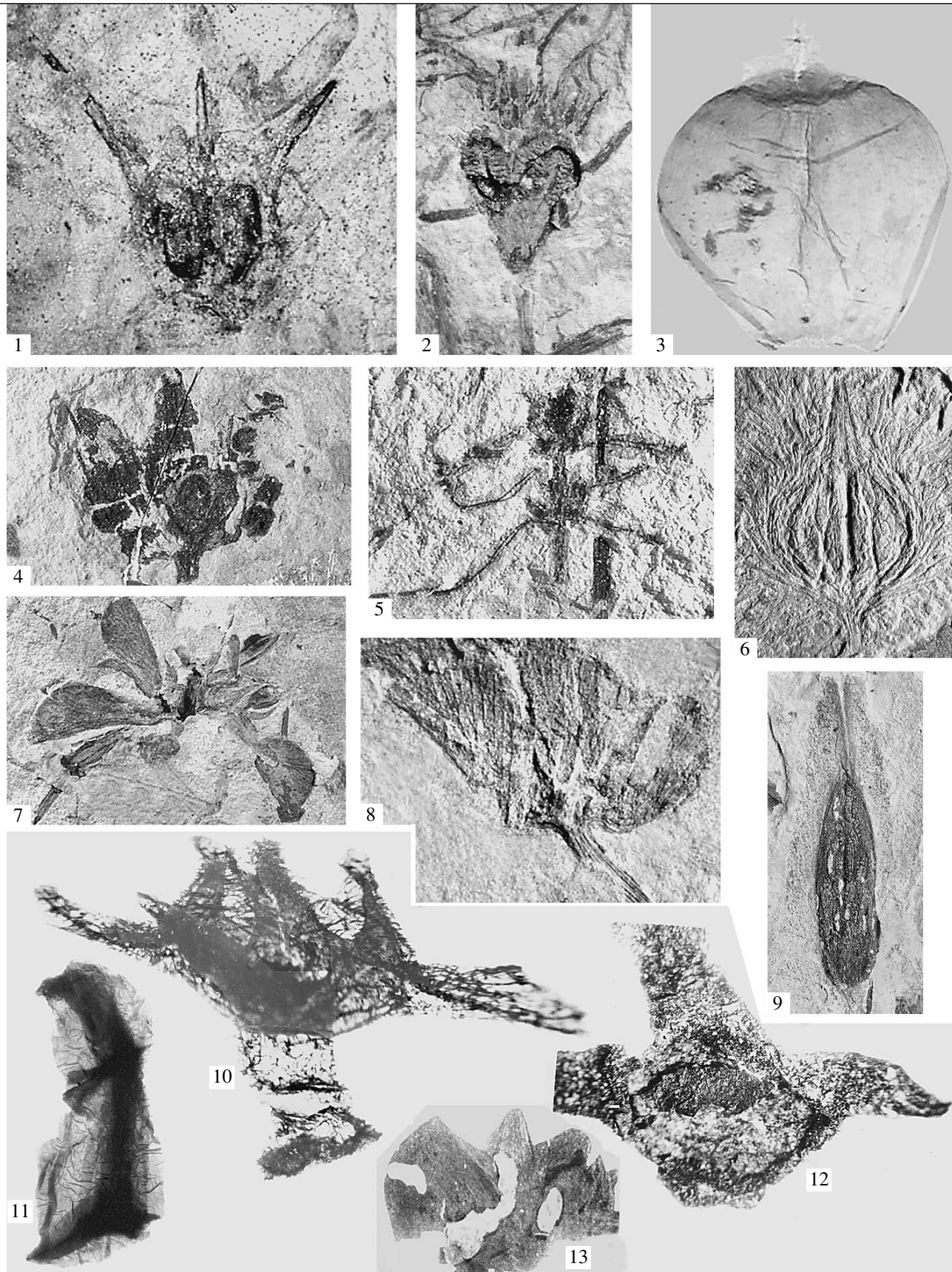
ered inflorescences had prevailed (Krassilov, 1987); and (2) the discovery of Mesozoic gnetophytes, the first macrofossil records of which were found slightly more than 20 years ago, but significantly altered our idea of Mesozoic vegetation since (Krassilov, 1982a, 1986, 1987). It was long suspected that the three modern genera are remnants of a once diverse group, but no direct evidence has been until recently available. To date, numerous Mesozoic gnetophytes are known, and the time is ripe to draw some interim conclusions.

The informal name *gnetophytes* is currently applied to fossil forms, which share taxonomically significant characters with living members of the Gnetopsida (Gnetophyta once formally designated the order of gnetalean plants, but is no longer used in this sense). Morphological limits of gnetophytes are difficult to define, if for no other reason than great morphological separation of the three modern genera, the taxonomic status of which is controversial: they are assigned to different

Explanation of Plate 21

Figs. 1–13. Cupules and ovules of Mesozoic gnetophytes: (1) *Eoantha ornata* Krassilov, Baisa locality, Transbaikalia, Lower Cretaceous, $\times 6$ (Krassilov and Bugdaeva, 1999); (2, 3) *E. zherikhinii* Krassilov, the same locality (Krassilov, 1986); (2) cupule, $\times 5$; (3) nucellus, $\times 50$; (4) *Preflosella nathania* Krassilov, the same locality, $\times 4$ (Krassilov and Bugdaeva, 1999); (5) *Prognotella minuta* Krassilov et Bugdaeva, the same locality, $\times 2$ (Krassilov and Bugdaeva, 1999); (6) *Gurvanella dictyoptera* Krassilov, Liaoning, China, $\times 6$ (Akhmetiev and Krassilov, 2002); (7, 8) *Vitimantha crypta* Krassilov et Bugdaeva, Transbaikalia, Lower Cretaceous (Krassilov and Bugdaeva, 2000); (7) $\times 2$; (8) $\times 4$; (9) *Heerala antiqua* (Heer) Krassilov, Ust'-Balei locality, Middle Jurassic, $\times 4$ (Krassilov and Bugdaeva, 1988); (10–12) *Dinophyton spinosum* Ash, Arizona, Upper Triassic (Krassilov and Ash, 1988); (10, 12) cupule, $\times 15$ (19) and 9 (12), (11) nucellus, $\times 30$; (13) *Hirmeriella muensteri* (Schenk) Jung, Odrowąż, Poland, Lower Jurassic, $\times 4$ (Krassilov, 1982a)

Plate 21



families or, occasionally, even to different orders. The most conspicuous differences concern their vegetative sphere. The growth form diversity of modern gnetophytes is very high for a taxon with only few members and includes xeromorphic shrubs and undershrubs, lianas, small trees with thin branching stems, and peculiar non-branching pachycaul forms. The leaf diversity is higher than in any other group of gymnosperms and ranges from petiolate leaves with broad lamina and reticulate venation of several ranks (*Gnetum*) as those typical of dicots, to scaly and nearly completely reduced leaves (*Ephedra*), and to phyllodes of inflated petioles growing with their bases during the entire life of the plant (*Welwitschia*). The conductive tissues consist of tracheids with bordered pits, vessel tracheids, and vessels, one more character shared with angiosperms. The diversity of palynological characters is as high: there are apertural and non-apertural, striate, echinate, and smooth pollen grains. The divergence in embryological traits is greater than in any type of seed plants, angiosperms included. *Ephedra* has distinct archegonia, whereas in *Gnetum* and *Welwitschia* female sex organs are lacking. Repeated fusions of nuclei take place in their multinuclear embryo sacs. *Ephedra* shows double fertilization of a sort, which is analogous or, in my opinion, homologous to that in angiosperms (Krassilov, 1997).

A question arises: what are the distinctive features of Gnetopsida underpinning their coherence as a natural group of seed plants? Primarily, these are the morphological features of seed organs that although morphologically diverse, are reducible to a common prototype of a cupule formed of bracteoles, typically bearing one orthotropic ovule (or, exceptionally, two orthotropic ovules) and supported by bracts, which may participate in dispersal as parts of a compound disseminule, analogous to fruit. The homology of these and angiospermous gynoecial structures is not yet unequivocally established and merits special studies. However, seed organs of Gnetopsida differ from any known in gymnosperms, fossil cupules included. Thus, the cupules of pteridosperms are commonly held to have originated from syntelomic systems or else derived from convolute sterile phyllomes (*Caytonia*). In contrast, the cupules of gnetalean plants are of a synphyllomic origin. Their pollen organs are also peculiar: cupulate and with sporangia fused into synangia, a feature shared with angiosperms and, within gymnosperms, with pteridosperms and bennettites. Though it may seem logical to apply these distinctions as diagnostic of fossil gnetophytes, the latter show even wider range of morphological diversity. Moreover, extinct forms show combinations of modern and supposedly archaic non-gnetophytic characters.

THE STRUCTURE OF DIVERSITY

This paper is the first attempt to reveal structure of higher rank diversity in Mesozoic gnetophytes by taxo-

nomic grouping based on similarities with modern Gnetopsida as well as on general trends in morphological evolution of gymnosperms. The architecture of ovulate structures is used as the main differentiating character (Pl. 21, figs. 1–13). The seed structures can be arranged in strobili, as in modern Gnetopsida, or in apical whorls on reproductive shoots, as in angiosperms. Comparable differences exist between typical gymnosperms, represented nowadays by conifers and cycads on the one hand, and the extinct pteridosperms and bennettites on the other. Such approach has led to clustering the so-called Mesozoic pteridosperms (peltasperms and caytonias) with cycads, that does not contradict their other characters of both reproductive and vegetative spheres (Krassilov, 1997).

As it is often the case in evolutionary systems, no one differentiating character is absolute. In particular, destrobilation of female reproductive system took place in modern *Cycas* and *Ginkgo*. Apparently, similar exceptions occurred in gnetophytes as well. Nonetheless, the separation between strobilar and anthoid genera by their ovulate structures seems fundamental and sufficient for the highest rank groups, which I here designate as eugnetophytes and anthognetophytes. All living gnetophytes belong to the first group. In *Gnetum*, ovulate strobili can be reduced to two nodes, and further reduction of the distal node is conceivable leading to an *Eoantha*-type anthoid structure.

The next iteration relates to composition of disseminules (fruits) that may include bract or bracts persistent on the cupule and serving as wing appendages. The fusion of bracts and seed cupules is associated with the symmetry of ovulate structures, which is radial in some cases and bilateral in the others, providing the next iteration of ordinal rank. Traditionally, the symmetry of ovule is held to be essential in the taxonomy of gymnosperms, among which radiospermic and platyspermic lineages are defined. Characters of pollen organs and pollen grains are given significance at the lower ranks of the gnetophyte macrosystem.

Among recent systems, Cleal (1993) included the order Bennettiales into the class Gnetopsida. Indeed, gnetophytes and bennettites show such a high degree of convergence that their derived forms can be considered as members of the same class. However, typical members of Bennettiales have ovules protected by peltate seed scales without formation of cupules. Anderson et al. (2007) included in the class Gnetopsida the orders Dinophytales Krassilov et Ash and Eoanthales Krassilov, And. et And. (contributed by Krassilov) as well as Bernettiales Konijn.-Citt., Fraxinopsiales And. et And., Dechellyiales Ash, and Nataligmatales And. et And. of a questionable gnetalean affinities. For the Bernettiales, the comparison with the Gnetales is based on the microsporophyll morphology (*Piroconites*) alone, whereas the seed organs are insufficiently studied (Van Konijnenburg-van Cittert, 1992). The Fraxinopsiales and Dechellyiales are closer to conifers by the mor-

phology of seed organs. There are no significant differences between the Nataligmatales and Pentoxylales.

On the other hand, I propose to include into the Gnetopsida the orders Fredlindiales, Cheirolepidiales, and Axelrodiales that are assigned to different classes in Anderson et al. (2007): the Pinopsida (two former orders) and Axelrodiopsida (the last order).

SYSTEMATIC PALEOBOTANY

Class Gnetopsida Thomé, 1898, emend.

As a whole, the Gnetopsida are characterized by:

—decussate or verticillate branch and leaf arrangement;

—association of helical, reticulate and pitted conductive elements;

—cupulate sporangiophores (anthers);

—synangiate sporangia;

—polylicate or echinate, monosulcate, leptomate, or inaperturate pollen grains with granular or granular-columellate infrastructure;

—cupulate ovules formed by decussate bracteoles;

—persistent subtending bract(s) and often winglike in disseminule, and

—orthotropic ovules with a strongly cutinized nucellus and distinct pollen chamber.

Dealing with such a broad range of characters and their mosaic combinations, one can hardly expect the presence of all typical characters in each member of the group. In this case, the Adansonian principles of classification are particularly pertinent, allowing the absence of one or another diagnostic character. Thus, Mesozoic gnetophytes show along the typical of the group also more archaic character states that occur in other gymnosperms as well, such as:

—peltate sporangiophores,

—free sporangia, and

—saccate pollen grains with alveolate infrastructure.

All these are related to male reproductive sphere, the evolution rates of which appear low and irregular at this stage.

The subclass Eugnetidae, subclassis nov. embraces all forms with strobili, including the three modern genera, which are considered here as members of three orders; Gnetales, Ephedrales, and Welwitschiales.

The order Gnetales Luersson, 1879 is characterized by radial cupules, situated in whorls at the thickened nodes of a non-branching fertile shoot and supported by bracts fused in an annular collar. Such morphology is extremely rare in fossil forms. It is approached by the Early Cretaceous genus *Prognotella*, which has free, linear, radiating single-veined bracts (Krassilov and Bugdaeva, 1999).

Verticillate branching strobili with cupulate synangiate microsporophylls were found in the Early Cretaceous *Baisianthus* (Krassilov and Bugdaeva, 2000).

Pollen grains of this genus have little in common with those of *Gnetum*. They are characterized by a nexine separating from the sexine as an inner body. Reticulate leaves of *Gnetum* are virtually indistinguishable from leaves of dicots and can be easily misinterpreted as such in fossil state. This type leaves from the Late Triassic of North America (Cornet, 1993) might have been produced by a gnetalean plant.

The order Ephedrales Dumortier, 1829 is characterized by decussate arrangement of seed cupules and supporting bracts in spikelike strobili. The cupules occasionally contain two ovules, as well as pollen organs. Bilateral symmetry of subterminal cupules originates by means of reduction or fusion of lobes. Fossil forms of this type are commonly assigned to *Ephedra* (Yang et al., 2005; Rydin et al., 2006; Cladera et al., 2007), although some of them probably belong to extinct genera.

In terms of shoot morphology and few known anatomical characters, *Leongathia* from the Lower Cretaceous of Australia is comparable with *Ephedra* (Krassilov et al., 1998). *Drewria potomacensis* Crane et Upchurch has dichasial fertile shoots with cupules supported by pairs of bracts and arranged in spikes (Crane and Upchurch, 1987). Although these organs were described as seed cupules, the occurrence of pollen masses suggests their interpretation as pollen cupules containing sporangiophores. This plant is comparable to *Ephedra*, at the same time being obviously related to a roughly coeval *Welwitschia*-like plant from Brazil (Dilcher et al., 2005).

The order Welwitschiales Skotts. ex Reveal, 1993 is characterized by one-ovulate bilateral cupules of two lateral bracteoles, transformed into wings in disseminule. A wide spatulate bract is attached to the cupule with a slightly encircling base and persists at fruit. *Welwitschia*, with its highly peculiar life form, is so far the only genus in the order.

A welwitschialean affinity of foliar organs with phyllodes and associated microstrobili from the Lower Cretaceous of Brazil, described by Dilcher et al. (2005), could have only be confirmed by a find of their seed organs. Phyllodes occur not only in the Welwitschiales, but also in other groups of gnetophytes. The microsporophylls are not very well preserved. A goniopteroid venation of seedling leaves from the same deposits is characteristic of *Welwitschia* (Rydin et al., 2003), but may also indicate a relation to *Drewria potomacensis* (see above).

The order Fredlindiales Anderson et Anderson, 2003 includes large monoaxial strobili bearing whorls of scaly organs interpreted as gynoeical (Anderson et al., 2003). However, the nature of the scales remains so far enigmatic, their alveolate structure being most probably sclerenchymous. In any case, the supposed reproductive nature of alveoli is improbable in terms of gnetalean morphology. The sequential whorls of scales

apparently correspond to the bract whorls of *Gnetum* and *Eoantha*.

The order Heerales, ordo nov. is characterized by the laterally symmetrically winged one-ovulate cupules (*Heerala*) analogous to those of *Welwitschia* (Krassilov and Bugdaeva, 1988). The bract is relatively narrow, smaller than the cupule, apparently deciduous, with an arcuate abscission scar at base. The pollen organs (*Aegianthus*) are large strobili with peltate scales bearing adaxial clusters of free sporangia. First found in the Jurassic of eastern Siberia (*Aegianthus*) in association with *Heerala*, this type pollen organs have been later described from the Cretaceous of Transbaikalia (*Loricanthus*: Krassilov and Bugdaeva, 1999). Gnetophyte affinities of the Heerales are solely based on the seed organs *Heerala*, whereas the microstrobili and pollen grains are of generalized gymnospermous types. On the other hand, the microstrobili are like those producing *Eucommiidites*-type pollen and assigned to the order Erdtmannithecales (Pedersen et al., 1989; Kvaček and Pacltová, 2001). The order was erected on the basis of pollen organs and dispersed seeds linked by the same type of pollen grains found in situ and in pollen chambers. However, none of these fossils, pollen grains included, exhibits typical gnetophyte morphology. Their gnetopsid affinity can only be supported by their similarity to *Aegianthus*, the pollen organ of the Heerales. *Eucommiidites*, a peculiar trisulcate pollen morphotype (Tekleva et al., 2006), might have occurred in some but not all genera related to the Heerales, the rest producing rather inconspicuous monosulcate pollen grains.

The order Cheirolepidiales Anderson et Anderson, 2007, here emended, includes a widespread Mesozoic family Cheirolepidiaceae traditionally assigned to the Pinopsida (Anderson et al., 2007). The shoots are scale-leaved as in *Ephedra* and some conifers. The pollen strobili bear peltate scales with adaxial sporangial clusters, atypical of gnetophytes, but not unlike those of the Heerales (above). In contrast, the pollen grains of *Classopollis* morphotype are highly peculiar. They belong to an extinct group of rimulate pollen with a circular subequatorial groove, often showing a distinct tetrad scar and a variably developed distal leptoma ("cryptopore"). Pollen grains of this type were found in intestines of fossil insects suggesting entomophilous pollination (Krassilov et al., 1997). The seed organs are one- or two-ovulate samaroid cupules developing in the axils of lobate bracts persistent in fruit. This interpretation is based on my study of a seed organ from the Jurassic of Poland identified as *Hirmerella* sp. (Krassilov, 1982a) and, later, as *Hirmeriella muensteri* (Schenk) Jung (Barbacka et al., 2007). The cupule clearly shows an inner cuticle lining the locule. Traditional assignment of Cheirolepidiaceae to conifers is based on supposed homology of their cone scales with those of the Voltziaceae (Clement-Westerhof and van Konijnenburg-van Cittert, 1991), which, in my opinion, testifies merely to possible phylogenetic relationships

between these morphologically widely divergent groups of gymnosperms.

The subclass Anthognetidae subclassis nov. includes non-strobilate seed-bearing cupules, which are situated solitary or in groups, terminal or subterminal on the fertile axes. The subtending bracts often persist in disseminule (fruit) as wings or pappuses.

The order Dinophytonales Krassilov et Ash is characterized by having spherical petiolate one-ovulate cupules of four decussate bracteoles, which are proximally fused, but distally forming a propeller-like samara (Krassilov and Ash in Anderson et al., 2007). Two pairs of decussate lobate bracts are fused to the base of the cupule and persist in fruit. The pollen organs are cupulate sporangiophores subtended by a whorl of four fused bracts (by this character similar to the seed cupules, but with a much smaller propeller). The pollen grains are bilobed monosaccate with alveolate infrastructure. The only genus *Dinophyton* from the Upper Triassic of North America has heteroblastic shoots with scaly leaves showing such a foliar character as circinate coiling of leafy axes (Ash, 1970; Krassilov and Ash, 1988). The nucellus of ovules is trilobate, which implies a possible relation to trigonocarps.

Preflosella from the Lower Cretaceous of Transbaikalia is here linked to the Dinophytales, although it possibly merits to be separated into a special order. The genus is characterized by a solitary shortly petiolate two-ovulate cupule subtended by the basally adnate bracts. However, *Preflosella* was monoclinal, with synangiate microsporophylls coaxial with the cupule. As in *Dinophyton*, the pollen grains were saccate, with alveolate infrastructure (Krassilov and Bugdaeva, 1999).

The order Axelrodiales Anderson et Anderson, 2007 is characterized by capitate agglomerates of bracteate cupules with adnate winged bracteoles (Cornet, 1986, 1989), a gnetophytic morphology making separation into a distinct class Axelrodiopsida (Anderson et al., 2007) unjustified. At the same time, a similarity of ovulate structures of the Axelrodiales and the Paleozoic Vojnovskyales Neuburg (re-interpreted in Krassilov and Burago, 1981) may indicate phylogenetic relatedness, which is consistent with their leaf morphologies. Interpretation of the Vojnovskyales still remains controversial, but their assignment to cordaites, a group with compound strobili, does not seem the best option, whereas their inclusion in the Gnetopsida awaits a comprehensive discussion, which is beyond the scope of this paper.

The order Eoanthales Krassilov, J. Anderson et H. Anderson is characterized by radially symmetrical petiolate cupules of decussate basally adnate bracteoles (Krassilov in Anderson et al., 2007). The floral axis is apically protruding. The bracts are numerous, linear, distinct, spreading from the base of cupule and in some species also from the apical protrusion. Massive orthotropous ovules develop in the axils of bracteoles.

Pollen grains preserved in the pollen chambers are polylicate. The cupules of *Eoantha* are associated with parallel-veined graminoid leaves of *Praeherba* morphotype (Krassilov and Bugdaeva, 2000). Apart from *Eoantha*, this order apparently includes *Vitimantha*, which differs in having broader petaloid bracts with reticulate venation (Krassilov and Bugdaeva, 2000). Tetrads of polylicate pollen grains were found stuck to the cupules.

A problematic plant *Afrasita* from the Lower Cretaceous of Egypt and Israel has compound cupules of numerous radially arranged segments, fused along their entire length, containing the axillary slightly curved ovules. This structure was interpreted as a variant of the *Eoantha*-type gynoecium (Krassilov et al., 2004).

The bilaterally flattened two-ovulate winged cupule (fruit) of *Gurvanella* from the Lower Cretaceous of Mongolia and Central China is a possible derivative of the radial *Eoantha*-type cupule (Krassilov, 1982b; Akhmetiev and Krassilov, 2002). Yet inclusion of *Gurvanella* in the Eoanthales would violate the logic of the system, which requires separation of radially and bilaterally symmetrical seed organs at the level of orders. On the other hand, separation of *Gurvanella* into a distinct order will be premature.

A peculiar *Gerofitia* group is described from the Upper Cretaceous (Turonian) of the Negev Desert in Israel including fertile shoots with terminal fascicles of one-ovulate cupules subtended by paired bracts (Krassilov et al., 2005). The systematic position of *Gerofitia* and allied genera remains so far unclear. Their gnetophytic affinity is suggested by the macromorphological similarities of their cupulate structures with those of the Eoanthales, but microscopic details are not available. Taking into consideration the relatively young geological age of the *Gerofitia* group and the habitual resemblance to the Podostemales, a fairly isolated order of aquatic angiosperms, one can surmise an extinct angiosperm affinity.

The order Baisiales ordo nov. is characterized by radially symmetrical solitary achene-like cupules situated on a massive receptacle and surrounded by filamentous bracts, which form a pappus in fruit. The pollen grains (preserved in the pollen chambers of several ovules) are asaccate and monosulcate with alveolate infrastructure. The receptacle bears short scaly appendages. This structure is comparable with the bennettitalean flower-like gynoecia and seems derivable from them by reduction of numerous ovules surrounded by few interseminal scales, typical of bennettites, to a solitary terminal ovule. The Jurassic *Problematospermum* and Cretaceous *Typhaera* (Krassilov, 1982b) are potential members of the Baisiales. This is the case when strong convergence between end members of gnetophytic and bennettitalean lineages might have brought them into one and same order of the Anthognetidae. The Baisiales might have included herbaceous wetland

plants, the prolific producers of wind born achene-like fruits as in extant reedmace (Typhaceae).

Courtesy of Barbara Bohr (Museum of Natural History, Berlin) I could examine a vast collection of well-preserved plants from the Crato Formation of Santana, Brazil, which apparently contains diverse gnetophytes, comparable with those described above or representing new orders. Yet in a number of cases, the assignments to gnetophytes or early angiosperms are tentative and a matter of opinion (e.g. Mohr and Friis, 2000).

A similar situation may occur in the other Early Cretaceous gnetophyte localities. At least some plants from the Lower Cretaceous of Mongolia which I once considered to be the most ancient angiosperms must be reinterpreted as gnetophytes (Krassilov, 1982b). Reproductive structures described from the Lower Cretaceous of China as angiosperm fruits *Beipiaoa spinosa* Dilcher, Sun et Zheng (Sun et al., 2001) are cupules of *Eoantha ornata* Krassilov (Krassilov and Bugdaeva, 1999). The angiospermous affinity is questionable of some other plants from this important locality of Early Cretaceous gnetophytes. By what is now known, the samaras of *Erenia* from the Lower Cretaceous of Mongolia (Krassilov, 1982b) and China are angiospermous, showing two persistent stylodes. However, the plant is insufficiently studied, and its transitional position between anthognetophytes and true anthophytes cannot be excluded. The fruit-like structures with spiny appendages from the Lower Cretaceous of Australia were compared with *Trapa* (Douglas, 1969) and *Ceratophyllum* (Dilcher et al., 1996). However, by having massive nucelli in shed achenes, they are similar to the *Baisia* type aquatic gnetophytes.

A system of gnetophyte morphotaxa is presented as a dichotomous key in Table 1.

Assemblages of Gnetophytes and Early Angiosperms

The oldest gnetophytes are reported from the Permian, represented so far by solitary finds (Wang, 2004). Their Mesozoic history reveals two bursts of taxonomic diversity. The first took place in the Middle–Late Triassic and is best represented in the Molteno Formation of South Africa and the Chinle Formation of North America. Apparently, the basic diversification of gnetophytes was accomplished at this stage (Krassilov and Ash, 1988; Cornet, 1996; Anderson and Anderson, 2003).

Apart from the Cheirolepidiales, gnetophytes are inconspicuous through the Jurassic. However, they are not uncommon in the mid-Jurassic Ust'-Balei locality of East Siberia, from where they have been first described by Heer (1876) and revised by Krassilov and Bugdaeva (1988). At about the same time, angiosperm characters appeared in other groups of gymnosperms, such as the Caytoniales, Czekanowskiales, and Bennettitales (Krassilov, 1997). This period of cryptic evolution was marked by the appearance of only one gnetophytic order, the Heerales.

Table 1.

1	Seed cupules decussate or verticillate in spicate or catkin-like strobili	2
–	Seed cupules solitary or clustered, terminal or subterminal on fertile axes	11
2	Cupules radiospermic	3
–	Cupules platyspermic	7
3	Cupules in many-membered whorls, subtended by a collar of fused bracts	<i>Gnetum</i>
–	Bracts free or only slightly fused	4
4	Consecutive whorls widely spaced, bracts linear, 1-nerved, radially spreading	<i>Prognatella</i>
	Bracts massive adaxially concave	<i>Fredlindia</i>
–	Cupules in axils of decussate bracts, arranged in spicate strobili	5
5	Cupules 2 or 3 per node, radiospermic, subterminal ones solitary platyspermic. Bracts scaly	<i>Ephedra</i>
–	Spikes in dichasial clusters. Subtending bracts paired	6
6	Bracts foliose	<i>Drewria</i>
7	Cupules with lateral wing-like bracteoles	8
8	Bracts persistent in fruit	<i>Welwitschia</i>
–	Cupules samaroid	9
9	Cupules 1-ovulate with symmetrical lateral wings	<i>Heerala</i>
–	Bracts persistent on floral axis	10
10	Cupules 1-2-ovulate, wing orbicular of numerous lobes	<i>Hirmeriella</i>
11	Cupules radiospermic of two or more pairs of decussate bracteoles	12
–	Cupules platyspermic, of paired bracteoles	18
12	Cupules 1-2-ovulate	13
–	Cupules containing four or more ovules axillar to bracteoles	15
13	Cupules lobate, 1-ovulate, fused to a propeller-like whorl of four bracteoles	<i>Dinophyton</i>
–	Cupules entire, 2-ovulate	14
14	Bracts petaloid, radially spreading	<i>Preflosella</i>
15	Cupules of numerous fused lobes with axillary seeds	<i>Afrasita</i>
–	Cupules 4-lobed dehiscent	16
16	Bracts free, linear, spreading. Cupules 4-lobed, dehiscent. Seeds shed from open cupules	<i>Eoantha</i>
–	Bracts petaloid	17
17	Cupules in distal fascicles. Bracts free, verticillate, foliose	<i>Vitimantha</i>
	Cupules in capitata gatherings. Bracts linear	<i>Axelrodia</i>
18	Cupules indehiscent, flattened. Fruit samaroid with two seeds	<i>Gurvanella</i>

At the beginning of the Early Cretaceous, a new burst of diversification gave gnetophytes the status of a regionally dominant group. A rich gnetophytic assemblage has been first described from the Lower Cretaceous of Transbaikalia (Krassilov, 1986; Krassilov and Bugdaeva, 1982, 1999, 2000). Recent discoveries have shown that such assemblages were widespread at about the same stratigraphic level in Mongolia and central China. They are also known from Brazil (Santana) and southern Australia (Koonwarra).

These finds reveal certain regularities in distribution of gnetophyte assemblages. Geologically, most of them are confined to extensive rift zones and, in terms of paleogeography, to fossil rift valleys filled with lacustrine deposits. The association with lacustrine black

shales is particularly evident in Transbaikalia. The Chinese and Mongolian localities mark continuation of the same structural zone, which belongs in the Mongolo-Okhotsk rift system. The gnetophyte-containing deposits of central Negev, Iberia, northern Brazil, and Victoria also represent the facial type of rift bound meromictic lakes.

The advent of gnetophyte assemblages is correlated with a decline of fern assemblages, a dominant type of Jurassic peat-forming wetlands. The Mesozoic sequences of central Mongolia show a narrow transition from the immense diversity of fern remains through the Jurassic to their near absence in the Early Cretaceous. A similar transition might have occurred in central-eastern China and other regions affected by

voluminous basaltic volcanism near the Jurassic/Cretaceous boundary. The volcanic impact and associated climate change could have led to degradation of fern communities, their vacated niches being then occupied by a new type of wetland communities with herbaceous gnetophytic plants, the diversity of their life forms being enhanced by colonization of new habitats. On the other hand, gnetophyte communities are underrepresented in the areas where fern communities persisted during the Early Cretaceous, such as on the Pacific coast (Krassilov, 1967). Angiosperms first appeared there about one geological stage later than in the inland rift valleys.

Hughes and McDougall (1987) noted that through the Early Cretaceous the ratio of *Ephedripites* and *Eucommiidites* pollen morphotypes tends to increase simultaneously with the first appearance of angiosperm pollen. Similar correlation between gnetophytes and angiosperms was detected in the fossil plant localities of Central Asia and other regions.

As noted above, it is not always possible to differentiate between anthognetophytes and anthophytes in the Early Cretaceous herbaceous wetland assemblages. Taxonomic affinities of several forms remain uncertain, waiting for further studies. Yet ambiguous forms as such testify to short morphological distance between angiosperms and gnetophytes growing side by side on the shores of taphrogenic lakes. It will be premature and probably incorrect to assign all early angiosperms to this type communities. However, it seems reasonable to suggest that a considerable diversity of initial angiosperms appeared as a component of a morphologically continuous eognetophyte – anthognetophyte – anthophyte diversity in the new type plant communities formed under conditions of a major ecosystem crisis at the beginning of the Cretaceous.

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