

PALAEOBOTANY OF THE MESOPHYTICUM: STATE OF THE ART

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Abstract

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Only a small number of the Mesozoic floras of the world have received full-fledged up-to-date treatment. No wonder that a lot of problems remain unsolved while the existing solutions are no more than tentative. The image of the Mesophyticum has changed gradually from "the era of cycads" to the "era of bennettites, czekanowskialeans and gnetophytes". Major evolutionary changes have taken place in the bryophytes, conifers and earliest angiosperms. On a phytosociological level, the Mesozoic vegetation was amazingly conservative but changed rapidly toward the end of the era, causing extinctions at the higher trophic levels, notably of the dinosaurs. The palaeogeographical significance of Mesozoic plants is still not fully appreciated and the importance of their records is often obscured by current tectonic dogma.

Introduction

In this review I have tried to focus in on problems which seemed most important to me though another reviewer might have selected differently. An introductory problem is the definition of the Mesophyticum. Popularly seen, it is an era when conifers, cycadophytes and ginkgophytes were the dominant plants. Though the term Mesozoic, "middle life", was originally meant to encompass both plants and animals, the latter were too plainly privileged and thus the Mesozoic period may or may not coincide with the Mesophyticum. In the opinion of many authors, the Permian *Callipteris-Walchia* and *Pseudovoltzia-Ulmannia* assemblages belong in the Mesophyticum rather than in the Palaeophyticum, while the Late Cretaceous floras with abundant angiosperms are Cenophytic. However, both callipterids and walchians had appeared before the Permian and neither of them seem closely related

to the dominant Mesozoic plants (the relationships of the walchians and pseudo-voltzians to the modern conifers is outlined below). Thus it seems more logical to draw the lower limit of the Mesophyticum at extinction rather than at the appearance of these archaic pteridosperms and conifers.

In northern Asia, the Palaeophyticum ends and the Mesophyticum begins with the extinction of the cordaitalean and voynovskyaean gymnosperms which dominated through the late Palaeozoic. As to when this happened, in terms of the age/stage scale, opinions vary (see Dobruskina, 1982). In any event, the extinction was abrupt and coincided either with the conventional Permian/Triassic boundary or with a somewhat earlier event, possibly as early as the lower limit of the Tatarian stage — palynologists could hopefully say which. Because correlation of the Tatarian with the more normal marine record remains uncertain, it would be premature to speak of any large

discrepancies between the floristic and faunistic era-making events.

On the southern continents, some elements of the *Glossopteris* flora, including *Glossopteris* itself, cross the Permian/Triassic boundary but lose dominance.

As to the upper limit, angiosperms became taxonomically more diverse than gymnosperms from the Turonian onward. However, conifer forests still covered most of the land up to the end of the Cretaceous while the precursors of broad-leaved deciduous forests, tropical rain forests and grasslands (major angiosperm-dominated plant formations) appeared not earlier than the Palaeocene. Such characteristic Mesophyticum plants as bennettites, caytoniales and nilssoniales made their last appearances in the Senonian, close to the Cretaceous/Tertiary boundary. Taking a holistic view of the biota, Mesophyticum can be seen as an integral constituent of the Mesozoic.

Another and more practical problem is just how much we know of the Mesophyticum. Disregarding small, scattered localities, we have about a dozen fairly rich fossil floras per continent, each comprising several to a few dozen localities within a sedimentary basin. Most of these floras had already been discovered in the nineteenth century and were studied by at least three generations of palaeobotanists. Oswald Heer, as a leading figure, was trained on extant flora, still had not quite digested the idea of extinct plants, assembled various fossil organs freely and often chimerically, made ingenious but seldom sound taxonomic decisions and used artistic drawings for illustrations. The next generation, headed by A.C. Seward, attempted to order nomenclature using organ-genera, practised rational if somewhat shallow taxonomy and began to use photographic documentation. Such men as T.G. Halle, E.W. Berry, A.N. Kryshchov, H.C. Sze, and Seward himself laid down the foundations of modern paleofloristics and provided a necessary substrate for the deeper morphologic work of A.G. Nathorst, G.R. Wieland, B. Sahni and H.H. Thomas.

T.M. Harris brought to palaeofloristics a new style which combined the comprehensiveness of Seward with the thoroughness of Thomas. No fossil was neglected and each received a fair treatment. It took a lifetime to describe the large fossil floras of East Greenland and Yorkshire in this way. At present, only these two floras are studied completely to his standards. The rest are mostly at the Seward stage; a few selected groups incorporate studies by modern methods. Many floras, especially in the U.S.S.R., China and Canada are wholly Sewardian and a few, strangely enough the older Mesozoic flora of Virginia among them, remain at the Heer stage.

At present, the discoveries of new fossil floras are rare, but those of Mongolia (Krassilov, 1982a), Madagascar (Appert, 1973) and Alexander Island (Jefferson, 1982) were described during the last decade and many important contributions to Mesozoic palaeofloristics were made, especially by Chinese workers. Major discoveries can be expected in the huge marginal basins of Africa, South America and Australia in which palynological explorations are still much ahead of the megafossil studies.

Most Mesozoic plant fossils are either compressions or so called impressions. The latter are usually produced by mineralizing solutions creeping in under cuticles which have completely or partially decayed. Uncompressed permineralized fossils are comparatively rare. Microscopic studies were traditionally centred on cuticles. They greatly benefited from SEM which also made investigation of the cellular pattern possible on impressions which show interior relief of the cuticle. With these techniques practically any fossil can be made to reveal some cellular features.

Fewer workers have been attracted to the Mesophyticum than either the Palaeophyticum or the Cenophyticum. The conceivable reasons for this might be either the Mesozoic transgressions, which reduced terrestrial biomass and its input into sediments, or the notorious lack of coal balls, or just the historical intermediacy revealing neither head

nor tail of evolutionary lineages. At present, with more compression-oriented SEM studies, the perspectives are better. Using recent bibliographies, I counted 70 workers giving all or most of their time to megafossils of the Mesophyticum. Granted zeal, patience and academic freedom, theoretically they can advance all the major floras to present-day standards in about 20 years.

Taxonomy and phylogenetics

It seems futile to speculate on how many plant species or genera there were in the Mesophyticum before this work is completed. Counting leaf species alone we obtain the following numbers for some well known fossil floras:

Molteno, South Africa, Triassic (Anderson and Anderson, 1985) — 115

Scoresby Sound, East Greenland, Rhaetoliasic (Harris, 1937) — 150

Yorkshire, Middle Jurassic (Harris, 1961, 1964, 1969, 1979) — 150

Bureja, Amurland, Late Jurassic–Early Cretaceous (Vakhrameev and Doludenko, 1961; Krassilov, 1972a) — 105

Primorye, Soviet Far East, Early Cretaceous (Krassilov, 1967) — 153

Victoria, Australia, Lower Cretaceous (Douglas, 1969, 1973) — 90

Provided roughly a third of the vascular plant species growing in or around a sedimentary basin ca.300 km wide are available as fossils (Krassilov, 1972b), the standing diversity of local Mesozoic floras could be about the same as or somewhat lower than the average in the present day warm-temperate zone.

The Mesozoic species were at first pigeonholed in the classification of extant plants but with time more natural groupings have emerged. Some phylogenetic work was done on tracing structural homologies, but still the time is not ripe for formal cladistic analysis unless one is satisfied with mere arbitrary distinctions of the primitive vs. derived character states.

Diversity of the higher taxa depends on the

balance of extinction and origination events. Origination events are concentrated at the mid-Triassic and mid-Cretaceous times when the taxa of ordinal rank seem to appear in clusters. Such episodes of explosive evolution occurred in the Mesozoic history of many groups, from bryophytes to conifers.

Bryophytes

For bryophytes, the Mesophyticum appears the time of radical change, though most groups are still insufficiently understood (Krassilov and Schuster, 1984). In fact, though bryophyte remains occur in nearly all large plant localities, our knowledge is based on a very few

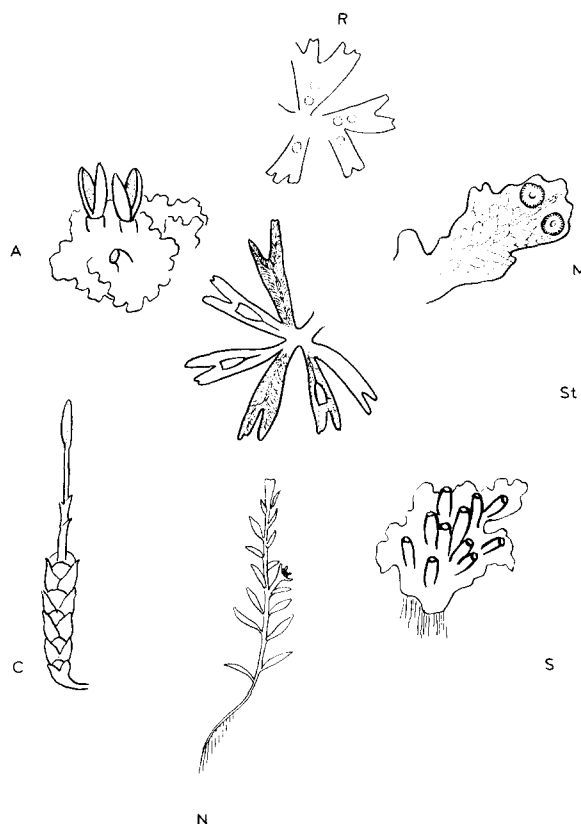


Fig.1. Presumed Triassic (bottom) and Cretaceous (top) radiations of bryophytes: A = Anthocerotales, C = Calobryales, M = Marchantiineae, N = Naiadales, R = Ricciineae, S = Sphaerocarpaceae, St = extinct group related to Corsiniineae, including *Striatothallus* (Krassilov, 1973a).

favorably preserved fossils. One of them is the Triassic *Naiadita*, an aquatic isophyllous form with scattered archegonia, a stem calyptra of four leafy appendages and a unistratose capsule wall. These are characteristic traits of Calobryales, but rhizoids suggest affinities with Sphaerocarpaceae to which it was allocated by Harris (1939). In my opinion *Naiadita* represents an order of its own which can be tentatively placed near the point where the Calobryales and Sphaerocarpaceae diverge.

At the same time primitive marchantialean hepatics appeared. In general habit they resembled *Riccia* or *Cyathodium*. Some of them even showed oblique partitions of the air chambers, numerous simple dorsal pores and small ven-

tral scales (Krassilov, 1973a). But capsules, when preserved, were not like those of *Cyathodium*. They were mostly superficial, stalkless, containing numerous small trilete spores without elaters — a mixture of sphaerocarpacean, marchantialean and anthocerotalean characters. On the evidence of these, they could originate from some ancestral sphaerocarpaceans and in turn, in the next tour of the mid-Cretaceous adaptive radiation, gave rise to the higher marchantialeans, *Riccia* and probably also Anthocerotales (Fig.2).

A heretic view of close relationships between the Ricciales and Anthocerotales can be substantiated by their rather late appearance in the fossil record, some structural homolo-

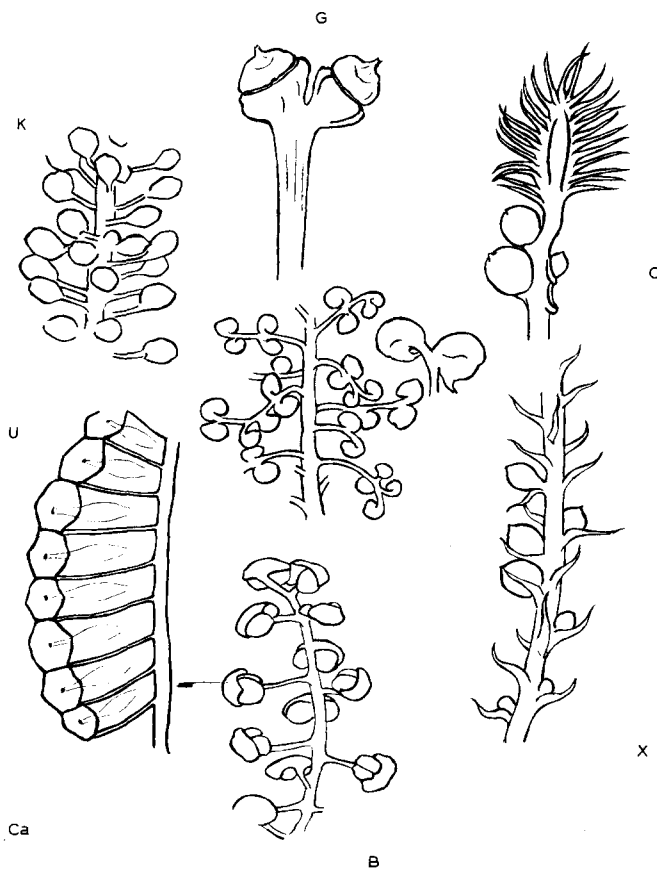


Fig.2. Putative gymnosperm radiation centered on corystosperms: B=Nilssoniales (*Beania*), C=Cycadales (*Cycas*), Ca=Pentoxylales (*Carnoconites*), G=Ginkgoaceae, K=Karkeniaceae, U=Corystospermales (*Umkomasia*), X=an unnamed form transitional between pteridosperms and cycads.

gies, as between the lime canals and air chambers, and very similar development of gamentagia.

The leafy Jungermanniales which appeared in the Jurassic time were not like any living forms (Krassilov, 1973a). They seemed capable of producing pseudothallose variants resembling some higher metzgerialeans (such as *Pallavicinia*) with the phylogenetic implication of being close to their most recent common ancestor.

Little can be said of the Mesozoic mosses except that, notable among them, were forms with dimorphic leaf cells (Krassilov, 1973a; Anderson, 1976; Pant, 1977) probably inherited from the Palaeozoic Protosphagnales of Neuburg (1960). Their sphagnalean affinities seem doubtful since *Leucobryum* and some other bryalean mosses also have dimorphic leaf cells.

Vascular spore plants

Mesozoic horsetails and ferns belong mainly in the extant families of Equisetaceae, Osmundaceae, Schizaeaceae, Matoniaceae, Gleicheniaceae, Cyatheaceae and Dicksoniaceae. These include both extinct and extant genera. Among the latter, *Equisetum*, *Marattia*, *Osmunda*, *Matonia*, *Cyathea*, *Dicksonia* had appeared as early as the mid-Triassic. The camptopteridaceous ferns including *Camptopteris*, *Thaumatopteris*, *Clathropteris* and *Dictyophyllum* are the only large extinct branch of the Triassic radiation. Their alleged affinity with the living *Dipteris* is not supported by the spore morphology. They might be, instead, a blind offshoot of the matoniaceous line.

The subsequent Cretaceous radiation gave rise to such extant genera as *Gleichenia*, *Anemia* ("Ruffordia"), some insufficiently known *Polypodium*-like forms as well as peculiar *Tempskya* and *Weichselia* which might represent extinct families. The latter could be related to water ferns which appeared in the late Cretaceous. *Onoclea* and *Woodwardia* occur in the terminal Cretaceous.

A number of peculiar extinct forms existed among the lycophytes. They range from the

massive Triassic *Pleuromeia* and its allies (Retallack, 1975) to the tiny Late Jurassic *Synlycostrobus* with inflorescence-like fertile parts (Krassilov, 1978a). Evidently, the evolutionary potential of this ancient group was much greater than at present.

Cycads and their allies

At one time all the Mesozoic gymnosperms seemed closely allied to the living cycads, ginkgos and conifers, and the Mesophyticum was even named "the age of cycads". The first surprise came when, to the resentment of some eminent botanists of the time, the cycadeoid foliage was linked with the williamsonialean flowers. Mesophyticum turned out to be the age of bennettites and cycads. But the "cycads" caused further troubles. The most common of them had *Nilssonia*-type leaves, which occasionally were found clustered, as if on a dwarf shoot. This was first seen by Schenk in 1867 and then repeatedly, each time as a fresh surprise, by other palaeobotanists. The dwarf shoots are very uncycad-like. *Beania*, the ovulate organ of the *Nilssonia* plant, is a loose strobilus, lateral appendages of which have been described as having a supposed analogy with *Zamia*, as peltate scales, but they actually compare more favorably with the recurved biovulate cupules of *Umkomasia*, a Triassic corystosperm. In fact, some species of *Umkomasia* were previously referred to as *Beania* (see Playford et al., 1982), and the distinctions seem rather vague.

Nilssoniales may be kept separate from Corystospermales on account of their compact pollen cones (*Androstrobus*) and unforked leaves, but the ovulate organs are emphatic in demonstrating phyletic relationships between them.

Dirhopalostachys, with closed cupules, has allegedly descended from the Nilssoniales (Krassilov, 1975a). Whether any true cycads, which first appeared in the Late Cretaceous (Krassilov, 1978b), also originated from the latter is an open question. An unnamed ovulate organ from the Lower Cretaceous of the

Transbaikal region presently under study shows large erect ovules, sessile in the axils of lanceolate bracts (Plate I). Distally the bracts are empty. It resembles extant *Dion* (*Dioon*), the more so because in some species of the latter ovules show a chalazal appendix (Sabato and De Luca, 1985) which suggests some kind of supporting bracts. While in *Dion* lateral appendages seem pinnate, in the Cretaceous spike they are definitely spiral, and if these two types of ovulate structures were phylogenetically related than the extant one might have been secondarily leaf-like and unrelated to the Palaeozoic ovulate phylloids (Mamay, 1976) which are too remote in time.

The above-mentioned ovulate spike associates with bipinnate leaves showing interstitial pinnules as in callipterids and peltasperms. Intermediate forms between pteridosperms and cycads are known also among the Mesozoic fossil woods. *Antarcticycas*, for instance, shows a cycadalean stem anatomy but lacks the characteristic girdling leaf traces found in the modern cycads (Smoot et al., 1985).

Ginkgophytes and czekanowskialeans

The Siberian Mesophyticum was described by Heer (1876) as the age of ginkgos rather than cycads. The most abundant plants, *Czekanowskia* and *Phoenicopsis* were included in the *Ginkgo* family when it was defined by Engler and Prantl. Florin (1936) had shared and strengthened this view and it was almost unanimously accepted until the late sixties. Even the leaf dissection morphocline from *Czekanowskia* to *Ginkgo* became a text-book example of trait evolution in plants. However, in 1951a Harris suggested that *Leptostrobus*, a

putative ovulate cone of *Czekanowskia*, was made of bivalved cupules. This was confirmed in the Siberian species of *Leptostrobus* which belonged not only to *Czekanowskia*, but also to *Hartzia* and *Phoenicopsis* plants. Further morphological details of *Leptostrobus*, such as the inner cuticle and the papillate stigmatic fringe came to light and some evidence of the pollen cones (*Ixostrobus*) was obtained. All this enabled me to erect Czekanowskiales (the name was provisionally proposed by Pant in 1959) as a separate order of extinct plants (Krassilov, 1968). Subsequently, I considered the *Leptostrobus* capsule as a precursor of an ovary composed of two open carpels and provided with a ventral stigmatic crest, as in Winteraceae, the extant family of primitive angiosperms (Krassilov, 1973b etc.) As to the origin of *Leptostrobus*, its rippled valves with a single submarginal ovule per ridge suggest derivation by fusion of a few linear ovulate scales, and if so, its ancestry could be shared with the cordaitaleans or vojnovskyaleans which are also somewhat similar in epidermal characteristics.

The ginkgophytes thus diminished by the exclusion of the czekanowskiales nevertheless constituted a sizable fraction of the Mesozoic flora. Among them, the pseudotorellians had simple lanceolate leaves and bracteate ovuliferous stalks while the karkenians of various leaf morphologies (*Ginkgoites*, *Baiera*, *Sphenobaiera*, probably *Erethmophyllum*) had ovulate cones of many stalked upright ovules, much smaller than in *Ginkgo*.

Triassic species of *Karkenian* resemble, at least in general habit, *Umkomasia* from the same localities (see Retallack, 1983), but differ in that they have a simpler structure of the lateral appendages. On the other hand, the

PLATE I

Unnamed ovulate spike from the lower Cretaceous of Transbaikalie, studied by E. Bugdaeva and the author.

1. Spike with immature ovules showing distal empty bracts, $\times 1.5$.
2. Spike with larger ovules, $\times 1.5$.
3. Immature ovule subtended by the bract, $\times 10$.
4. Bract, $\times 13$.
5. Mature ovule overgrowing its subtending bract, $\times 8$.

PLATE I



1



2



3



5



4

bioovulate, short-cupulate stalks of modern *Ginkgo* are more like the *Umkomasia* cupules and seem easily derivable from them (Krassilov, 1975b). Supposedly there were several lines of adaptive radiation from the ancestral corytospermalean stalk; in some of these (*Karkenia*) the lateral ovulate appendages became more numerous and simplified while in others (*Ginkgo*), they, though destrobilized, have retained more ancestral features. Dichopodially branched *Dicroidium* leaves (Anderson and Anderson, 1983) and their decisively ginkgoalean stomata can be cited in support of the above suggestions.

Pentoxylalean gymnosperms, the ovulate cones of which (*Carnoconites*) are like *Karkenia* in principle, might belong in the same radiation gird. Anatomically, *Pentoxylon* is rather similar to *Rhexoxylon*, a putative corytospermalean stem (Archangelsky, 1968; Rao, 1974).

Conifers and gnetophytes

Conifers seemed the most secure group of the Mesophyticum, firmly rooted in the Palaeozoic walthians and with many living descendants. The voltzians were generally accepted as their radiation core from which the lines of descent might be extended to the modern Pinaceae via *Schizolepis* or *Borysthenia* (Stanislavsky, 1976), to Taxodiaceae via *Elatides* and possibly also to Araucariaceae and Podocarpaceae with *Doliostrobus*, *Rissikia* and *Mataia* as putative links (Miller, 1977). Bits of evidence for this scheme could be found in many Jurassic and Early Cretaceous plant assemblages where, e.g., *Schizolepis* merges in *Pseudolarix* (Krassilov, 1982a), or *Elatides* in *Cryptomeria*, at least as far as the leaves and ovulate cones are concerned. The latter were given priority in evolutionary studies traditionally, but pollen organs also pose phylogenetic problems. In the voltzians the pollen organs appear complex, with branched microsporophylls — "cone-fleur" of French authors (Grauvogel-Stamm and Schaarschmidt, 1978). Their derivation from the simple pollen cones of the walthians

goes against morphological intuition while among pteridosperms variously branched microsporophylls are common. One asks oneself whether the ancestry of Mesozoic conifers was not misplaced.

Generally, among conifers, the trend was from branched to simple microsporophylls, but the ancestral condition might occasionally reappear as in the Cephalotaxaceae.

A further problem with the Mesozoic conifers is similar to that posed earlier by the Mesozoic cycads and ginkgos, namely, are they all conifers?

Palaeobotanists seem fascinated by the needle and scale leaves as if they were unique coniferous traits. They are not and a number of Mesozoic plants labelled conifers on account of their leaves may well belong in different extinct or extant groups. For instance, the Palissyaceae, a small group of Triassic and Jurassic gymnosperms, usually allied to the conifers, had shoots of needle leaves, but their ovules were orthotropous, provided with a short cupule and aligned in two rows on each cone bract. Now in conifers the ovules are anatropous or pseudorthotropous, while the upright cupulate ovules are more characteristic of gnetophytes. In *Stachyotaxus*, a late Triassic member of Palissyaceae, the ovules show long micropylar tubes (Harris, 1935; Kräusel, 1952) and their nucelli are free from integuments — gnetalean features also. In *Gnetum*, cupulate ovules seem axillary to the perianth-like bracts but their primordia are at the base of the bracts, their vascular supply branches off from the bract traces and they can occasionally be displaced on the bracts. Thus it seems not unlikely that the Palissyaceae were closer to gnetophytes than conifers.

In the famous Ust-Balei locality of Heer (1876) there are dagger-shaped leaves with one, two or occasionally three apically converging veins (Plate II), exactly like in the extant *Ephedra chilensis* in which the leaves are similarly thickened in the middle due to the amply developed transfusion tissue (Foster and Gifford, 1974). Associated with these leaves there are large samaras described by Heer

(1876) as *Ephedrites antiquus* and subsequently transferred to *Schizolepis* (a coniferous cone scale genus) by Prynada (1962). The samaras have an elongate central body surrounded by a membranous unvascularized wing which is bifid at the apex — this alone reminds one of *Schizolepis*. They show abundant resin bodies in the median zone and a prominent callous scar at the base. Bracts with an exactly matching resiniferous median zone and basal scar occur in the same bed. Both bracts and samaras are like corresponding organs in *Welwitschia mirabilis* and, if referred to in the same plant as dagger-shaped leaves, might represent a gnetophyte which combined the *Ephedra*-like foliar and *Welwitschia*-like ovulate organs.

Similarly in *Hirmerella*, an ovulate cone of a widespread Mesozoic family Hirmerellaceae (Cheirolepidaceae), samaras develop from axillary ovules and bracteoles which are free from subtending bracts. They have several short wing-like outgrowths formed by bracteoles and contain one or two ovules in a cuticle-lined locule (Krassilov, 1982b). Leafy shoots of these plants have been invariably described as coniferous in spite of the axillary branching (Alvin and Hlutek, 1979) but the prevailing decussate leaf arrangement is more characteristic of gnetophytes than conifers except in the Cupressaceae, an advanced family appearing in the Late Cretaceous (earlier records may actually belong in the Hirmerellaceae).

No less peculiar are the hirmerellean pollen grains of *Classopollis* with their decisively non-coniferous exine structure and distal porous aperture. The aperture resembles a distal porous leptoma in the pollen grains of *Gnetum africanum* which has revealed in TEM baculate structure (Orel et al., 1986) analogous to that of *Classopollis*. Taxonomic implications of these findings are self-evident.

Hirmerelleans dominate many Triassic to mid-Cretaceous localities all over the world. These alone are enough to underline the importance of gnetophytes in the Mesophyticum. But there were even more peculiar forms. *Dinophyton*, a Triassic plant from Arizona had

branching shoots of hairy needle leaves and propeller-like structures, supposedly ovulate (Ash, 1970). In the material kindly supplied by Dr. Ash I was able to prepare an ovule, orthotropous and basal in the four-valved hairy cupule attached at the base to the "propeller" of four perianth bracts (Plate III). Homology with the gnetalean perianth of connate bracts and the cupule of fused bracteoles is immediately evident. The ovule is notable for its three-angled nucellus showing a markedly thickened bottom of the pollen chamber — a plinth. These are characteristic trigonocarpalean features betraying a pteridospermous ancestry.

More advanced forms are represented by *Eoantha* from the Lower Cretaceous of the Transbaikalian region (Krassilov, 1986) — an ovulate organ consisting of a whorl of four longitudinally folded cupules surrounded by linear perianth bracts and crowned by a fascicle of similar bracts. The cupules appear dehiscent along the dorsal sutures showing relief venation inside. Each cupule contains a single orthotropous ovule in the pollen chamber of which there were *Ephedripites*-type pollen grains.

Due to its carpel-like cupules, I considered *Eoantha* as a possible transitional form between gnetophytes and primitive angiosperms. Indeed, with so many diverse Mesozoic gnetophytes at hand, it is the time to think more seriously of the gnetalean ancestry of at least some angiosperm lineages. Forms with a basal orthotropous ovule, trimerous ovary (according to Pearson, 1929, in *Gnetum* the cupules were initially trimerous) and simple perianth are common among the early angiosperms (Friis, 1985). Also the tricolpate condition of pollen grains was approached by *Eucommiidites* showing gnetalean exinal characters (Hughes, 1961; Trevisan, 1980).

Bennettites and their derivative forms

Related to gnetophytes and evolving along grossly parallel morphological pathways, bennettites are so far the best known extinct group

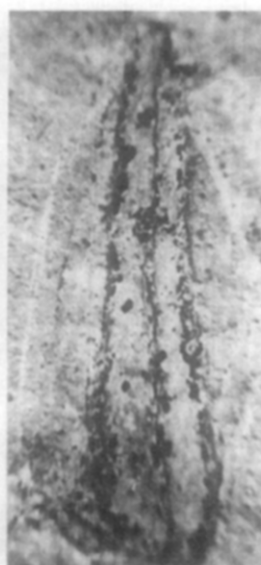
PLATE II



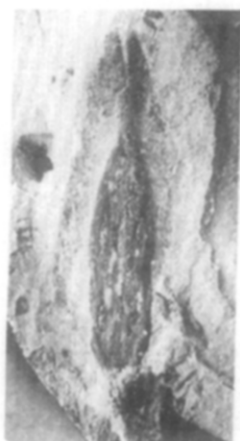
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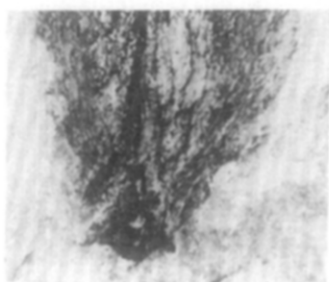
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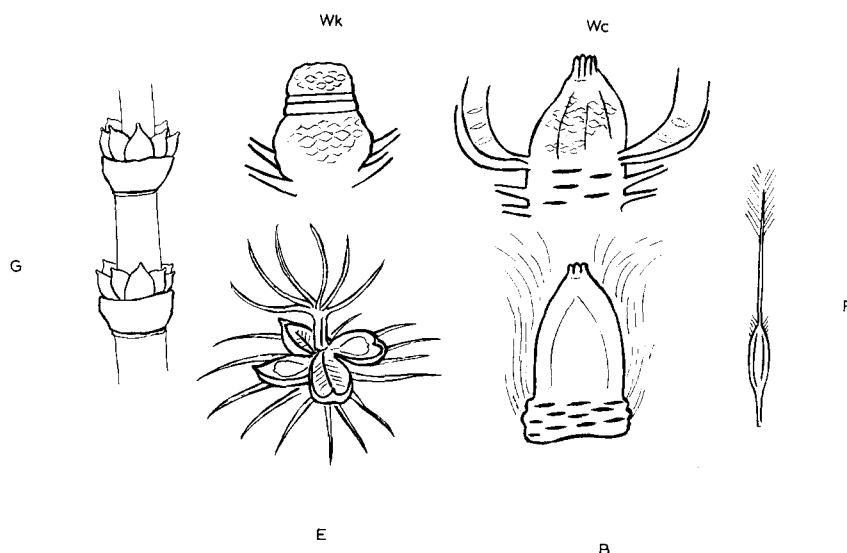


Fig.3. Possible transformations of a second floral node in gnetaleans, bennettites and allied forms: B = *Baisia*, achene-like Early Cretaceous fossil related to bennettites showing a vestigial corona of the bract tips forming the cupule (Krassilov and Bugdaeva, 1981), E = *Eoantha*, flower-like Early Cretaceous fossil related to gnetaleans, with a fascicle of bracts left from the second floral node (Krassilov, 1986), G = *Gnetum* with two fully developed floral nodes, P = *Problematospermum*, achene-like Jurassic fossil related to bennettites, showing a corona-derived pappus, Wc = *Williamsoniella coronata* from the Jurassic of Yorkshire, Wk = *Williamsoniella* sp. from the Jurassic of the Ukraine showing a slightly reduced floral node instead of a corona.

of the Mesophyticum. However, they also present some neglected or poorly understood features (see Delevoryas, 1968). One of them is a corona, or sterile bulge at the top of the gynoecium. A few underdeveloped sterile scales have been noticed on the corona of *Williamsonia leckenbyi* (Harris, 1969). In the Middle Jurassic of Kamenka (Ukraine) I found a ferruginous cast of *Williamsoniella* showing a comparatively large corona, in fact, almost as large as the receptacle itself, covered with sterile scales. On the evidence of this dumbbell-shaped structure, the corona is a vestigial floral node above the basal receptacle. This interpretation strengthens the comparison

with gnetophytes in which *Gnetum buchholzianum*, for instance, may have spikes of two floral nodes only (Pearson, 1929).

In *Eoantha* (above), the corona is represented by a canopy of perianth-like bracts above the gynoecium. In the development of a true flower, the corona-bearing axis is suppressed to make the gynoecial apex fertile. This condition is met in *Baisia*, another Early Cretaceous floral organ of a single cupulate ovule terminal on the hairy receptacle (Krassilov and Bugdaeva, 1982). The cupule is supposedly derived from concrescent sterile scales and a vestige of a corona can be seen on the top of it.

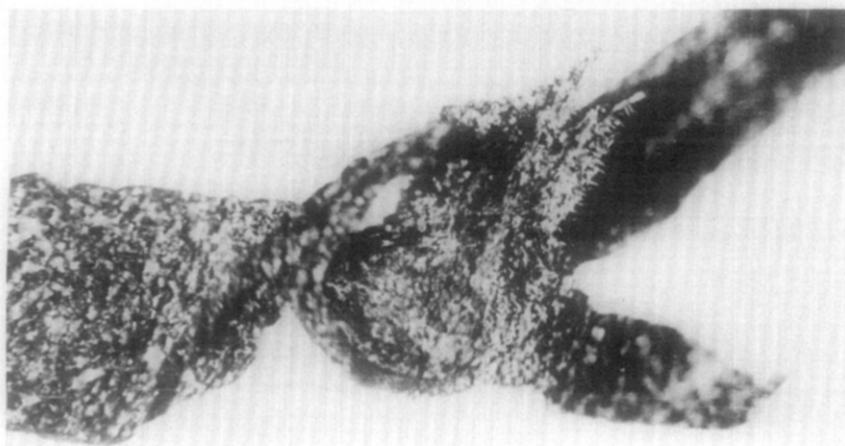
In still another related form, *Problematosper-*

PLATE II

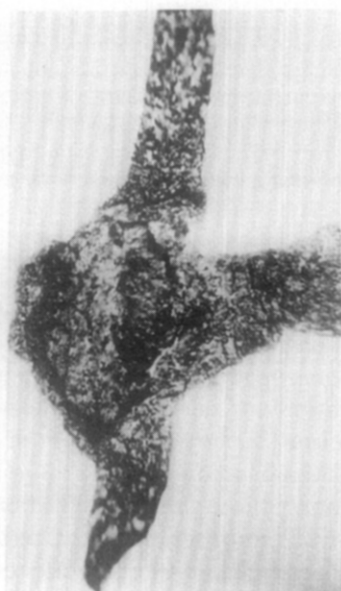
Gnetalean plant fossils from the mid-Jurassic of Ust-Balej, East Siberia.

- 1-4. "*Ephedrites*" *antiquus* Heer. 1, apical cleft in the wing. 2, a complete samara. 3, central part showing resin bodies. 4, basal scar of attachment, $\times 3$ and $\times 10$.
5. *Ephedra*-like leaf with three veins, $\times 10$.
- 6,7. Bracts showing resin bodies and an attachment scar as in the samara (1-4), $\times 4$ and $\times 8$.

PLATE III



1



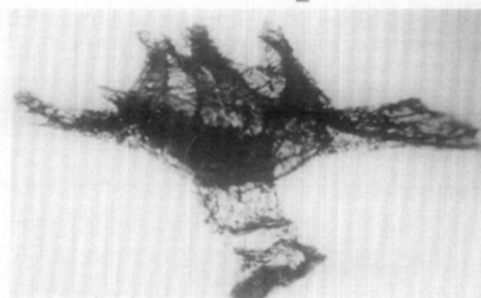
2



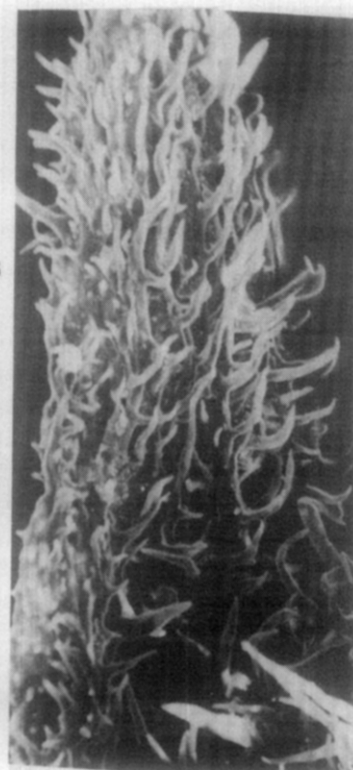
3



4



5



6

mum ovale Turutanova-Ketova (Krassilov, 1973b), the corona might have been transformed into a pappus of apical bristles. And if any pistillate structure had evolved from this or from a similar prototype, the corona could provide the morphological precursor of a branching stigma.

Vessels or vessel tracheids found in the midrib of a bennettitalean leaf *Otozamites lacustris* (Krassilov, 1982a), mesogenous paracytic stomata and stellate hairs (Ash, 1968) are further noteworthy characteristics which bennettites share with some gnetophytes and angiosperms.

Caytoniales

Angiosperm traits evolved independently in other groups of Mesozoic seed plants. One of them, a small order of Caytoniales was described in detail by Thomas (1925) and Harris (1951b). Their reconstruction of the caytonial-ean ovulate organ — a spike of many-seeded fleshy cupules with a mouth close to the base — was regularly reproduced in botanical textbooks. But recent studies have shown that on many critical points opinions vary, the most essential of these is placentation. While Harris apparently thought of it as parietal, according to Reymanowna (1973) and Krassilov (1977) it was actually basal-central. I have also argued that what was previously described as the eleurone layer was in fact the inner integument of a bitegmatic ovule (Krassilov, 1984). Until these features are finally cleared up any phylogenetic conjecture seems premature, but the caytonialean theory of angiosperm origin advanced by Thomas half a century ago is still viable. To it can be added a

possibility of deriving tricolpate pollen grains from the bissaccate (or bilobed monosaccate) as in *Caytonanthus*, with the bladder scars transformed into apertures.

Developmental studies

In the future phylogenetics could gain more from palaeodevelopmental studies which are rare but which nevertheless exist. I have tried to show that not only stomatal ontogeny but also some morphogenic patterns of epidermal topography can be traced on the cuticle of a bennettitalean leaf (Krassilov, 1978c). There are fine embryological studies on petrified material (Stockey, 1978) and even some attempts on material from compressions (Krassilov, 1972a). And occasionally one finds a fossil seed-plot as in the Jurassic of Ust-Balej where nearly half of several hundred *Samaropsis* seeds germinated and the seedlings became fossilized at different developmental stages (Plate IV).

Palaeoecology

Palaeoecology is a vast discipline embracing the questions of the growth, dispersal, interaction with other organisms and physical environments and fossilization of plants in past geological times. So as not to repeat what I said in my book (Krassilov, 1972b), I shall mention a few problems which appear comparatively underexplored.

Depositional environments

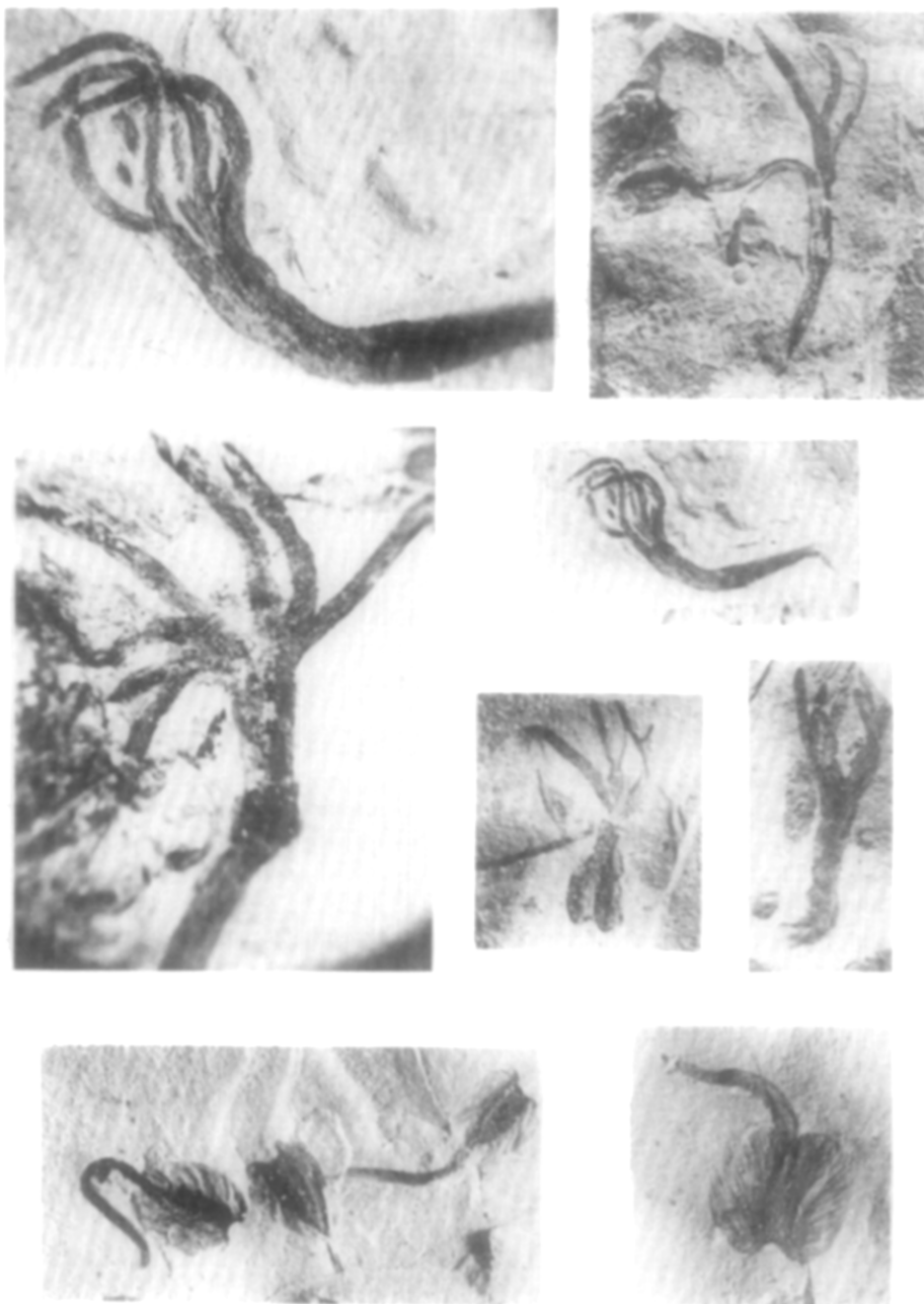
To begin with, the significance of fossil plants as indicators of sedimentary environ-

PLATE III

Dinophyton spinosum Ash from the Triassic of the southwestern U.S.A.

- 1,5. Four-lobed cupules basally attached to a propeller-like perianth of four bracts, $\times 15$ and $\times 12$.
2. Cupule, facing wall removed exposing a single ovule, $\times 9$.
3. Cleared ovule from fig.2 showing thickened bottom of the pollen chamber (plinth) as an arched line near the top, $\times 17$.
4. Another cleared ovule notable for a three-armed ridge at the base, $\times 17$.
6. Leaf showing dense hairs, SEM, $\times 100$.

PLATE IV



Germinating *Samaropsis* seeds and seedling of the same plant from the mid-Jurassic of Ust-Balej, East Siberia, $\times 3$ and $\times 10$.

ments is still not fully appreciated. For instance, in the ophiolitic cherts usually described as pelagic deposits, large araucarian logs were found (Abbate et al., 1980). To incorporate a log about half a meter in diameter into the slowly accumulating pelagic sediments would take no less than 5000 years and probably much more. On the other hand the existence of these wood remains agrees well with the idea of a siliceous turbidite which, if a member of ophiolitic sequence, might give evidence for a trench rather than a mid-ocean rift environment. If so, then the ophiolites were found not far from where they had been formed.

The concomitant melange deposits usually contain palynomorphs which are 50% or more reworked, so that only geologically younger forms count as age indicators. Occasionally the deposits also contain leaf fossils giving evidence of a near-by island arc (Krassilov et al., in press).

But abundant plant megafossils normally occur in different tectonic environments notable among which are the rift valleys, shallow epirift depressions, faulted marginal basins and compensatory troughs along the rising volcanic ranges. Rifting of cratonic areas in the Triassic time accounted for abundant deposition of plant debris in coarse clastic and volcanoclastic sediments such as Tunguska in Siberia or Molteno in Africa. These localities could be extraordinarily rich, comprising plant remains not only from lowlands but also from steep slopes.

In contrast, in the broad saucer-shaped depressions which develop over sagging rifted areas, as the Jurassic and Cretaceous West Siberian or North European basins, plant localities are comparatively poor, supplied mostly from near-by lowland sources.

More diverse terrestrial environments are reflected in the plant assemblages from deltaic deposits which fill the marginal faulted basins, as on both sides of the Atlantic (e.g. the Potomac flora of Maryland). In fact, we owe most of our knowledge of the Mesozoic vegetation to this process of large-scale faulting

which affected most continental margins in several stages from the mid-Triassic to the Early Cretaceous.

Lastly, the intermontane lacustrine plant-bearing facies are confined mostly to the circum-Pacific volcanic belt and its arm which extended across the Transbaikalian region and Mongolia. In this area wind transport, probably aided by storms from volcanic eruptions, was an important agent of the plant debris accumulations in which an upland flora has been fairly represented.

In other words, deposition of the plant material in various sedimentary basins can eventually be related to a tectonic style of the epoch which affected, albeit indirectly, the content and preservational qualities of the fossil plant assemblages.

Even the distribution of plant beds over a sedimentary sequence can bear important information on tectonic movements and climate. It is often cyclic, and in the simpler cases cyclicity might depend directly on migrational facies changes, such as the alternate succession of flood plain and channel beds.

Sometimes, however, the causes of cyclicity are less obvious. In the limestone/marl Cenomanian sequence of Crimea, plant debris is correlated with anoxic conditions at the sediment-water interface as evidenced by pyrite concretions and aragonitic shells. Periodical input of the terrestrial plant material could depend on influx of fresh waters (causing stagnation at depth) and eventually on the alternation of wet and dry periods of the order of a few hundred thousand years, a chief variable of the Cretaceous climate (Krassilov, 1985).

Similarly, in the lacustrine sequences of the Transbaikalian region cyclicity of plant beds — and especially of the *Czekanowskia* beds — seems to correspond to periodic lacustrine transgressions flooding swampy benches during the wetter periods.

In addition, the plant beds with chaotically disposed remains, often oblique to the bedding planes (suggesting very rapid sedimentation) could be tempestites caused by periodic storms.

Patterns of plant communities

Both tectonic and climatic conditions might determine to what extent the fossil plant assemblages can be expected to reveal a pattern of the contemporaneous plant communities. For this purpose many more fossil assemblages must be meticulously described, named and classified according to some convenient rules (Krassilov, 1972b) than was done previously or than we can hope for the near future with so few workers in the field. However, even now some crude patterns reveal themselves. For instance, a certain parallelism was found in the succession of plant beds deposited after the retreating seas in places as distant as Kamenka, Ukraine, and Bureja in the Far East. The lowermost plant beds contained abundant fern leaves. Then followed a *Czekanowskia* bed, the conifer-dominated assemblages and finally rather thick *Phoenicopsis* beds. Occasional *Ginkgoites* might represent an upland community in both cases.

It would seem premature to translate this sequence into a universal up-slope pattern, or catena, especially since many deviations did occur. It was noticed that equisetaleans could replace ferns; the brachyphyllous conifers, *Classopollis* producing hirmereleans and other gnetophytes could cancel *Czekanowskia*, especially in more southern localities, and along seashores where the fern belt was reduced. Bennettites occupied various catenic loci, most often those of the *Ptilophyllum*–*Otozamites* group at the lower end, in the near-shore and, judging by their occasional occurrence in carbonaceous and gypsiferous deposits, even mangrove habitats where they were joined by hirmereleans and peltasperms. Other forms, such as *Pterophyllum*, might grow in the conifer or *Phoenicopsis* belts or with nilssonialeans as a cycadophyte shrubbery, while *Nilssoniopteris* has repeatedly been found associated with coal-beds. There were also coals consisting of *Equisetum*, *Pseudotorellia*, *Sphenobaiera*, *Pityophyllum* or *Czekanowskia* cuticles.

It is obvious that catenic belts were them-

selves mosaic, interlacing and capable of wedging out or changing position in response to climatic events, especially to cooling which brought ubiquitous upland–lowland migrations. The vegetational pattern was dynamic and consequently there was probably no such thing as an upland flora permanently distant from depositional sites and thus impenetrable for palaeobotanists¹.

Nevertheless *Czekanowskia*, for example, always maintained one of the lowermost catenic loci and can be conceived as an active colonizer appearing early in seral successions. And indeed, in many Siberian sections, the *Czekanowskia* beds, usually a few centimeters thick, are succeeded by a much thicker sequence of *Phoenicopsis* or *Ginkgoites* beds.

A somewhat unusual situation was recently described by E. Bugdaeva (unpublished) in the Transbaikalian area where *Czekanowskia* dominated a thick mid-Jurassic sequence of volcanoclastic rocks while *Phoenicopsis* appeared in the overlying clastic deposits. Supposedly under heavy volcanic impact, a normal seral succession was suppressed at the pioneer *Czekanowskia* stage which lasted until volcanic activity decreased and the climax vegetation could restore itself. In less disturbed areas this could be accomplished in a few thousand years — that is accepting about 10 cm per 10³ years as an average deposition rate for short continental sections.

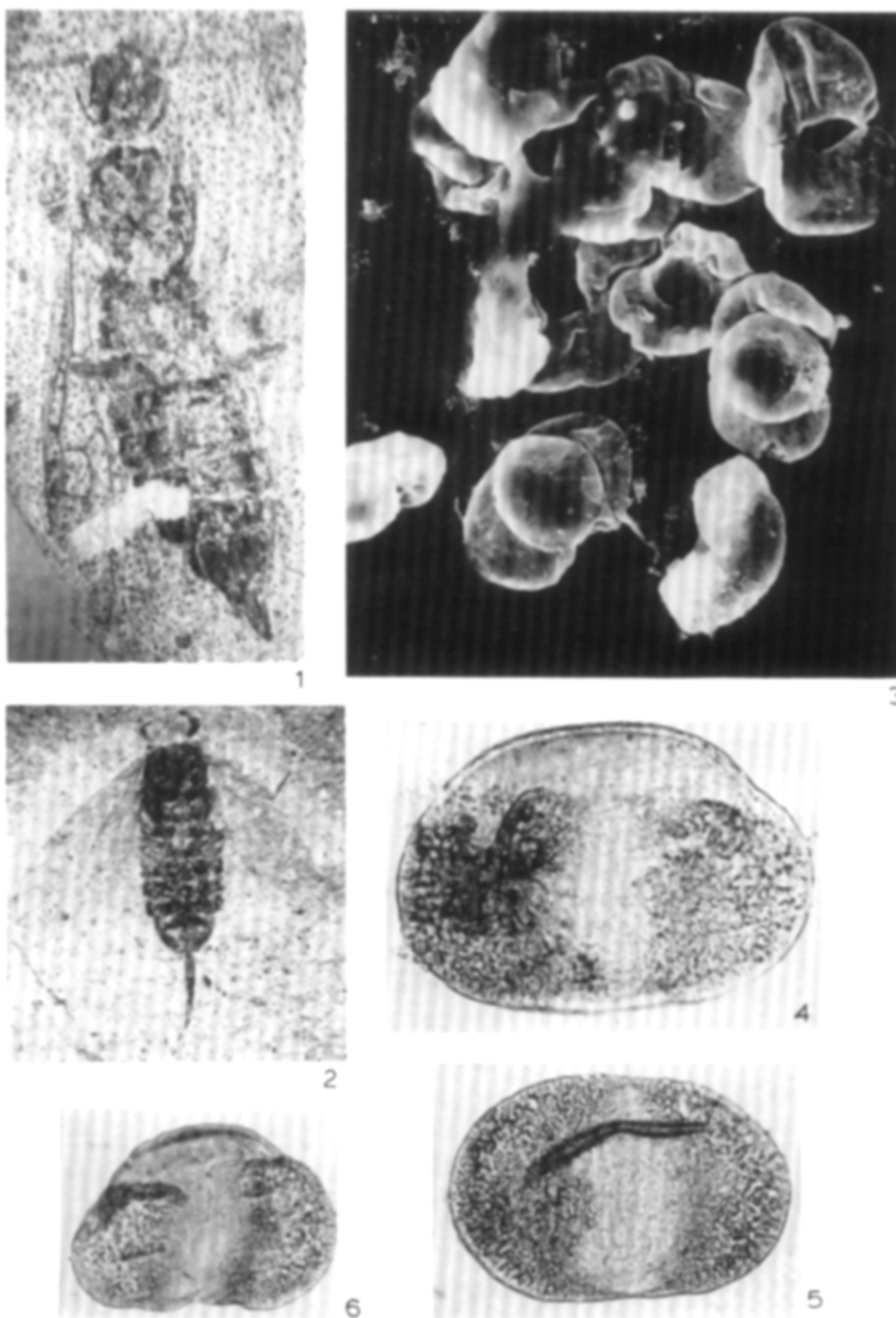
Another oblique piece of evidence comes from the classical Ust-Balej locality where *Czekanowskia* was first described by Heer. Its linear leaves are heavily and selectively tainted by parasitic fungi, a condition only a pioneer plant could withstand.

Plant–animal interactions

Evidence of plant–animal interactions can also, among other things, tell something about the catenic position of a plant. For instance, consider the peculiarly intricate caddis-cases from the Lower Cretaceous of Mongolia show-

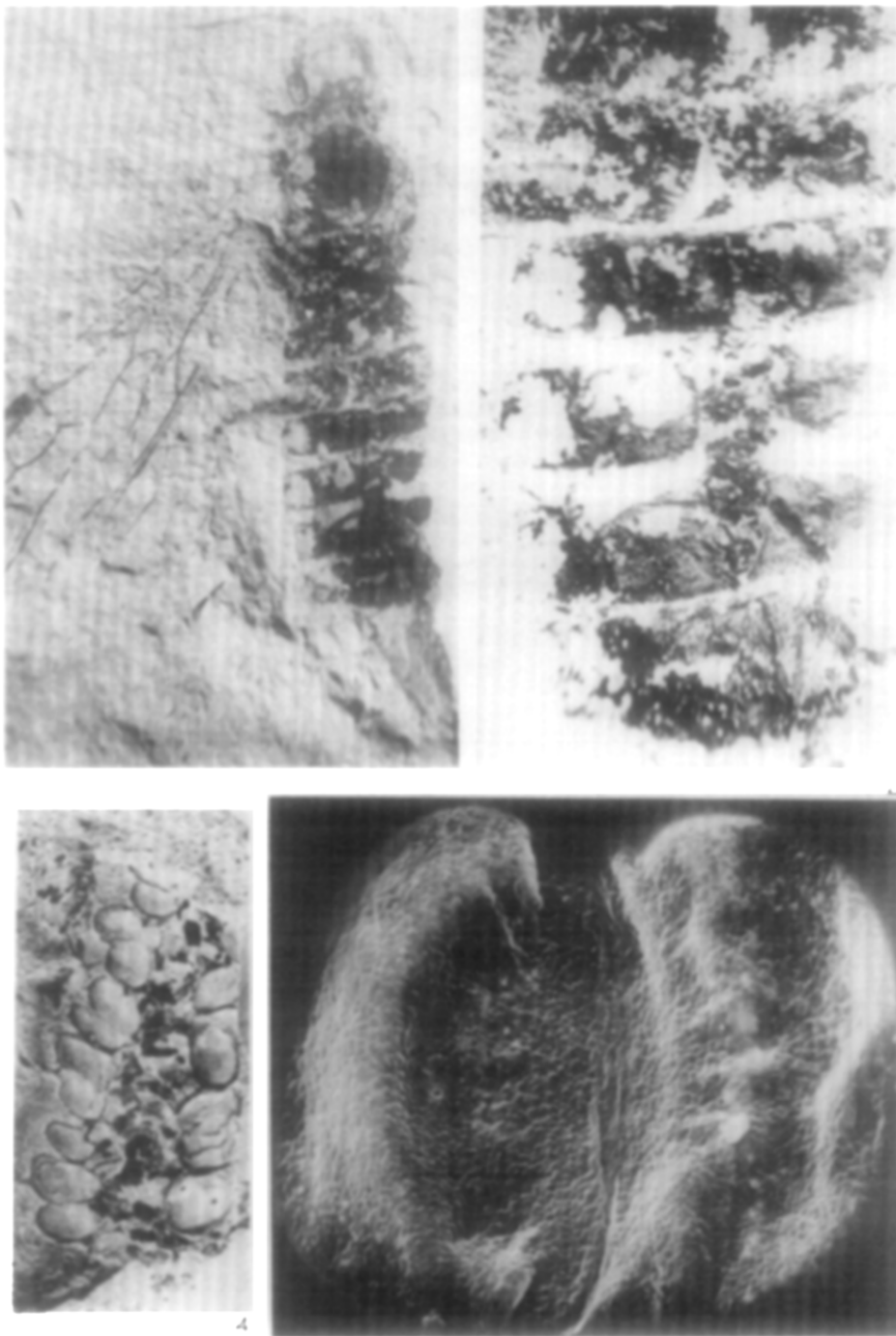
¹See Note added in proof (pp. 253–254).

PLATE V



- 1,2. Xyelidae insects *Ceroxyela* and *Spathoxyela* from the Lower Cretaceous of Transbaikalie with pollen grains in their guts and crops, $\times 7$.
3. *Pinuspollenites* pollen grains from the crop of (2), SEM, $\times 800$.
- 4-6. *Vitimipollis* pollen grains from the guts of fig.1, light micrographs, $\times 600$ and $\times 400$.

PLATE VI



ing *Karken* seeds attached as floats (Plate VI). These make it obvious that, for a caddisfly species to have found out how to use them, these seeds must have been constantly at hand, supposedly shed by a plant which grew profusely over the lake shores.

Among the taxonomically diverse insect fossils from the Lower Cretaceous lacustrine deposits of Baisa in the Transbaikalian region, three specimens, each belonging to a different species of Xyelidae, had their guts and crops full of well-preserved pollen grains (Krassilov and Rasnitsyn, 1982). Normally pollen grains remain in a crop for a short time only so the insect could not fly far from its feeding plant, supposedly a voltziacean or pinacean conifer. These considerations agree well with an idea of a coniferous forest growing around the lake.

It may also be a notable example of ethological conservatism that in early development the living Xyelidae larvae still feed on coniferous pollen cones while imago have turned to flowering plants. It could be that flowering plants initially acquire most of their insect retinue in this way.

It would be interesting to know just as much about the diet of the larger Mesozoic herbivores, but stomach contents have been preliminarily examined for plant remains in only a single hadrosaurian specimen (Kräusel, 1922).

Given the available evidence most herbivorous dinosaurs are conceived of now as having been gregarious. They seem to have needed a fast growing, rapidly repairing type of vegetation to support their herds. This could not be a closed forest. I suggested an open vegetation like extensive fern-horsetail marshes or cycadophyte (and cycadophyte-gnetalean-coniferous) shrublands (Krassilov, 1981). Notably, following the decline of cycadophytes in the mid-Cretaceous and their replace-

ment by angiosperms with much smaller leaves and succulent fruits, dinosaurs developed new mastication structures and various beaked forms have appeared as the witnesses of dietary innovation. No wonder these animals were deeply affected when the fern-horsetail marshes as well as cycadophyte-gnetophyte-primitive angiosperm shrublands disappeared to be replaced by the rapidly advancing forests in the terminal Cretaceous. These changes occurred most dramatically in the broad temperate/subtropical ecotonal belt to which most prosperous dinosaur communities were confined.

Phytogeography and crustal motions

Flora of the Mesophyticum was once described as uniform all over the world. Such extreme uniformity implied some kind of connection between the continents — either by land bridges or by continental drift. And, of course, land connections were needed for the early angiosperms to march over the world from their place of origin wherever it was.

We know at present that the Mesophyticum was not spatially uniform, though it was less distinctly differentiated than the late Palaeophyticum. If the latter was the time of Pangaea then uniformity paradoxically increased while Pangaea broke up.

Migration routes

No matter which tectonic theory is considered, Pangaea just did not exist in the mid-Cretaceous and could not help early angiosperms to spread. On the other hand, *Aquilapollenites* plants, for instance, could disperse along the Thulean (Greenland-Jan Mayen-Faeroe) route (Croxtton, 1980). In the Cretaceous, when oceans were shallower,

PLATE VI

1. Xyelidae insect *Anthoxyela* from the Lower Cretaceous of Transbaikalia with pollen grains in the guts, $\times 7$.
2. Abdomen of fig.1 with a lump of pollen grains seen as a longitudinal body in the middle, $\times 15$.
3. *Allisporites* pollen grain from (2), SEM, $\times 1400$.
4. Caddisfly case with *Karken* seeds as floats from the Lower Cretaceous of Mongolia, $\times 2$.

many plants could use this and possibly also the De Geer route between Greenland and Spitsbergen (McKenna, 1972). Drawing Europe and North America closer would inevitably create a gap between Chukotka and Alaska, while the undeniable similarity between the Cretaceous floras of eastern Asia and western North America shows that the Bering route was functional at that time. To have both the Thulean and Bering bridges intact should better keep the continents in their places.

In the southern hemisphere, shallow-water Cretaceous deposits occur at places on the submarine Walvis Ridge and Rio Grande Rise which might form at least a stepping-stone route between Africa and South America while the Mcquarry Ridge might link Antarctica and New Zealand. But by what route could India be reached in the Late Cretaceous if it were drifting freely midway between Antarctica (or Australia) and Tibet?

Nevertheless, on the ample palynological evidence (Herngreen and Chlonova, 1981; Nandi, 1983; Srivastava, 1983), a lot of African and Asiatic taxa found their way to India in the Maastrichtian time. Evidently, the plate tectonic scenario should not be taken so much for granted.

What is now southern Asia in the Mesozoic time was a mosaic of plates not necessarily separated by oceans but merely by gaping faults evolved into ophiolitic troughs. Obduction of the ophiolitic rocks in Zagros, Oman, Macran, Farahrud and the Indus-Tsangpo-Aracan Yoma belt in the pre-Maastrichtian time signifies that the ophiolitic troughs between Anatolia, Arabia, Lut, Gilmend, Lhasa and India were healed, welding these and smaller plates into a single continent (see Krassilov, 1985, for review). In effect new migration routes had been established and India became accessible for African plants.

Phytogeographical boundaries

I suggested a deceleration of the Earth's angular velocity as a common force under the crustal shortening in the Alpine-Himalayan

belt and the flattening of the global hypsometric curve which caused shallower oceans and marine transgressions over cratonic areas (Krassilov, 1985). Shallow seas strewn with islands and with some larger areas of dry land emerging from time to time probably presented lesser obstacles to plant dispersion than climatic barriers. That is why a purely floristic subdivision of the Mesophyticum is impractical. The boundaries were ecotonal, marked by the changing species frequencies rather than endemism.

In the northern areas which can be described as temperate on the ample evidence of marked seasonality, the ginkgoalean, czekanowskialean and coniferous trees had in common such features as deciduous dwarf shoots and drooping cones which were shed after dropping their seeds. Prevailing among the seeds were samaras with a one-sided propeller wing of the kind often met in the trees which drop their seeds or fruits on or into snow. Ferns and horsetails were dwarfish, not larger than their extant descendants in the modern temperate forests.

To the south, abundant scaly conifers and hirmereleans together with xeromorphic benettitalean *Ptilophyllum* or *Otozamites* leaves gave the plant assemblages a sclerophyllous "mediterranean" aspect suggesting a summer-dry climate.

In practice, the boundary between these major phytoclimatic zones can be defined by a sharp decline of *Phoenicopsis*, a dominant tree of the deciduous temperate forests and by the rise of brachyphyllous conifers, pachycaul cycadeoids and the *Otozamites*-*Ptilophyllum* group. The latter mix with *Phoenicopsis* in several Mongolian and Transbaikalian localities along latitude 50°N. Minor constituents of the plant assemblages also felt this boundary. Schizaealean ferns, *Coniopteris* with aphlebioid proximal basiscopic pinnules, equisetaleans thicker than 2 cm, pteridosperms and araucarians almost never crossed it.

In many ecotonal localities the boundary can be drawn over the areas with a certain confidence. In the Early Cretaceous it was

several hundred kilometers north of its mid-Jurassic location. Such shifts were obviously due to climatic fluctuations.

The boundary can be traced approximately along 50°N further west, but in western Europe it turns to the north, passing through Scotland where the Jurassic flora includes both *Phoenicopsis* and *Ptilophyllum*. This deflection might have been caused by the Tethys waters flowing through the Carpathian corridor and between the Ardenian and Brabantian land masses.

In North America, the corresponding boundary can be placed between British Columbia with *Phoenicopsis* (Bell, 1956) and the Black Hills of Dakota with abundant *Cycadeoidea*, but, surprisingly, the Rhaeto-Liassic and Cretaceous Greenland assemblages are ecotonal at 70°N. With the warm-water Cretaceous fauna found on the Flemish Cap and the Orphan Knoll in the North Atlantic (Berggren and Hollister, 1977) we can tentatively attribute this anomaly to the proto-Gulf Stream current.

If we follow the law of parsimony, one hardly needs a better explanation for evergreen plants in high latitudes than a warmer polar climate (Axelrod, 1984). Even now a number of species growing over the polar circle are evergreen and one can see the unfolding of photosynthetic organs when the growing season is so short as a waste of precious time.

In the southern hemisphere, the boundary analogous to that just described should lie somewhere between the Fossil Bluff fossil forest of Alexander Island (Jefferson, 1982) and southern Patagonia with *Ptilophyllum*, that is about 60°N.

The equatorial Cretaceous zone defined palynologically falls on the present-day equator in Africa and South America (Herengreen and Chlonova, 1981). Its extension to the east is poorly known but probably also not far from the equator.

Thus the framework of three belts — equatorial and two ecotonal temperate/subtropical — can put constraints on both continental drift and climatic fluctuations, but much more work is still needed to place it more precisely for each of the Mesozoic epochs.

Conclusion

In conclusion I must apologise again for expounding my own views at the expense of the others — but this cannot be helped — and I admit the vagueness of many ideas presented in the paper. But my impression of the Mesophytic palaeobotany state of the art is that it is making mediocre progress and can fare better with more competing ideas in the trade.

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Note added in proof

This was one of the arguments against the upland theory of angiosperm origin when, more than two decades ago, it was forcefully promoted by D.I. Axelrod and had a

few opponents like N.F. Hughes and myself. But the opposite coastal theory (e.g. Retallack and Dilcher, 1981, in *Paleobotany, Paleoecology and Evolution*, vol. 2. Praeger, New York, N.Y., pp.27–77) is also questionable because the earliest angiosperm fossils came from both

coastal and inland basins. Strictly coastal and especially tidal flat flowering plants are specialized species from advanced families rather than generalists which the primitive angiosperms probably were. They might arise at different catenic loci as various life forms. When still poor competitors they could invade those communities which

suffered from environmental hazards — first cycadophyte shrublands and then riparian forests where they gave platanoid and salicoid forms. But the coastal fern marshes remained impenetrable at places such as Sakhalin where I described several Maastrichtian fern-dominated paralic localities without a single angiosperm fossil.