Syngenesis of Xeromorphic Plant Communities in the Late Paleozoic to Early Cenozoic

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Abstract—The methods and terminology of plant community reconstruction are considered. The successive late Paleozoic to early Cenozoic xeromorphic coniferoid-peltasperm, bennettite-brachyphyll and debeyo-dryophyll communities are briefly described. They sequentially replaced each other within the coastal–littoral facies domain forming a continuous syngenetic series. Their xeromorphism was related to their helophyte and littoral habitats rather than to arid climates. Xeromorphic communities played a significant evolutionary role as a cradle for new higher taxa, in particular angiosperms. The evolution of xeromorphic communities apparently corresponds with the general model of plant syngenesis (Krassilov, 1992).

INTRODUCTION

Reconstructions of biotic communities through geological times of tens to hundreds of million years are relevant to our growing concern for long-time natural, as well as anthropogenic, ecological processes. This paper deals with the historic development of xeromorphic plant communities that appeared in the late Paleozoic and evolved through the Mesozoic and early Cenozoic (their late Cenozoic history relates to the present day Mediterranean-type vegetation that is beyond the scope of the present analysis). The xeromorphic communities are here chosen for syngenetic reconstruction because of their relatively complete geological record, as well as their climatological significance and the outstanding role they played in the evolution of seed plants.

The xeromorphic aspect is characteristic of plant communities inhabiting intracontinental areas of sharply seasonal, mostly summer-dry climate, as well as of coastal–littoral shrubland and woodland vegetation. Xeromorphism relates also to helophytic, calciphilous and psammophytic adaptations occurring in both intracontinental and coastal environments. It is not always possible to distinguish between the respective morphologies. Some plant sociologists (e.g., Ilyin, 1947) consider littoral habitats as "laboratories" for xeromorphic transformation of mesophytic plants which then spread inland.

Reconstructions of the Mesozoic and Paleocene communities are based on the materials studied by the present author from the Jurassic of the Donets Basin, Jurassic–Early Cretaceous of the Bureya Basin, Early Cretaceous of Primorye in the Far East, Transbaikalia and Mongolia, Late Cretaceous of Sakhalin, the Albian–Cenomanian of Northern Crimea, the Maastrichtian–Paleocene of the Zeya-Bureyan Depression, the Sikhote-Alin Ranges, and the Lesser Kuril Islands

(Krassilov, 1967, 1972a, 1972b, 1976, 1979, 1982a, 1984; Krassilov et al., 1987). These studies were based on the approaches outlined in the next chapter. In several cases it was possible to deduce a position maintained by xeromorphic communities in spatial and temporal successions, the latter encompassing a long-time evolutionary series. For the Paleozoic fossil floras there is only general paleoecological and taphonomic information allowing for a preliminary consideration of xeromorphic communities at most.

METHODOLOGY AND TERMINOLOGY

Since the methods and approaches of terrestrial plant paleoecology were reviewed (Krassilov, 1972a) a number of fossil floras have been analyzed for their plant community structures by my collaborates and myself. These studies have raised some methodological and terminological problems that are briefly dealt with below. In the first place, it is necessary to emphasize the significance of the basinal approach. The material for paleoecological reconstructions is provided by stratigraphic successions of plant-beds as well as by their facial domains in a sedimentary basin, the latter defined as a depositional area of a hydrographic basin. The sedimentary basin serves as a natural geological framework for paleoecological research.

It is worth noting that the basinal approach is currently widely used in modern ecology as well. In essence, a hydrographic basin is considered as an integral landscape system that determines the development of both natural and anthropogenic processes. Basinal vegetation is a dynamic system of climax and seral communities. Their catenic or mosaic patterns influence the deposition and facial distribution of plant remains. Therefore it seems appropriate to introduce the basinal approach in the practice of plant community reconstruction. In particular, the basinal approach per-

tains to definitions of such important paleoecological notions as taphoflora, fossil plant assemblage, paleo-catena, etc. They are based on the terminology worked out by Clements (1916), Du Rietz (1921), Braun-Blan-quet (1932), Sukachev (1964) and other authors (see Krassilov, 1972a). The following definitions reflect the present author's understanding of the frequently used, but semantically ambiguous terms.

Clisere: a chronological succession of climax communities replacing each other within a landscape or a facies domain.

Coenoseries (*sere*): a sequence of syntaxal developmental stages from the pioneer to the climax.

Fossil plant assemblage (FPA, including palynological assemblage, PA): all fossil plant species found in a stratigraphic unit. A basic fossil plant assemblage comes from a single plant-bed or a bedding plane.

Fossil plant spectrum (FPS, including palynological spectrum, PS): species frequencies in the fossil plant assemblage.

Paleocatena: a spatial sequence of plant communities from the basinal facies domain (proximal members) to the borderlands (distal members).

Paleosuccession: a stratigraphic sequence of fossil plant assemblages.

Plant community: a vegetation unit composed of a set of life forms represented by a species combination sustained over a range of habitats. Plant community of the past (paleocommunity) is an inferred vegetation unit based on the fossil plant assemblages confined to a certain facies domain.

Syngenesis: a historical development of biotic communities ("coenogenesis" should not be used in this sense as a primarily embryological term).

Taphoflora: all fossil plant assemblages occurring in a sedimentary basin.

Classification of plant paleocommunities is based on dominant species that define a general aspect (physiognomy) of the community. Names of reconstructed communities are derived from the roots of generic names of the dominant species by adding suffixes -*etum* for the basic units and -*ion* for the higher rank units. Their formal correspondence to the names of, respectively, associations and unions of the modern phytosociological classification does not implicate correspondence of classification criteria and scopes. It is just a practically convenient nomenclature applied for formalized descriptions of reconstructed syntaxonomic units. Such descriptions should contain diagnoses of new syntaxa and information on their type localities.

The dominance-based paleocommunities usually correspond to the higher units than basic associations of the modern syntaxonomy that are based not so on dominants as on determinants, i.e., species characteristic of certain habitats, although not necessarily frequent there. As a rule, more detailed reconstructions are achievable for proximal paleocommunities, while for the distal vegetation there is generalized evidenc at most.

The influx of plant material to a deposition site controlled by tectonic, geomorphological and climat conditions in the sedimentary basin. These condition determine the proportions of autochtonous (hypoa tochtonous) and allochtonous components in a taph flora as a whole, as well as in the basic FPA that ma reflect more than one natural association.

A reconstruction of plant paleocommunities star with a survey of basic FPS's and their facial occu rences. A FPS can be considered as a sample of veget tion within the radii of about 150 m for macroscop plant remains and about 500 m for pollen grains (the estimates are averages of those obtained in a number studies by comparing subfossil leaf and pollen spect with their source vegetation, reviewed in Krassilo 1972a). Naturally, the quantitative structure of FI reflects mostly a composition of proximal commun ties, their dominants prevailing in most spectra inspi of the possible taphonomic biases. Numerical represe tation of distal communities depends on both the dep sition and transportation environments. Due to the la ter, the distal dominants can be preserved either abundant or as rare fossils. In any case, a FPS is r more than raw material for the reconstruction of pale community that should be based on a comparative ana ysis of a series of contemporaneous, as well as succe sive, FPS's.

Dominants of reconstructed plant communities a recognized not only by their numerical prevalence in fossil plant spectrum, but also by their frequencies in series of spectra. These two values are combined in tl importance value:

$$Iv = D + P = \frac{100di}{M} + \frac{100pi}{M},$$

where D is relative dominance, P is relative frequenc di is the number of FPS's dominated by species i, pi the number of FPA's containing species i, and M is tl total number of assemblages involved in the plant con munity analysis. Due to their larger P, dominants regional communities are, as a rule, marked off by higher importance value than the occasionally prevai ing dominants of local proximal communities (se Krassilov, 1979 for an example of paleoecologic analysis using the importance value).

Of great importance for the reconstruction of extin vegetation as a system of paleocommunities are tl data on the dynamical relations of the latter within sedimentary basin. In particular, a paleosuccession the regressive stratigraphic sequences that reflect build-up of plant communities following the retreat the coastal line gives an idea of a sere, as exemplifie by the regressive paleosuccessions in the Donets Basi Bureya, Sakhalin and other regions (see Krassilo 1972a, 1972b, 1979, 1984). At the same time, the dist (allochtonous) components might change their relativ

frequencies in a series of successive FPA's reflecting a shift of catenic communities on the slope of the sedimentary basin.

Such observations provide evidence of secular vegetational changes constituting a clisere. Syngenetic processes are then reconstructed on the basis of cliseres involving paleocommunities that replaced each other within a facies domain. In this type of reconstruction, a syngenetic continuity of successive plant communities is substantiated by the following criteria:

—the persistence of certain adaptive features (in particular, xeromorphic characters of leaves, stomata, etc.) through a succession of plant communities composed of different plant taxa;

—the confinement of successive communities to a particular facies domain;

—the phylogenetic links between the successive dominant species;

—the persistent plant taxa that survived from one of the successive communities to the other, usually changing their phytosociological status; in particular, the survival of a former dominant form as a relic form of a derived community (see examples below).

CONIFEROID-PELTASPERM COMMUNITIES

In the Paleozoic paleobotany and palynology, the FPA's are traditionally divided into the hydrophytic lowland and meso(xero)phytic upland types. The former usually include the FPA's of ferns, lycopods, and sphenopsids, while the latter comprise cordaites, pteridosperms, and conifers. The assignments to upland communities is based primarily on the xeromorphic aspect of Paleozoic seed plants, especially the peltasperms and coniferoids. The latter group includes not only early conifers, but also some similar in the leafy shoot morphology, although phylogenetically distant forms. A traditional placing of all the fossils with scale-leaves or needles to conifers is unfounded, for such leaves occur also in pteridosperms, cordaites, gnetophytes, and perhaps other gymnosperm groups.

The increase of peltasperms and coniferoids in the Permian is usually conceived of as evidence of aridity on a global scale and especially in the mid-latitudinal Euramerian and Subangarian paleofloristic provinces. Widespread in the latter was the Late Permian *Tatarina* Flora and the corresponding *Vittatina* PA's of taeniate pollen grains. It is known that taeniate pollen was produced by xeromorphic peltasperms and conifers. Therefore, such pollen is also considered as an indicator of a relatively dry climate. Although these ideas are firmly embedded in palynological thinking, they seem in need of a radical revision. The following considerations seem pertinent to the habitats of the supposed xerophilic communities.

(1) The cordaites were of at least two ecological types: the hydrophilic Cordaixylon with adventitious roots (Rothwell and Wagner, 1984) and the relatively mesophytic Mesoxylon lacking adventitious roots (Trivett and Rothwell, 1985). The latter, judging by their coal-ball occurrences, might also belong to the waterside or proximal flood plain communities. Both had the *Cordaites*-type leaves that in the hydrophilic group showed more xeromorphic microstructural features than those of the mesophytic group. Still more xeromorphic were the externally similar *Rufloria*-type leaves produced by the vojnovskialean gymnosperms, a dominant group in the late Paleozoic flora of Siberia and the Urals. Characteristic of some *Rufloria* species are such xeromorphic microstructural characters as the sunken stomatal grooves (Meyen, 1966). In the Kuznetsk Basin, large accumulations of *Rufloria* leaves are usually confined to coal-bearing facies, while in the Fore-Urals they are dominant in the shallow water marine facies (Naugolnykh, 1996).

(2) The walchiacean coniferoids are traditionally assigned to conifers, although they are closer to the hydrophilic cordaites in the morphology of reproductive structures, including the fairly similar prepollen grains that set them apart from the true conifers. Since the hydrophilic cordaites had heteroblastic shoots with needle-leaves in the proximal zone, the walchians can be considered as a xeromorphic version of the latter, with the needles produced all over the shoot system. In both the walchians and hydrophilic cordaites, xeromorphism relates to helophyte or littoral adaptations rather than to aridity.

(3) Recent studies of the Permian coniferoids from Alpine localities (Clements-Westerhof, 1987; Kerp, 1996) have shown that their mass occurrences are confined to marine carbonate deposits suggesting coastal or littoral habitats. Taphonomically these assemblages are similar to the mass occurrences of brachphyllous coniferoids characteristic of the same facies domain through the Mesozoic (see below).

(4) The peltasperm-dominated FPA's are found in the coal-bearing or calcareous littoral facies, often as mass accumulations of compressions or dispersed cuticles. One such locality occurs in the marly clay lense above the major coal seam of the Bogoslovskoye Coal Field in the eastern Urals (Prynada, 1940; Vladimirovich, 1965; Krassilov, 1995). Compressions of *Scytophyllum vulgare* (Pl. 1, Figs. 5 and 6) constitute about 80% of the FPS. Compressions are preserved under an estuarine regime with anoxic conditions in the near-bottom zone. Mass accumulations of dispersed cuticles are sometimes interpreted as allochtonous, representing a distal plant community. However, fragmentation of plant material might be caused by redeposition in a tidal environment rather than by long-distance transport. Such plant remains could be both allochtonous and hypoautochtonous, with a prevalence of the latter in the mass occurrences. Since "estuarine regime" with inflowing deep waters and outflowing surface waters (Berger, 1970) excludes a considerable influx of terrigenous material brought in by rivers, a long-distance

transport is improbable, whereas the source peltasperm vegetations might grow at or near the site of deposition.

(5) Taeniate pollen grains of three different morphotypes were recently found in the gut compressions of three species of Permian insects (Rasnitsyn and Krassilov, 1996a, 1996b). Large well preserved hypoperlid and grylloblattid insects where neither long-distance fliers, nor could they withstand long-distance transportation intact. These insects might conceivably feed in the proximal coniferoid-peltaspem communities.

Data on the plant–insect interaction in the Permian give some support to a hypothesis ascribing taeniate structures in the pollen grains produced by gymnosperms of different taxonomic orders to horizontal transfer of the gene controlling this peculiar exinal character. Insects feeding on these pollen might transfer microorganisms that transduced genetic material (by analogy with the insects spreading viral plant disease in extant plant communities). The taeniate structures were thought to correlate with arid conditions because of their supposed volume regulating (harmomegathy) function. However, harmomegathy is no less important in a slow and irregular pollen transfer by unspecialized insect vectors irrespective of climatic conditions.

BENNETTITE-BRACHYPHYLL COMMUNITIES

Peltasperms still played a dominant role in the early Mesozoic xeromorphic communities (e.g., in the Triassic of the Urals, see above). They declined in the Jurassic, with the glandular axes and small thickly cutinized pinnae of *Pachypteris* alone still widespread, although never dominant, components of the late Mesozoic mid-latitudinal taphofloras. Harris (1964) pointed out that *Pachypteris* preferentially occurred in shallow water marine or estuarine facies. He suggested a reconstruction of *Pachypteris* as a littoral, perhaps mangrove, shrub or small tree. This genus, thus, links the Permian–Triassic coniferoid-peltasperm communities with their replacing Mesozoic xeromorphic communities. The latter are typically dominated by scale-leaved coniferoid plants assigned to the shoot genera *Brachyphyllum, Pagiophyllum, Cheirolepis, Pseudofrenelopsis*, etc. They constitute a morphological group of brachyphylls including conifers of different families (the Voltziaceae, Araucariaceae, Taxodiaceae, etc.), as well as the superficially similar Hirmerellaceae. The latter have been previously assigned to conifers, but their winged cupules and peculiar rimulate pollen grains (*Classopollis*) suggest a gnetalean affinity (Krassilov, 1982b). The similarity of leaf characters in brachyphylls from different taxonomic groups might be due to a widespread leaf convergence characteristic of xeromorphous vegetation in general.

The ecological significance of *Classopollis* is a matter of general concern. Vakhrameev (1981) considered this pollen type as an indicator of a dry climate. Other authors related *Classopollis* to halophytic or psammo-phytic habitats (Watson, 1982). Recent studies have shown that at the time of major transgresssions the *Classopollis*-dominated assemblages have spread as far north as the Yamal Peninsula occurring mostly in marine facies (Rovnina, 1996). The in situ preserved vertical stems of the *Classopollis*-producing brachy phylls (Francis, 1983) give direct evidence of their coastal–littoral habitats. An increase of *Clossopolli* frequencies with transition from continental to marin facies was repeatedly observed in palynological stud ies. On the sum of the evidence, Classopollietum i here interpreted as a coastal–littoral community with diversity of helophilic and calciphilic adaptations, pe haps penetrating inland along alluvial or lacustrine we land corridors.

A waterside habitat of the bennettite-brachyphy communities is further confirmed by anatomical stru tures of their constituent plants, such as aerenchym tous tissue in the mesophyll, with the stomata deep sunken in it (Pl. 1, Figs. 3 and 4) in a xeromorphic be netite *Otozamites lacustris* from the Lower Cretaceo of Mongolia (Krassilov, 1982a). Some bennettites a brachyphylls show anatomical features associated wi C4 photosynthesis perhaps related to high atmospher carbon dioxide concentrations.

Similarity of the Paleozoic and Mesozoic xeromo phic communities is manifested also in their produci the most advanced pollen morphologies of the respe tive geological periods, i.e., the taeniate pollen grains the Paleozoic and the rimulate *Classopollis* poll grains in the Mesozoic. Both morphotypes were fou in the gut contents of large pollinivorous insects. In t case of *Classopollis* the insects were katydids of t dominant Jurassic genus *Aboilus* (Rasnitsyn a Krassilov, 1996b). In addition, cuticles of brachyp lous plants were also found in the intestines of a lea eating insect from the Jurassic Karatau entomofauna Kazakhstan. For the same taphonomic reasons th were given above for the Permian pollinivorous insec these findings testify to the proximity of the brach phyll communities to the deposition sites of the respe tive FPA's.

The morphology of reproductive structures sugge phyllogenetic relatedness of some Mesozoic brach phylls to their precursory Paleozoic coniferoids. In p ticular, a Permian genus *Majonica* is similar to *Hirm ella*, a dominant Mesozoic brachyphyll genus (Cleme Westerhof and van Kohijnenburg-van Cittert, 198 The endostriate girdle of *Classopollis* may indicate t pollen type derivation from one of the late Paleozoic–ea Mesozoic striate (taeniate) morphotypes.

These comparisons, alongside with the ecotoj correspondence, may suggest a syngenetic continu of the Paleozoic and Mesozoic xeromorphic commu ties. A gradual autochtonous replacement of the cor eroid-peltasperm communities by their derived benn tite-brachyphyll communities was accomplished to t

end of the Triassic Period. The community restructuring was manifested primarily in the replacement of dominant species belonging to different taxonomic groups, but of similar life form aspects. The Mesozoic dominant types might derive from subordinate, perhaps the pioneer or seral, components of the Paleozoic communities, but much more paleoecological work has to be done until such relationships can be established with a certain degree of confidence.

BRACHYPHYLLION EXPANSION AT THE JURASSIC–CRETACEOUS BOUNDARY

Paleoecological analysis of Mesozoic FPA's (the procedures of which are briefly outlined above) has shown that in the Middle and Late Jurassic the bennettite-brachyphyll communities prevailed on sea coasts, as well as in the inland wetlands, behind the fern marshes or forming with the latter a mosaic of wetland communities. Incidentally, in the regressive sequences of the Talynjanskaya Formation in the upper reaches of the Bureya River, as well as in the Kamenskaya Formation in the northwestern periphery of the Donets Basin, the upper horizons of the shallow marine deposits of retreating seas contain abundant fern remains, mostly *Dicksonia*, that are replaced upsection by the brachyphyll-dominated FPA's of Elatidetum association (a variety of the Brachyphyllion) containing diverse bennettites. In the Kamenskaya localities, the leaf accumulations of a bennettite *Ptilophyllum pecten* occur in the gypsiferous clayey facies of the littoral domain. The subsequent seral stages are represented by Phoenicopsietum in the Bureya Basin and by Ginkgo-Phoenicopsietum in the Donets Basin (Krassilov, 1972a, 1972b).

A radical restructuring occurred at the Jurassic–Cretaceous boundary. The changes were most spectacular in central Asia where the basinal paleocatenae lost their proximal fern marsh members that were replaced by the bennettite-brachypyll communities. In the Mesozoic sections of western and central Gobi (Mongolia) the fern–brachyphyll replacement even serves as a stratigraphic criterion of the Jurassic–Cretaceous boundary (Krassilov, 1982a). Fern marshes were simultaneously reduced in Central and Western Europe and elsewhere. However, xeromorphic coastal fern growths with *Weichselia* still played a considerable role in the European Wealden. The least significant were the corresponding vegetational events across the Jurassic–Cretaceous boundary in the temperate zone of northern Asia where fern marshes maintained their position in the Cretaceous, with the dominant replacements at the species level alone (Vakhrameev and Kotova, 1980).

## THE MID-CRETACEOUS RESTRUCTURING OF XEROMORPHIC COMMUNITIES

A radical restructuring of xeromorphic communities took place in the mid-Cretaceous time. The bennettites and brachyphylls have lost their dominant status surviving as subordinate components of the Late Cretaceous communities of a similar xeromorphic aspect and represented by FPA's of the same facies domain. Their replacing dominants were sclerophyllous angiosperms of the *Debeya–Dryophyllum* group characterized by the narrow entire or deeply dissected to compound palmate and transitional coriaceous leaf blades, thick cuticles, sparse deeply sunken stomata with peristomatal rings, and other xeromorphic microstructures (Pl. 1, Figs. 1 and 2). They are morphologically related to such early appearing morphotypes as *Sapindopsis* and suggesting a possibility of autochtonous derivation from angiosperm components of the Early Cretaceous xeromorphic communities.

Typical for this type of communities are FPA'x coming from the mid-Cenomanian marine carbonate deposits of northern Crimea (Krassilov, 1984) where the small-leaved sclerophyllous angiosperms associate with still numerous brachyphylls and occasional peltasperms of an early Mesozoic aspect. Such FPA's are widespread in the Late Cretaceous of Western Europe. They correlate with PA's dominated by *Normapolles* group pollen grains that were conceivably produced by some dryophylls or other representatives of Dryophyllum communities. Such xeromorphic FPA's are relatively rare in the intracontinental areas of northern Asia. However their frequencies increase again towards the Pacific border. Large accumulations of dispersed cuticles mostly belonging to a xeromorphic angiosperm species *Debeya pachyderma* are found in the shallow marine Senonian deposits on the eastern coast of the Tatar Strait (Krassilov, 1979). Leaf fragments and cuticles of this or closely related species occur in the early Paleocene island arc volcanoclastic deposits of the Lesser Kuril Islands (Krassilov *et al.*, 1987). Debeyo-Dryophylletum retained its position of a widespread community type through the Paleogene of the Gelindenian Floristic Province (as defined by Kryshtofovich, 1955).

What is known of the mid-Cretaceous restructuring of xeromorphic plant communities appears compatible with the general syngenetic scheme of ecosystem evolution by cutting-off the climax phase by environmental impacts that truncate seral sequences at some early or transitional phases (Krassilov, 1992). As a consequence, the climax species are driven to extinction or are reduced to a subordinate status as in the case of the Late Cretaceous brachyphylls. A new climax phase is formed of the pioneer and seral species (proangiosperms and early angiosperms in the case of the bennettite-brachyphyll communities). High rates of morphological evolution are characteristic of such species at the time of the community restructuring, while their diversity rapidly increases, as in the explosive evolution of the mid-Cretaceous angiosperms.

Truncation of seral sequences responsible for the wholesale restructuring of vegetation in the mid-Cretaceous time can be, in the most general form, ascribed to

Plate 1
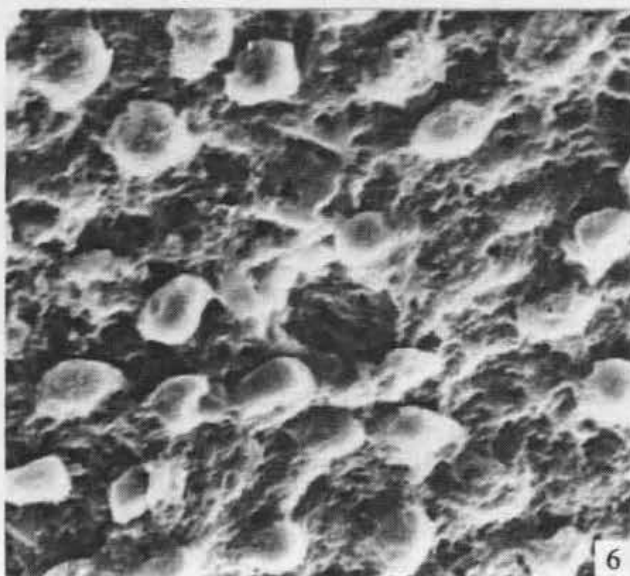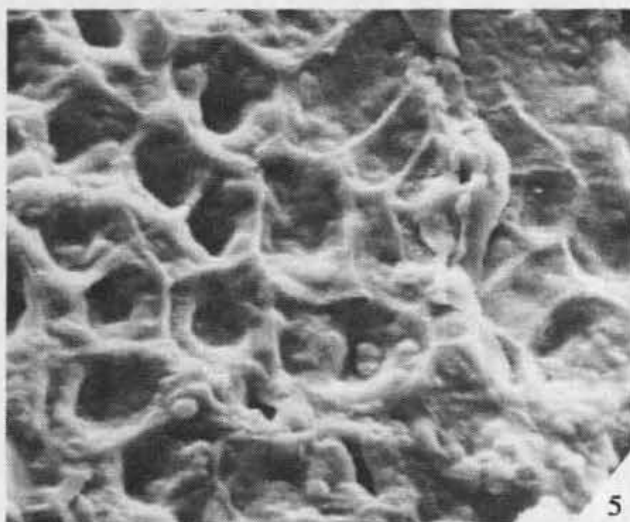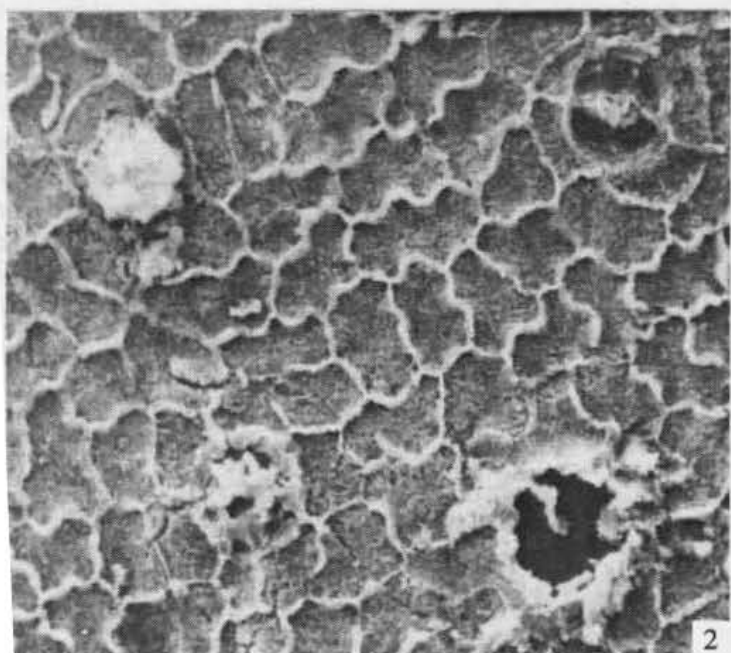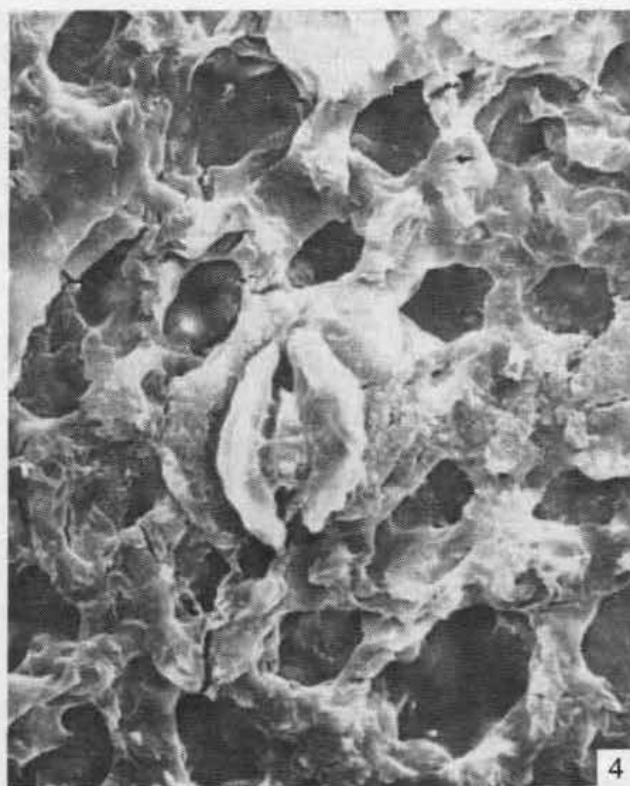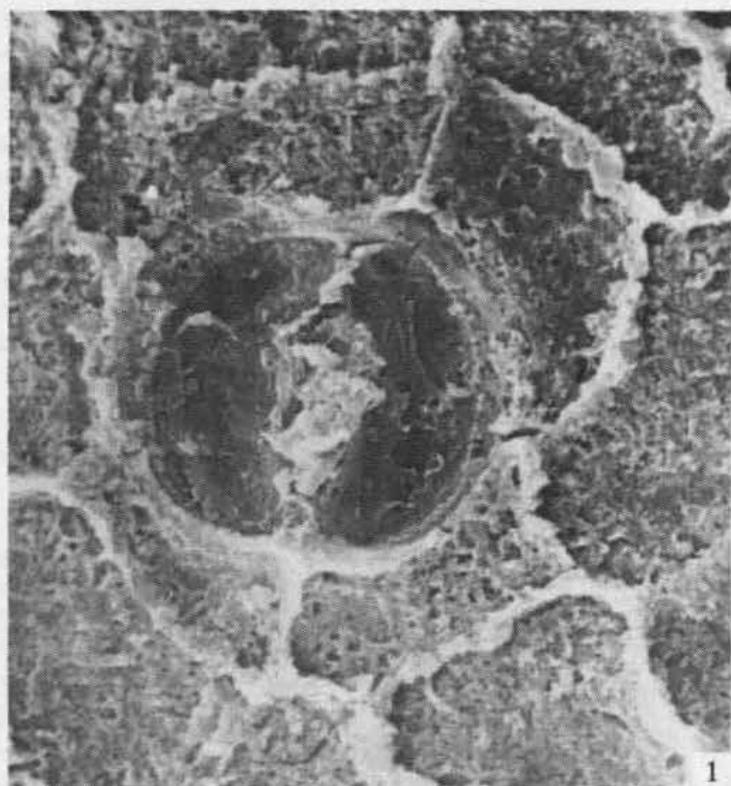
he multiple environmental impacts in turn related to he global tectono-magmatic events of the Austro-lpine folding phase that affected major fold belts at bout the Albian–Cenomanian boundary, and the associated submergence of cratonic areas (Krassilov, 1985). A more direct correlation occurs between the major egetational and volcanic events. Thus, the replacement of xeromorphic communities through the Paleozoic–Mesozoic transition on continents was associated ith the Siberian Trap magmatic phase. The Jurassic-Cretaceous boundary vegetational changes in central Asia were accompanied by the appearance of one of the world's largest basaltic provinces in northern Mongolia nd adjacent countries. Eventually, the mid-Cretaceous estructuring corresponded to the emergence of the iant circum-Pacific volcanic belt. Such large-scale olcanic events might have many-sided environmental onsequences affecting vegetation either directly or idirectly, by their associated climatic events. Devastating disturbances could be caused by acid rains following massive discharges of volcanic gases. It is well nown that conifer forests and wetland communities re most sensitive to acid rains. Indirect evidence of eir effects comes from the mass mortality of aquatic isect larvae, fishes and other pH-sensitive organisms overing bedding planes of the finely laminated lacustine deposits at the Baisian and other Early Cretaceous calities in the Transbaikalian segment of the Mongolo-Okhotian rift system. In several cases (studied by .V. Bugdaeva) a massive deposition of volcanic material actually correlates with a long-time persistence of arly seral phases, such as Czekanowskietum represented by the *Czekanowskia*-dominated FPA in the rassic Shadoron Series.

The restructuring of plant communities has evidently affected terrestrial insects and vertebrates. The cline of bennettites might have caused extinctions nong their insect symbionts part of which, notably etles, may have switched to early angiosperms. As a insequence, the latter acquired the solitary cantharoilous flowers of many parts that appeared not earlier an the Cenomanian. At the same time, the replacement of the sparsely branched large-leaved bennettites the copiously branched small-leaved early igiosperms might increase the total shoot mass at the pense of the total leaf mass (Krassilov, 1981). These anges required an adaptive response on the part of rge herbivores, and, in fact, there was a replacement the dominant herbivorous dinosaur groups, the forms

with new dental morphologies appearing in the mid-Cretaceous time.

AROGENIC SIGNIFICANCE OF XEROMORPHIC COMMUNITIES

Macroevolutionary significance of xeromorphic communities is implied by the great evolutionary potentials of their dominant groups, such as peltasperms that gave rise to the Czekanowskiales, Nilssoniales and perhaps other widespread Mesozoic gymnosperms. The bennettites and gnetophytes might derive from trigonocarpalean pteridosperms that, judging by their coal-ball occurrences, might also belong in the xeromorphic wetland communities. Even a more important role in terrestrial ecosystem evolution was played by the Mesozoic xeromorphic communities that included diverse proangiosperms—plants showing typical angiosperm characters but yet not fully angiospermous. A number of adaptive features, such as glochidia, pappose dispersal structures, as in *Problematospermum* (Krassilov, 1973), etc., have appeared in the xeromorphic communities. These morphological innovations forecasted the advent of the angiosperms.

The experimental nature of xeromorphic communities as laboratories of plant evolution can be exemplified by the Early Cretaceous bennettite-brachyphyll assemblages of Transbaikalia and Mongolia. First angiosperms appeared there in the Late Hauterivian–Early Barremian, that is considerably earlier than in other vegetational types (Vakhrameev and Kotova, 1977; Krassilov, 1982a). They were accompanied by diverse proangiosperms, such as *Baisia, Eoantha, Graminophyllum*, etc., their remains often occurring in the same plant-beds (Krassilov and Bugdaeva, 1982 and in press; Krassilov, 1986). The appearance of angiosperms was not, thus, an occasional event, but was rather an outcome of parallel development involving the whole community of proangiospermous plants representing different taxonomic groups. Such communities deserve to be designated as type-forming, or arogenic (by analogy with arogenic populations: Sinskaya, 1948) for in them new types of plants have emerged as a product of parallel evolution.

Chronologically the appearance of angiosperms correlates with expansion of the bennettite-brachyphyll communities that replaced fern marshes at the Jurassic–Cretaceous boundary in the vast territories of central Asia and other parts of the world (see above). The pro-

Explanation of Plate 1

Figs. 1 and 2. *Debeya* cf. *pachyderma* Krassil., a xeromorphic angiosperm from the Early Paleocene of Yurii Island, the sser Kuril Islands: stoma and epidermal topography with stomata and trichomes, SEM, ×1000 (1) and 250 (2).

Figs. 3 and 4. *Otozamites lacustris* Krassil., a xeromorphic bennettite from the Early Cretaceous of Mongolia: stomatal ne and stoma sunken in aerenchymous mesophyll, SEM, ×450 (3) and 1000 (4).

Figs. 5 and 6. *Scytophyllum vulgare* (Pryn.) Dobrusk., from the Late Triassic of the Eastern Urals: stomata sunken in mes-hyll and papillate cuticle, SEM, ×400.

See taxonomic descriptions in (Krassilov, 1982a, 1995, Krassilov *et al.*, 1987).

cess of ecological expansion might promote pioneer adaptations that enabled xeromorphic communities to colonize new habitats. Both the first angiosperms and their accompanying proangiosperms were represented in the xeromorphic communities by herbaceous or small woody forms in which the pollen and seed productivity was greatly enhanced (e.g., in the case of *Classopollis* pollen grains or the bristled cupules of *Baisia*) relative to their reduced vegetative sphere. Developmental acceleration was conceivably a leading factor of their evolution in turn related to unstable environments and pioneer adaptations. Remarkably, the most productive localities of proangiosperm and early angiosperm FPA's came from lacustrine deposits of rift valleys of the major rift zones traversing Transbaikalia, Mongolia, northwestern China, southern Australia (the Koonwarra Fossil Bed), and other regions within the broad ecotone between the xeromorphic and mesophytic vegetation.

PHYTOGEOGRAPHICAL SIGNIFICANCE

The Mesozoic temperate deciduous forest zone is well marked by both morphological and taphonomic indications of deciduousness, in particular by accumulations of leafy dwarf shoots and leaf mats. This zone, with Phoenicopsis as a leading plant formation, occupied northern regions of Eurasia and North America. Its southern boundary occurred at about 50°N in Asia ascending to 60°N in Europe. To the south, there was a broad zone of evergreen (or winter-green) vegetation of entirely different life forms, such as the pachycaul *Cycadeoidea* (Krassilov, 1972c and elsewhere). Since the latitudinal temperature gradient was then much lower than at present, this boundary was conceivably controlled not so by the temperature differences as by the seasonality of precipitation.

In the Mesozoic, precipitation patterns might have been considerably different from those of the glacial climate. The present day pattern of a tropical humid zone and its bordering dry zones relates to a rapid cooling of the ascending equatorial air masses shedding rain over the tropics. Cool air descending on the periphery of the equatorial zone absorbs water vapor thus causing subtropical arid zones. In the warm ice-free climate, the ascending air masses cooled much slower retaining water vapor until they reached extratropical latitudes that, consequently, received more precipitation than the equatorial zone. Therefore, a typical precipitation pattern of the ice-free climate consisted of a dry equatorial zone and its bordering relatively humid subtropical zones with the prevalence of winter precipitation.

Spatial distribution of Mesozoic plant communities agrees with the latter pattern. To the very end of the Cretaceous Period, there was no fossil evidence of tropical rain forests, whereas xeromorphic communities spread over the tropical and subtropical areas, deeply penetrating the temperate humid zones along the routes

opened by marine transgression. The subtropical zo experienced large fluctuations of annual precipitati as indicated by sedimentary criteria. Characteristic this zone were the widespread red-bed accumulatio and carbonate lacustrine facies. In the Jurassic, massi salt deposition took place in the areas covered with x omorphic vegetation, whereas in the Cretaceous t salt-bearing deposits were locally replaced by the co bearing facies testifying to relatively high precipitatio At the same time, the richest xeromorphic assemblag were always confined to the lagoonal–lacustrine cal reous facies that never extended beyond the range xeromorphic vegetation.

Distribution of the xeromorphic coastal–littor communities may explain the sharpness of the Mes zoic subtropical to temperate zonal boundary (in co trast to the nearly homogeneous vegetation within t vast expanses of these zones), with more promine xeromorphism to the south of the boundary. Penetratio of xeromorphic communities in the temperate zone w controlled by marine transgression, seasonality of pr cipitation and, indirectly, by the global temperatu changes.

CONCLUSIONS

In this paper, I have attempted an analysis of syng netic processes involving xeromorphic communiti that underwent several major restructurings in the tin span of several geological periods. The successive xe omorphic coniferoid-peltasperm, bennettite-brach phyll, and debeyo-dryophyll communities of the Pe mian–Triassic, Late Mesozoic and the Late Cret ceous–Paleogene respectively have replaced each oth within the coastal–littoral domain. Contrary to t widely held views, a spread of xeromorphic commun ties might not necessarily indicate dry climate, for the xeromorphism was primarily related to helophyti psammophytic and calciphilic adaptations. At the sam time, widespread xeromorphism might indicate mo phological adaptation to elevated atmospheric carbo dioxide concentrations that are associated with a lo stomatal index (as in xeromorphous *Debeya pach derma*) and anatomical features of C4 photosynthesis

Syngenetic restructurings of xeromorphic commu nities were caused by environmental impacts, primaril the large-scale volcanic activity at about the Permian Triassic, Jurassic–Cretaceous, and the Early–Late Cr taceous boundaries. Environmental impacts truncate seral sequences at some early stages of their develop ment thus cutting off the climax phase and endangerin the climax dominants. Their niches were then filled b surviving species of the pioneer and successiona phases that underwent morphological restructurings i the process. This scheme relates to the appearance o xeromorphic angiosperm communities replacing th bennettite-brachyphyll communities in the mid-Creta ceous time.

Xeromorphic communities comprised the most advanced plant groups of their time. They served as experimental laboratories for new methods of plant dispersal and they cradled the dominant Mesozoic gymnosperms, as well as the angiosperms. The latter appeared in association with diverse proangiosperms that evolved in parallel in the direction of angiospermy. For xeromorphic communities direct evidence was obtained of the plant–insect interaction that played a significant role in the build-up of biological diversity.

Phytogeographically, the xeromorphic communities were confined to the broad zone of prevailing summer-dry climate that, in the warm ice-free epochs, extended in the Northern Hemisphere from the equator to 50°–60°N. Shifts of this boundary may indicate global climatic changes. Further analysis will trace the development of Cenozoic xeromorphic communities to the modern types of sclerophyllous vegetation.

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