MODELS OF PLANT AND PLANT COMMUNITY EVOLUTION: CRETACEOUS-PALEOCENE TRANSITION EXAMPLES

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Abstract: Vegetational changes at or close to the K/T boundary are related to the models of (1) sea level - CO_2 - biotic productivity feedback; (2) climax cutoff; (3) diversity-redundancy correlation; and (4) epicrisis macropolymorphism. Major K/T vegetational events caused the decline and fall of the dominant Cretaceous redwood-laurophyll forest and the fern marsh communities and then the appearance of progenitorial Arcto-Tertiary broad-leaved forests. The transitional stage shows a mosaic of the Cretaceous-type and Paleocene-type communities. Dominant plant taxa of this stage are characterized by extreme polymorphism and unusual combination of morphological traits. The low recovery rates of species diversity are due to the "fine-grained" population strategies of the epicrisis that encourage high rank macroevolutionary events rather than speciation.

Key words: Cretaceous - Paleocene transition; plant evolution; plant community evolution; models.

Изменения растительности на границе мела и палеогена или вблизи нее соотнесены с моделями (1) колебаний уровня моря – CO_2 – биологической продуктивности, (2) снятия климаксной фазы, (3) корреляции разнообразия и избыточности и (4) эпикризисного полиморфизма. Основными событиями мел-палеогенового рубежа были упадок доминирующих меловых сообществ – редвуда с лавролистными двудольными и папоротниковых маршей – и первое появление широколиственных лесов арктотретичного облика. На переходной стадии существовала мозаика сообществ мелового и палеогенового типов. Доминирующим видам этой стадии свойственны исключительно высокий полиморфизм и необычные сочетания признаков. Низкие темпы восстановления разнообразия связаны с тем, что "тонкозернистая" стратегия переживших кризис видов скорее способствовала макроэволюционным скачкам, чем дроблению видов.

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The K/T crisis, whatever the causes, is generally held to be one of the most severe in geological history. As such it provides a testing ground for ecosystem evolution models. Fortu-

nately, the simplistic approaches based on the asteroid impact hypothesis seem to have lost the attraction they had a few years ago, thereby clearing the way to a more comprehensive ecosystem analysis. The ecosystem evolution theory seeks to explain the interrelationship of physical environmental changes and biotic events. The following models seem pertinent to the K/T events (see also Krassilov 1978, 1992a, b):

1. Sea Level -CO_2 - Biotic Productivity Feedback

In addition to its role in regulation of global temperatures, atmospheric CO_2 concentration is a factor of biotic productivity, conceivably providing a feedback between eustatic events and ecosystem evolution according to the following scheme:

(1) Transgression reduces the area of terrestrial biota (as much as 40% globally in the Late Cretaceous) by expanding the area of marine biota. However, since productivity of the latter is negligible in comparison with the former, the overall biotic production decreases.

(2) Since biotic production is a major sink of atmospheric CO_2, concentration of the latter increases with transgression.

(3) Inasmuch as terrestrial biotic productivity is directly correlated with atmospheric CO_2 concentration, there should be a direct correlation with transgression also; a concomitant increase of marine productivity would result from a larger influx of nutrients from the continent due to the increase of chemical weathering in a greenhouse climate.

(4) Regression would reverse 1, thereby causing the reversal of 2 and 3. A decrease of biotic productivity in the lower trophic level would affect the superimposed levels, driving them to extinction.

This scheme is supported by the planktonic boom associated with the mid-Cretaceous transgressions, the enormous accumulation of oil and gas as well as coal in the Cretaceous transgressive epochs, the gigantism of Cretaceous terrestrial vertebrates, and the end-Cretaceous extinctions concomitant with the global regression.

2. Climax Cutoff Model

Resilience of an arboreal plant community depends on its pioneer and successional species filling gaps or windows caused by natural mortality of climax trees or catastrophic environmental impacts. However, under prolonged environmental stresses, succession can be truncated at a pioneer or transitional stage, never reaching the former climax. In effect, the climax species would find themselves at a disadvantage, and some or all of them would eventually perish. A new climax will be formed by the pioneer or successional species which undergo major evolutionary changes in the process, setting out new trends of adaptive radiation.

This is the climax cutoff model (Krassilov 1992a, b) which implies that major vegetational changes are induced by long-term environmental impacts rather than by occasional catastrophes, and that morphological evolution is guided by phytocoenotic evolution.

3. Diversity-Redundancy Correlation

Species diversity is a function of available resources divided by the mean niche overlap and the mean effective population density. Both the latter variables tend to decrease with ecosystem evolution, thereby enhancing diversity. However, the effective population density (that is, one sufficient for sustainable reproduction) correlates negatively with environmental stability (the less stable the environment the larger should be a redundant component buffering population from devastating environmental impacts). Redundancy thus underlies the diversity-stability correlation. The model predicts a dramatic increase of population densities in crisis survivors with concomitantly decreasing diversity.

4. Epicrisis Polymorphism

In undersaturated epicrisis communities the survivor populations tend to increase the polymorphism of the characters normally subjected to a strong stabilizing selection. The release of the latter allows the populations to reveal a full range of their genetic potentials manifested in macropolymorphic populations that might form a source of subsequent adaptive radiation.

The following analysis is based on monographic studies of several Cretaceous and Paleocene floras (Krassilov 1976, 1979, 1984; Krassilov et al. 1988; Krassilov and Makulbekov, this issue) and reconstructions of plant communities and climatic trends (Krassilov 1973, 1975, 1981). I have suggested that the K/T boundary as well as other prominent boundaries in the fossil record are of stratoecotonal character, the stratigraphic scope of stratoecotones depending on the abruptness of the change as well as on completeness of the record. The K/T stratoecotone was restricted to the lowermost Paleocene, or early Danian, thus a very narrow time span for the restructuring of the terrestrial ecosystems of a few hundred thousand years, not of the time scale of an asteroid impact (that is, a few hundred years at most). A cooling trend starting in Maastrichtian and culminating at the K/T boundary seemed to have been a major factor of vegetational change. The latter appeared more conspicuous at the communal than at the specific level. Progenitorial Arcto-Tertiary broad-leaved deciduous forests became dominant plant formation. They might have developed in several Early Paleocene florogenetic centers and advanced much south of the Cretaceous summergreen/evergreen zone boundary.

In this paper, further phytosociological considerations support the above suggestions. Previously I recommended a formal description of fossil plant communities with types and diagnosis, but the informal one would also suffice for the purposes of the present discussion. The basic unit of paleophytosociological analysis is a single layer or a single bedding-plane assemblage. Recurrent assemblages of similar taxonomic composition and relative species frequencies constitute an assemblage type supposedly reflecting a contemporaneous biotic community. Proximal and distant communities are inferred on the basis of autochthonous and allochthonous components.

THE K/T BOUNDARY

Chronostratigraphic boundaries are currently conceived of as time surfaces defined by nominal spikes on their type sections. In the K/T boundary this concept was strengthened by the discovery of an iridium anomaly forming the physically perceptible spikes in a number of sections. However, the notion of their synchroneity is based on the single-impact hypothesis alone. If there

were multiple sources of iridium, such as cosmic bombardment and/or volcanism, then the spikes might not be necessarily synchronous. Actually, some boundary sections contain more than one iridium spike.

A broader concept of the boundary is adopted here. It is defined as the time interval of the concentration of the earth crust and biosphere reshaping events such as regression (with climatic and biotic effects postulated by the sea level - CO_2 - biotic productivity model above); large-scale accretion in the Tethys-Himalayas and circum-Pacific belts (including the emergence of island arcs, such as the Lesser Kuril Islands discussed later); transition from ignimbritic to basaltoid volcanism in the marginal Pacific volcanic belt, Deccan traps, etc.; and magnetic and geochemical (e.g., iridium) signatures of cosmic impacts and/or mantle upwellings (Krassilov 1985). In marine sediments the boundary is, as a rule, lithologically distinct as a result of the dramatic rise of the carbonate compensation level resulting in the widespread hardgrounds and metallic clay horizons formed in anoxic environments. In terrestrial sections are multiple hiatuses and condensed clayey tuffaceous horizons with iridium concentrated in diagenetic spherules.

Biotic signatures of the boundary are here conceived of as low diversity monodominant assemblages of highly polymorphic species comprising few relics of the typical Cretaceous dominant groups. There could be a number of successive horizons containing this type of assemblages summarily defining the boundary.

In plant macrofossil assemblages, additional control is provided by spore-pollen and faunistic assemblages, notably from marine intercalations. In the following examples, spore-pollen control was regularly implemented. In the Tsagajan Formation of Amur Province the floristic boundary is drawn above major dinosaur beds, although some dinosaur bones, perhaps redeposited, were found above it. In Sikhote Alin' it corresponds to a switch from a compressional to a tensional tectonic regime and the related changes of igneous activity. In Sakhalin the boundary occurs above the marine Maastrichtian, within continental section grading laterally into the transitional and lowermost Paleocene marine deposits. In the Lesser Kurils, the boundary layer is a turbidite with marine fauna and terrestrial plant remains.

THE K/T PLANT EXTINCTIONS

There could be a long list of species binomials not transcending the K/T boundary. But, insofar as paleobotanical species are very conventional and as many of the more strictly defined species are known from a single or few localities only, such lists have little meaning. Less biased comparisons could be made between regional floras studied by one researcher. The latter condition seems important insofar as very different species numbers were given by different researchers for the same flora (e.g., Kryshtofovich and Krassilov for the Tsagajan flora). In the examples given later in the paper, the regional Lower Paleocene floras with no more than 50 species each are typically 20% less diverse than their preceding Cretaceous floras. There might be quite a few disappearances among dominant taxa, such as *Parataxodium* ("*Cephalotaxopsis*"), although most of them (notably *Sequoia*) have lost their dominant status.

Remarkably, a few relics of the typical Mesozoic flora, such as *Bennettites* and *Czekanowskia*, vanishingly rare in early Senonian, reappeared as Lazarus species in the Late Maastrichtian. The boundary-layer plant assemblage of the Boshnyakovian Section in Sakhalin looks pretty "Mesozoic" with *Pterophyllum* and *Cycadites* (see below). Such assemblages are known also in the

far northeast (Krassilov et al. 1988). However, of the Mesozoic cycadophytes, *Nilssonia* alone is widespread in boundary sections. In Sakhalin it was used as a guide fossil for separation of Cretaceous coal-bearing strata from the Paleocene, but it could occasionally transcend the boundary, as in the Boshnyakovian Section. Generally, taxonomic changes across the boundary seem subordinate to the phytosociological ones.

LATE CRETACEOUS PLANT COMMUNITIES

Typical Late Cretaceous communities have been inferred from the repeated occurrences of certain assemblage types in the Late Cretaceous of Sakhalin (Krassilov 1979). Comparisons with the Crimean assemblages studied by the author (Krassilov 1981) as well as the survey of collections from Kazakhstan, Mongolia, Bohemia, etc. showed these types to be of at least continent-wide extent, though regional dominant species could be different. In the northern midlatitudes there were:

(1) Redwood-laurophyllous communities dominated by *Sequoia* or *Geinitzia* with *Cupressinocladus* (of *Chamaecyparis* type), *Protophyllocladus* and *Araucarites* as subdominants, and with *Laurophyllum, Araliaephyllum, Magnoliaephyllum, Liriophyllum*, and other laurophylls as well as *Debeya, Trochodendroides*, and a few platanophylls, the latter numerically increasing northwards. This type assemblages came primarily from coal-bearing deposits (fig. 1). Their source communities seem to have been dominant in the flood-plain and delta-plain environments.

(2) Redwood-platanophyllous communities dominated by *Parataxodium* ("*Cephalotaxopsis*") and broad-leaved hardwoods with platanoid leaf morphologies. They seem to substitute type 1 in northeast Asia and Alaska, while in Sakhalin they became conspicuous in the terminal Maastrichtian. The dominant conifers left masses of leafy shoots suggesting deciduousness.

(3) Fern-platanophyllous communities commonly represented by abundant platanoid leaves forming leaf mats in levee facies in association with cyatheoid (conventionally described as gleichenioid) fern fronds and scattered conifer twigs. These might be riparian woodlands and were the earliest terrestrial communities dominated by angiosperms. They may have caused a widespread notion of angiosperm dominance in the Late Cretaceous, although their actual role might have been greatly exaggerated by their overrepresentation in fluviatile facies.

(4) Fern and fern-nilssonialean marshes. These merge with type 3 but with far fewer platanophylls and tending to occur in the vicinity of coal seams in the levee and oxbow as well as tidal flat facies. Fern marshes were ubiquitous through the Mesozoic, but in the Late Cretaceous they lost most of their formerly dominant *Coniopteris* species, substituted by the *Anemia* ("*Asplenium*") *dicsoniana-Cladophlebis frigida* association.

(5) Aquatic communities. These are characterized by Krassilov and Makulbekov in the present issue.

(6) Slope shrublands. This is a hypothetical type of Cretaceous communities inferred on the basis of the angiosperm wood remains, mostly representing shrubs or small trees and such occasionally predominant fragmentary xerophytic leaves with a thick cuticle as *Debeya pachyderma* (Krassilov 1979). More evidence is to be expected from dispersed cuticle and fossil wood studies.
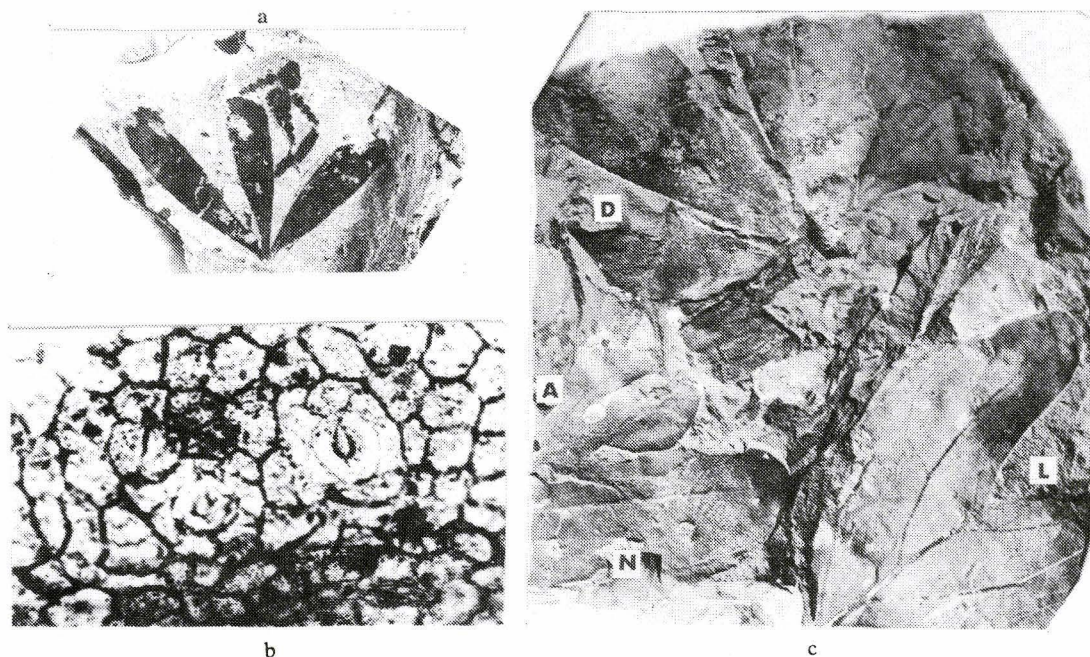
Fig. 1. Angiosperms of the Late Cretaceous redwood-laurophyll assemblage (Krassilov 1979): *a*, *b* - *Debeya*, leaf and cuticle, ×395; *c* - slab association of *Debeya* (D), *Sassafras*-like *Araliaephyllum* (A), *Liriophyllum* (L) and *Nilssonia* (N).

EARLY PALEOCENE PLANT ASSEMBLAGES

Vegetational types seemed to have been more prominently differentiated according to the basin types in the Paleocene than in the Cretaceous. Four major basin types are distinguished in the area between the Far Eastern cratonic massifs and the Pacific coast (Krassilov 1991): (1) inland intractonal basins, including the Zeya-Bureyan Basin of Amur Province; (2) intermontane depressions of the marginal Okhotsk-Chukotka volcanic belt; (3) miogeosyncline foredeep of the marginal volcanic belt extending from western Kamchatka to the western Sakhalin Mountains and central Honshu; and (4) island arc belt of eastern Kamchatka, eastern Sakhalin and the Lesser Kuril Islands (fig. 2). The Early Paleocene plant localities occur in each of these environments, representing different types of contemporaneous vegetation.

TSAGAJAN INLAND ASSEMBLAGES

Tsagajan Formation of the Zeya-Buryan Basin consists of conglomerates, sands, sand-stones, and shales containing large dinosaur localities in the lower coarse-grained member. In the dinosaur beds have recently been found a diverse Maastrichtian spore-pollen assemblage and
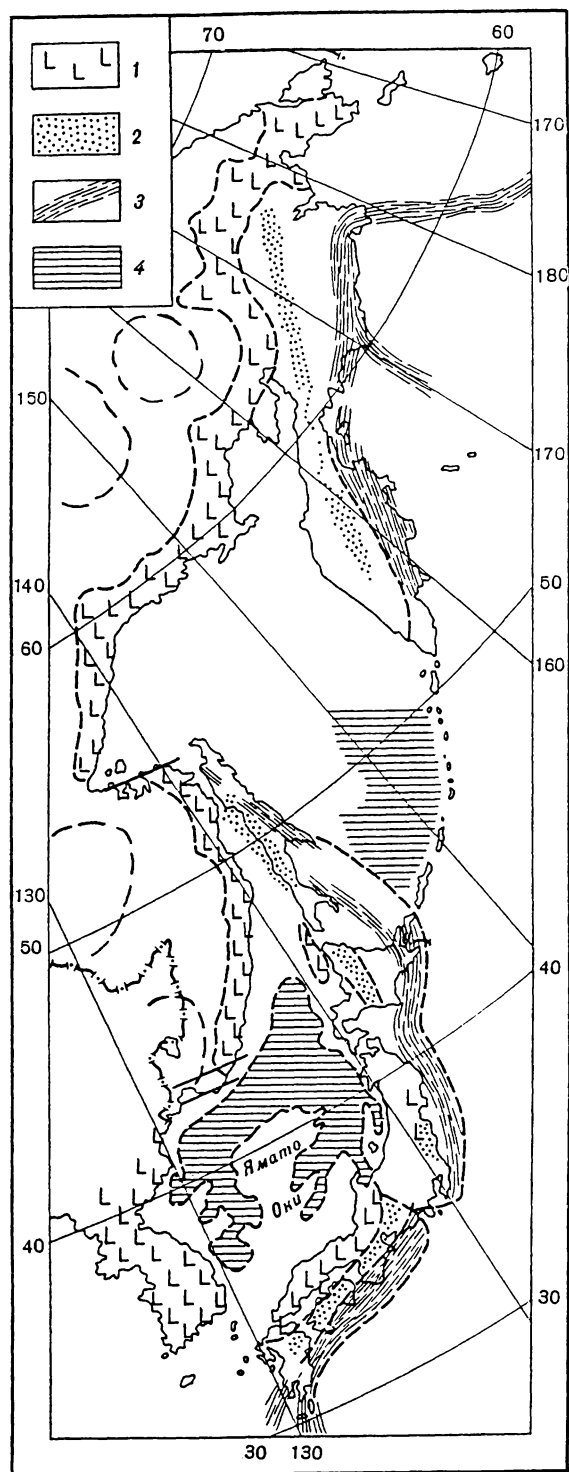
Fig. 2. Tectonic belts of the western North Pacific coast: 1 - terrestrial volcanic belt; 2 - foredeep; 3 - island arc-trench system; 4 - putative spreading areas.

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Fig. 3. *Tiliaephyllum* leaf mat from the Lower Paleocene of Tsagajan locality representing ripari
woodlands.

a fern-platanophyll assemblage with occasional *Czekanowskia* (Markevich et al. 1994) con
to the silty levee sandstones.

In the Upper Tsagajan above the dinosaur beds are 23 plant beds, most belonging i
two types of sedimentary facies: (1) levee facies of laminated puff-pastry light coarse-graine
dark silty sandstones with leaf mats, and (2) gravely to conglomeratic debris flow de
comprising lenticular oxbow silts with root horizons. A conspicuous feature of this taphofl
the predominance—about 60%—of plant beds with single or few species.

Type 1 plant assemblages represent riparian vegetation dominated by *Trochodendı*
leaves accompanied by twigs with spur-shoots, *Trochodendrocarpus* panicles and *Troch*
drospermum seeds. These, on the evidence of repeated association, are attributed to the
plant—supposedly a small to medium-sized deciduous tree with aspen-like polymorphic l
on both the long and short shoots and large inflorescences emerging from the crown as in e
Aralia. Subordinate to *Trochodendroides* in these localities are typically much larger, t
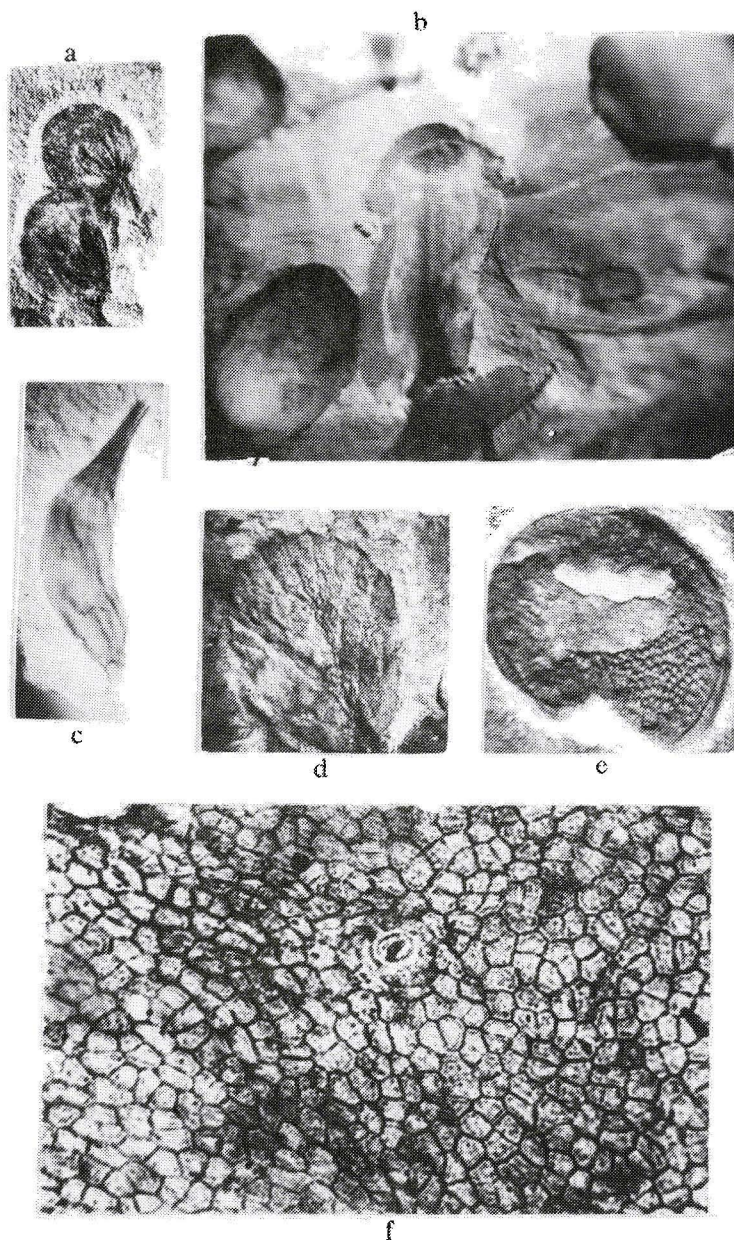
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Fig. 4. Lower Paleocene Tsagajan aquatic assemblage: *a* - *Hydrocharis*; *b* - arilloid seeds; Nymphaeaceae; *c* - *Carex*, ×2; *d* - *Quereuxia*, an extinct nymphaeoid plant, ×3; *e, f* - *Limnobiophyllum*, aroid genus, floating leaf, ×3, and cuticle, ×195.

larger, but of variable size, guilder roselike leaves belonging to one of the three similar but distinct morpho-types, *Viburniphyllum, Grewiopsis,* or *Tiliaephyllum* (fig. 3), normally not occurring together in a single plant bed. They might represent deciduous shrubby plants forming a patchy single species shrub stratum under a uniform single-species tree cover of a two-story riverside hardwood community.

A single type 1 locality contains *Protophyllum* and *Gleichenites*, a residual Cretaceous fernplatanophyll community which might conceivably survive as a singular patch of riparian vegetation. The coarser levee facies contain abundant plant debris but determinable drifted plant remains are infrequent. Notable among the latter are occasional *Ginkgo* leaves and dispersed leaf cuticles as well as the thick scale-leaves of *Araucarites pojarkovae* Krassil.

Type 2 assemblages are obviously heterogeneous and separable into at least four distinct subtypes:

(*2a*) Aquatic angiosperm community of *Potamogeton, Hydrocharis, Limnobiophyllum, Nuphar, Nymphaeites, Nelumbo,* and *Quereuxia* (fig. 4). It is much more diverse than any of the Cretaceous precursors consisting mostly of nymphaeoid dicotyledons. A distinctive feature of this community is the appearance of aquatic herbs belonging to both extinct (*Limnobiophyllum,* Araceae) and extant monocot genera. Notably, the geological time-scale succession of the Early Cretaceous aquatic moss-fern assemblages, Late Cretaceous nymphaeoids, and Paleocene herbs is reiterated in the present-day ecological succession of oligotrophic to eutrophic lacustrine macrophyte communities.

(*2b*) Waterside or semiaquatic herb community, including the ill-defined *"Arundo"* and *"Phragmites"* morphotypes as well as *Carex*-type fruits. Though the generic assignments of grass fossils may indicate the life form rather than taxonomic affinities, a primeval grass-sedge community replaces the Mesozoic-type fern-horsetail marshes still widespread in the Cretaceous. This could be a modest beginning of grasslands evolving from hydrophytic to mesophytic and xerophytic types.

Fig. 5. *Taxodium* and *Nyssa* from the Lower Paleocene Tsagajan oxbow clays representing a swamp cypress-gum-tree community (Krassilov 1976).

(2c) *Taxodium - Nyssa - Myrica - Nordenskioldia* swamp forest community. The flood-plain lobe, silty clay lens assemblages are invariably dominated by *Taxodium* (leafy twigs, pollen cone bearing shoots, seed cones) which, together with the gum-tree (fig. 5) and bogmyrtle fruits, represents an early example of an exceptionally longeval community that survived through all the stages of Arcto-Tertiary floristic evolution up to the present. *Nordenskioldia*, a putative climber with a long drooping fruiting axes making a distinctive fossil of the type 2 localities, was shed from the swamp forest community in Miocene time (Manchester et al. 1991).

(2d) Upslope mixed woodland. This problematic community is represented in the type 2 localities by occasional samaras, cone scales, fragmentary leaves, and *Ginkgo* leaf cuticles, which are preservationally different from the dominant fossils of the 2c assemblage. Insofar as the fossiliferous lenses are imbedded in the bottom-slope debris flow deposits, the drifted plant remains might represent upslope vegetation of a single or more than one altitudinal belts. The considerable thickness of the debris flow deposits make this upslope vegetation probably woodland rather than closed forest. Conifers are fairly diverse (if actually coming from a single community), comprising both "northern" (*Metasequoia, Sequoia, Cupressinocladus, Pseudolarix, Pinus*) and "southern" (*Araucarites, Podocarpus*) genera. (Actually, they might grow in successive belts rather than side by side, whereas the subsequent elimination of the "southern" group might result from deletion of the respective belt, but this is mere conjecture at the moment.)

While the conifer component is essentially Mesozoic, the hardwood genera *Alnus, Cyclocarya, Papilionaceophyllum*, and *Celtis* testify to a rapid modernization of the mixed conifer-broad-leaved communities, which evolved at much higher rates in the uplands than in the lowlands. Altitudinal segregation of archaic and advanced genera might have been sharper in the Early Paleocene than in any other age.

SIKHOTE-ALIN' INTERMONTANE DEPRESSION ASSEMBLAGES

The Okhotsk-Chukotka coastal ranges emerged in mid-Cretaceous time as a result of granitization and volcanic buildup over the earlier Mesozoic island arc-trench structures napped upon the continental margin. The Cretaceous sequence of liparitic and andesitic volcanites ends with the exceptionally thick ignimbrites of the terminal Maastrichtian *Woodehousia fimbriata-Ulmoideipites krempii* palynozone (Markevich 1994). Slumped liparitic tuffs of this age contain a diverse, though fragmentary, conifer assemblage including *Sequoia, Glyptostrobus, Cupressinocladus, Androvettia, Pseudotsuga*, and *Pseudolarix* as well as fern pinnules and angiosperm detritus. Notable among the latter are wind-borne trilobed bracts of *Betula lacinibracteata* Krassil. and betuloid leaf fragments indicating proximity of a birch-dominated community. While the conifer assemblage might represent a slope belt analogous to the present-day Sikhote-Alin' montane taiga, it is conceivable that allochthonous birch remains came from a different altitudinal belt comparable with the present-day Sikhote-Alin' stone birch, *B. ermanni*, woodland occurring above the mixed cedar pine-broad-leaved forest.

At the K/T boundary the tectonic regime had changed from compressional to tensional, and the volcanic belt was rifted along several transcurrent fault zones. The downfaulted intermontane depressions were filled with tuffaceous dark brown to black shaly deposits of stratified lakes with marginal debris flow accumulations and thin coals covered with basalts.

Shales contain rich localities of *Metasequoia-Pinus-* ulmoid-betuloid assemblages. A dominant species, *"Betula" pomoera* Krassil., is represented by abundant leaves with cuticles (Krassilov 1989a) and trilobed bracts occasionally preserved in dichasial clusters. Obviously, the source community occurred closer to the site of deposition than in the Late Maastrichtian, evidencing a downslope shift of altitudinal belts (fig. 6).
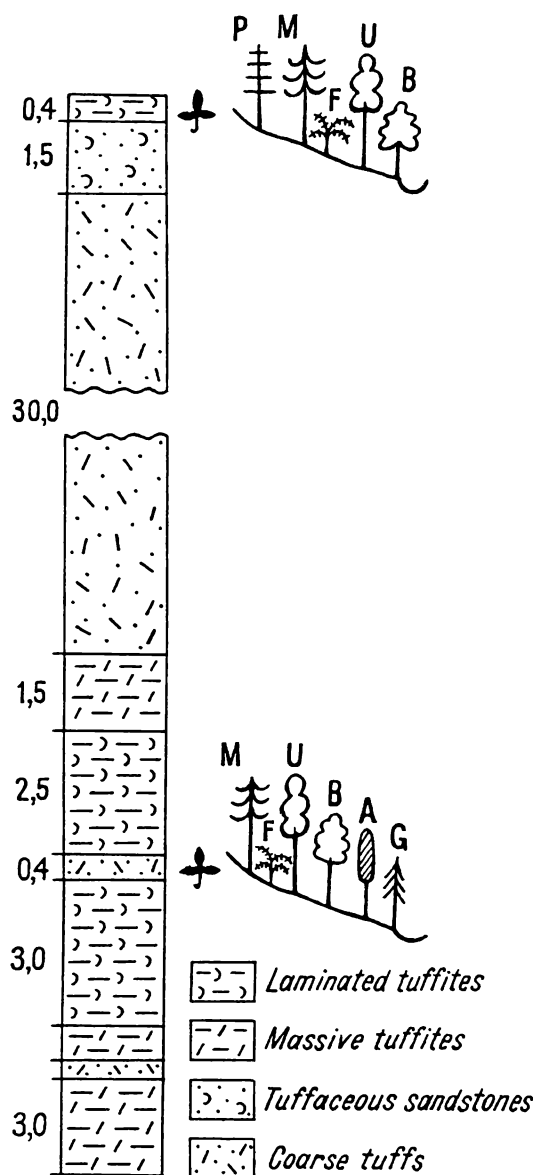

Fig. 6. Floristic change due to upland-lowland migration at about the K/T boundary in the Ustinovsky Section, Kavalerovo District, Sikhote-Alin': A - *Androvettia*, B - betuloids, F - ferns, G - *Glyptostrobus*, M - *Metasequoia*, P - *Pinus*, U - ulmoids.

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FOREDEEP ASSEMBLAGES

The foredeep of the Cretaceous Sikhote-Alin' volcanic belt extends as a trough filled with deltaic and marine turbiditic deposits along the Tatar Strait. Its eastern flank is uplifted as the western Sakhalin Ranges. The boundary between the predominantly deltaic and the predominantly flyschoid marine sedimentary provinces occurred at about 50° N, but shifted north and south with eustatic events producing intercalation of horizons with terrestrial and marine fossils.

Cretaceous plant species have been ranked according to their importance value (sum of their total frequencies and the frequencies as dominant elements) and assigned to three major types of terrestrial plant assemblages: (1) delta-plain and flood-plain fern—*Nilssonia* marshes with *Anemia dicksoniana* (Heer) Krassil., *Cladophlebis frigida* (Heer) Sew., and *Nilssonia* spp.; (2) platanoid-tree fern (*Cyathea sachalinensis*) stream border assemblages; and (3) marsh border conifer *Sequoia - Cupressinocladus - Protophyllocladus - Araucarites* forest with laurophylls, *Debeya* spp., *Liriophyllum sachalinense*, and *Trochodendroides sachalinensis* as undergrowth or pioneer species (Krassilov 1979).

Early Maastrichtian transgression flooded the delta plain, leaving shell beds with giant ammonites and inoceramids. Deltaic facies reappeared in the terminal Maastrichtian, above the *Pachydiscus gollevilensis* zone. The K/T boundary is unconformable throughout the basin, with thick conglomerates above, except at a few loci of continuous deposition. In the Augustovka River Section west of Boshnyakovo Village, the Late Maastrichtian coaly sandstones and shales contain both the marsh species *Cladophlebis frigida* and *Nilssonia gibbsii* and the riparian species *Cyathea sachalinensis* and *Protophyllum schmidtianum*. *Parataxodium* and *Trochodendroides arctica* are added to the typical assortment of Senonian taxa. The overlying coarse tuffaceous sandstones have an unusual assemblage of Paleocene species, *Glyptostrobus nordenskioldii* and *Trochodendroides arctica*, accompanied not only by *Nilssonia gibbsii* but also by relic cycadophytes *Pterophyllum* and *Cycadites*. It must be noted that cycadophytes and other Mesozoic relics (e.g., *Czekanowskia*) are more prominent in the Maastrichtian than in the preceding Late Cretaceous (see Krassilov et al. 1990, for Chukotka occurrences). This assemblage is interpreted as a mixture of material coming from different source communities. Coarse preservation of twigs and pinnate leaves oblique to the bedding planes suggest instantaneous deposition in a thick tempestite bed damming a distributary channel which developed as a lake or lagoon later on.

The overlying sequence of tuffs and tuffaceous shales about 200 m thick, with occasional coarse debris flow interbeds, contains 9 plant beds, including a 10 cm-thick root bed at the base. *Metasequoia occidentalis* (Newb.) Chaney and *Corylites protoinsignis* Krassil. dominate six of them, with *Ginkgo, Trochodendroides arctica* (Heer) Berry, *Alnites protoschmalhausenii* Krassil., *Liriophyllum sachalinense* Krysht., and *Macclintockia kanei* (Heer) Sew. as subdominants. A single fern bed—a 50 cm-thick coaly shale with *Woodwardia* and *Cladophlebis columbiana* Dawson—occurs in the lower part of the section. In addition, ferns and *Nilssonia gibbsii* are present as rare components in most of the plant beds. Thick conglomerates truncating the tuffaceous sequence contain a few sandy plant beds with typical Paleogene *Ulmus* dominated assemblages. To the south, the tuffaceous Boshnyakovian sequence is replaced by the marginal marine Sinegorskiy horizon with an Early Paleocene foraminifer assemblage (Kalyshevich et al. 1981).

Major vegetational change at the base of the tuffaceous sequence consists in the disappearance of the characteristic Cretaceous *Sequoia* and platanophyll-dominated communities (and a near disappearance of the fern marshes, residually represented by a single fern bed). A

few members of these communities, such as *Nilssonia* and *Liriophyllum*, have survived as subordinate components of the *Corylites*-dominated assemblage, giving it a transitional Cretaceous-Paleocene aspect. The abundance of *Corylites* throughout the tuffaceous sequence may suggest postfire pioneer growths on extensive clearings caused by volcanic eruptions (similar *Corylus* beds occur sporadically in the subsequent Tertiary volcanomictite). Conceivably, this early Paleocene community was halted at an early successional stage by incessant volcanic activity.

ISLAND ARC ASSEMBLAGE

The Lesser Kuril Islands north of Hokkaido are built of Maastrichtian inoceramid shell containing clastic flysch sequence piled upon thick lavobreccias, intruded with doleritic sills and covered with alkalic basalts showing pillow structures. On Yuriy Island these basalts are overlain with conglomerates and silty turbidites containing foraminifers, bivalves, sea urchins and plants (Krassilov et al. 1988). Both foraminifers and spore-pollen assemblages, studied by Serova and Markevich, indicate a transitional terminal Maastrichtian-lowermost Paleocene age correlative with the upper Nemuro Group of Hokkaido, Sinegorskiy Horizon of Sakhalin and the *Rzehakina epigona* zone of Kamchatka. The associated terrestrial plants may demonstrate emergence of the island arc after the accretion of submarine ridge-trench deposits and alkalic volcanism. Typically, turbidite deposition on island arc slopes starts several thousand years after emergence of the island. The overlying deposits are terrestrial basalts and breccias with silicified conifer wood.

The Yuriy Island turbidite assemblage reflects at least two catenic conifer belts: (1) *Sequoia reichenbachii-Cupressinocladus cretacea* lowland Cretaceous belt represented by numerous relatively well preserved shoots, and (2) *Picea-Pseudolarix-Androvettia-Amentotaxus* upland Paleocene belt represented by samaras, cone scales, and dispersed needles. Among angiosperms, *Corylites protoinsignis* is the only frequent leaf type supposedly representing a postfire growth, as in the Sakhalin localities (above). The remaining angiosperm morphophytes are either Cretaceous (*Debeya* cf. *pachyderma* Krassil.) or Paleocene (*Trochodendroides arctica* (Heer) Berry, *Viburniphyllum asperum* Newb., and *Menispermites katiae* Krassil. similar to *M. favosus* Krassil. from the Lower Paleocene of Sakhalin) affinities.

VEGETATIONAL CHANGES AND MORPHOLOGICAL EVOLUTION

The regional Early Paleocene (lower Danian) floras with — after taxonomic revision — no more than 50 well-defined species show a considerable, about 20%, decrease in taxonomic diversity in respect to their predecessor Cretaceous floras. In addition, most of the Early Paleocene plant localities are either single-species or few-species plant beds of which one or two species are, as a rule, extremely abundant. Thus, the decrease of diversity apparently correlates with the increase of population densities.

The subsequent rise of diversity occurred in the Middle and Late Paleocene. The low-diversity interval is here considered as transitional, or stratoecotonal, retaining such Cretaceous relics as *Nilssonia* and *Gleichenites* (and typically about 10% of *Aquilapollenites* and other Cretaceous palynotaxa). Furthermore, a unique feature of the Early Paleocene floras was the predominance of extinct hamamelids *Trochodendroides* and *Platanus*-like *Grewiopsis*, which extended well into the Eocene but were no longer as prominent as at the K/T boundary. Their assignment to the families based on extant plants is ambiguous, for they combined features of

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Fig. 7. *Nordenskioldia borealis* Heer, an extinct "synthetic" genus: *a-g* - opened calyptrae persistent on the inflorescence axis, ×3 and ×5; *h, l* - detached calyptra, ×3 and ×7; ×5; *i* - flowering axis bearing flower buds proximally and fruit distally; *j* - flower scar with persistent bract, ×5; *k* -bud with bract scars, magnified from *i*, (arrow) ×5; *m* - split fruit with fruitlets showing styles, ×5.

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more than one such families. A typical example is *Nordenskioldia* (fig. 7), superficially resembling *Trochodendron* but with solitary ovules and protruding floral axis, as in the Illiciaceae, and with calyptrae as in Winteraceae and other magnoliids.

At the phytosociological level, the above Early Paleocene assemblages show various stages of advancement from the slightly modified Cretaceous to the progenitorial Arcto-Tertiary vegetation. Major vegetational types were: (1) archaic fern marshes, residual in the foredeep localities; (2) archaic fern-platanophyll riparian communities, residual in the inland localities and elsewhere; (3) archaic *Sequoia-Cupressinocladus* delta-plain conifer forest, relic in the island arc locality; (4) transitional *Corylites* shrublands with *Nilssonia, Liriophyllum,* and other Cretaceous relics occurring in disturbed environments impacted by igneous activity; (5) riparian broad-leaved deciduous low-diversity community of primitive hamamelids, *Trochodendroides* and "*Platanus*"; (6) taxonomically diverse mixed conifer-broad-leaved upland forest with "northern" and "southern" (*Araucaria, Podocarpus*) conifers, Juglandaceae, Ulmaceae, etc.; (7) montane conifer *Picea-Pseudolarix* forest, and (8) montane protobirch woodland.

The two latter types are known from allochthonous localities or from downslope migrations. They might be more fully represented in the north where the Arcto-Tertiary precursors have appeared in the Late Maastrichtian (Golovneva 1994; Herman 1994).

In the Koryak Uplands in the northeast, a floristic change in the Late Maastrichtian is claimed to be even more pronounced than at the K/T boundary (see papers by Golovneva and Herman, this issue), this has yet to be confirmed by vegetation structure analysis. Moreover, in the case of the Koryak sections, stratigraphic resolution is scarcely enough to define how far from the K/T boundary the major change was.

Types 1 to 3 are little-modified survivors of the dominant Cretaceous plant communities. Fern marshes have been the most productive coal-producing plant formations through the Late Mesozoic. The platanophyll woodlands have been the earliest community type dominated by dicotlyledons. The Cretaceous redwood-laurophyllous communities 3 are considered to represent a lowland maritime climax of both the circum-Pacific and peri-Atlantic realms and are a source of the most diverse fossil plant assemblages.

The decrease of these plant formations at or close to the K/T boundary has brought about a major vegetational change and a substantial decrease of biotic productivity scarcely compensated by the appearing type 4 and 5 lowland communities. This is what is to be expected according to the sea level-productivity model (above). The stratoecotonal interval lacks any appreciable coal measures. Although coal accumulation resumed soon after the boundary event (e.g., Fort Union coals in North America or Kivda coals in Amur Province), it was far below the Cretaceous level.

Further changes might have been due to the Laramide orogenesis, greatly increasing differentiation of altitudinal belts in the course of which 6 and 7 might emerge as the newly formed types of montane vegetation.

Patch segregation of archaic and modernized communities in the flood-plain-delta-plain mosaics and even more distinct altitudinal segregation, with a tendency of downslope migration of altitudinal belts, showed a cooling trend. Critical for the archaic types 1-3 could be a more seasonal precipitation pattern and a lowering of ground-water table associated with regression.
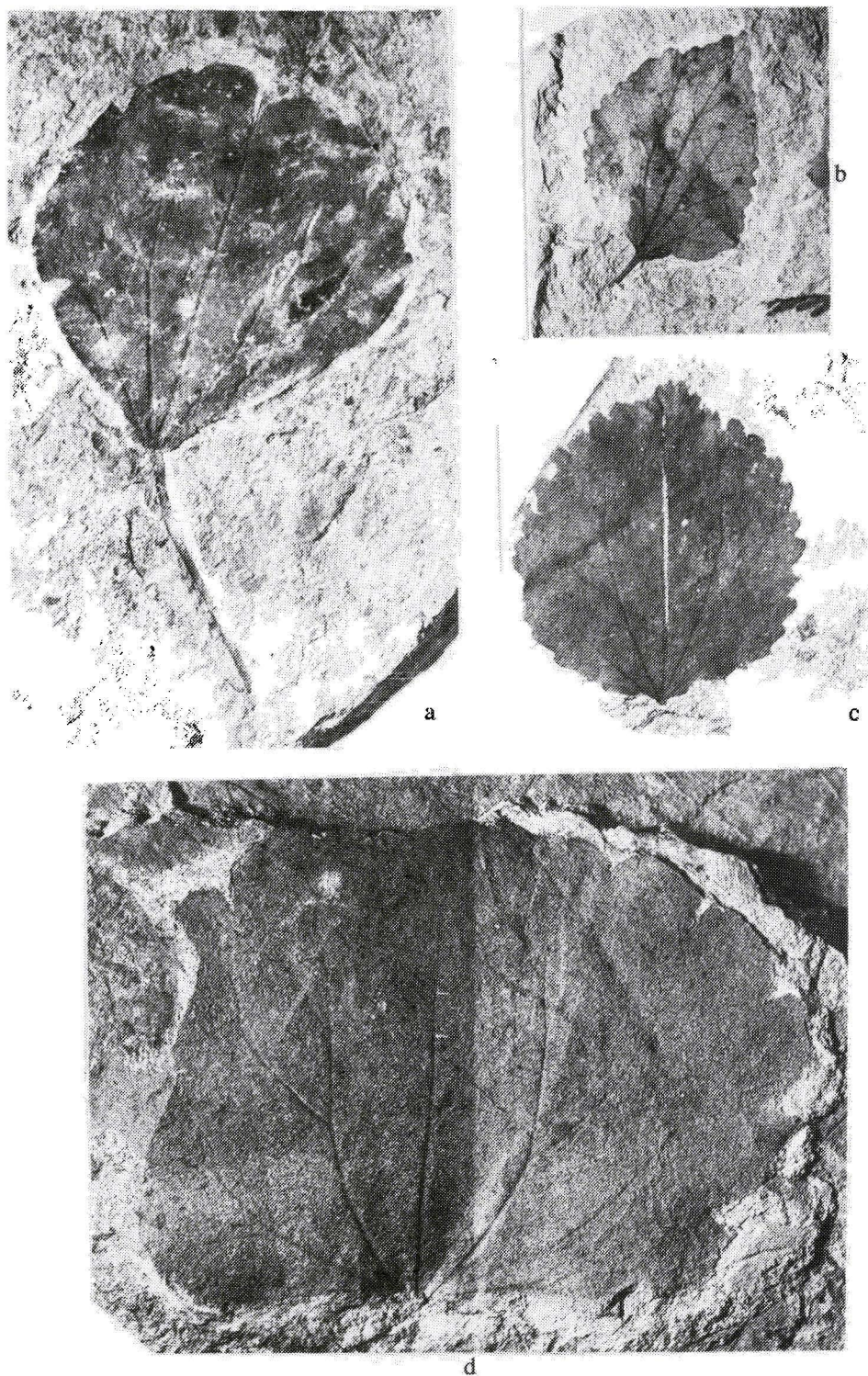
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Fig. 8. Leaf polymorphism in *Trochodendroides* from Tsagajan locality; *a - cuneata*, *b - speciosa*, *c - arctica*, *d - richardsonii* morphotypes.

Fig. 9. *Grewiopsis* ("*Platanus*") from Tsagajan locality, large protophylloid morphotype.

Type 4 provides an example of a halted successional community in stressed environments. However, because of the combined volcanic, eustatic, and climatic effects, all types of terrestrial environments were stressed at the K/T boundary (cosmic impacts could add to terrestrial stresses, but the simplistic model of vegetational change caused by a giant impact dust/fire can hardly account for the complexity of transition).
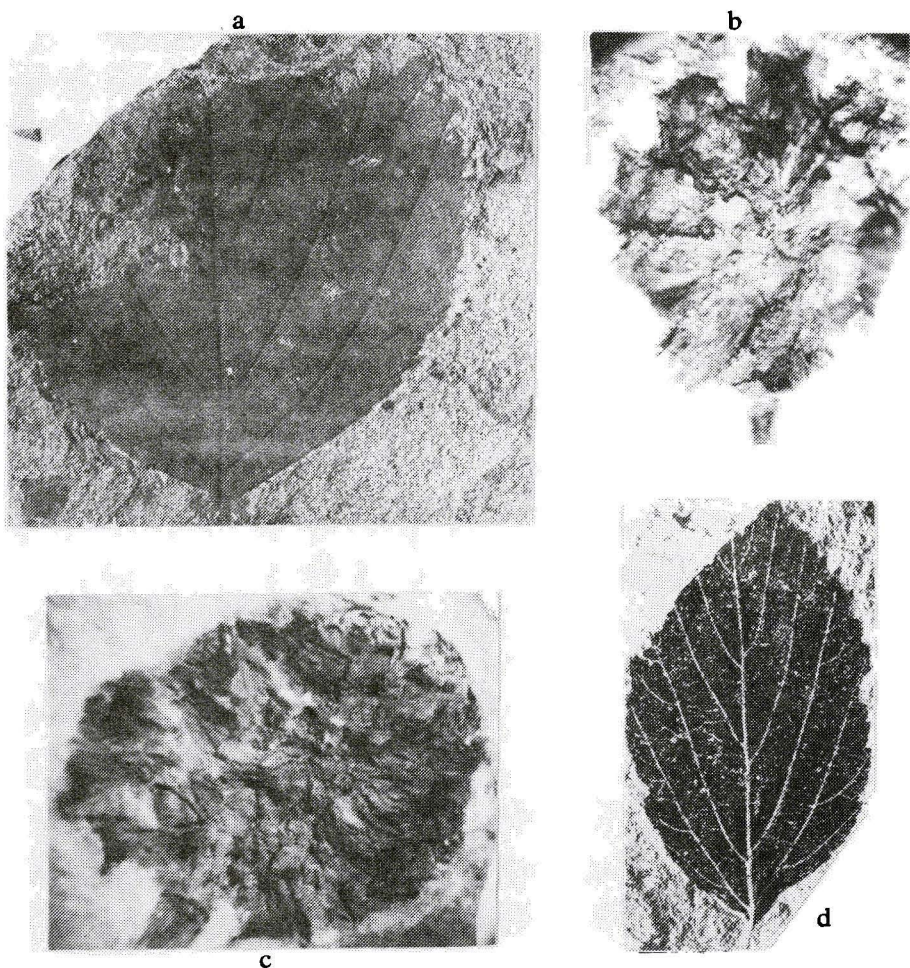
Fig. 10. *Grewiopsis* ("*Platanus*") and associated reproductive structures from Tsagajan; *a, d* - small alnoid morphotypes; *b* - *Tricolpopollianthus*, staminate head, ×7; *c* - *Steinhauera*, carpellate head, ×3.

Type 5 constitutes a core of the Early to Middle Paleocene floras of the Arcto-Tertiary realm extending to southern Mongolia (Makulbekov 1988). Its diversity was greatly exaggerated due to the extreme leaf polymorphism of dominant species (figs. 8-10). In the case of Tsagajan *Trochodendroides arctica* and "*Platanus*" *raynoldsii* I had to synonymize 23 and 16 previous identifications, respectively. At the same time I retained some of these identifications as nontaxonomic designations of distinct morphotypes. Thus, *T. arctica* includes morphotypes "*speciosa*," "*smilacifolia*," "*richardsonii*," "*genetrix*," etc. (such informal phenotype designations are widely used in genetics, e.g., "notch," "bobbed," "eyeless," etc., in *Drosophila melanogaster*). In this way, polymorphic leaf populations can be easily compared on the individual morphotype basis.

Actually, the polymorphism ranges are nearly the same in the contemporaneous Paleocene leaf populations but different in both Cretaceous and Eocene records. The Cretaceous precursors, such as *Prototrochodendroides*, typically had much smaller leaves, suggesting a herbaceous or shrubby habit.

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There was also a considerable increase in size and complexity of reproductive structures from the supposedly ancestral Mid-Cretaceous *Caspiocarpus* to the Early Paleocene *Trochodendrocarpus* (see Krassilov 1989b).

Another dominant species, *"Platanus" raynoldsii*, is also polymorphic, with *"credneriform"* morphotypes perhaps inherited from Cretaceous *Credneria*, in association with "alnoid" and "tilioid" morphotypes, variously described as *Grewiopsis, Alnites, Betulites, Pterospermites, Ficus, Quercus,* and recently *Ushia* (Boulter and Kvacek 1989; Kvacek et al. 1994). All the morphotypes have similar platanoid cuticular structures (Krassilov 1976). Their associated reproductive structures are *Tricolpopollianthus* staminate heads, *Steinhauera* carpellate heads, and *Carinalaspermum* seeds showing a mixture of platanoid-altingioid characters.

These are examples of macropolymorphism exceeding the typical range of intrageneric variation in woody plants. It is characteristic of species emerging as dominants of the newly formed undersaturated communities. These species might fill broad ecological niches revealing a full range of their genetic potentials in the process. Macropolymorphism forms a basis of subsequent adaptive radiation giving rise to the widely divergent higher taxa which retain a few characters of their founder morphotypes. Schematically, this is what might happen during the rapid phase of concomitant ecological and morphological evolution at the K/T boundary.

The low recovery rates noted by Frederiksen (1994) and related by him to the Rosenzweig-McCord (1991) model of speciation fostered by empty ecological niches, the Carr-Kitchell (1980) model of recovery hampered by low diversity, and the immigration dependence model (Barry et al. 1991) are, according to the present model, explained by the fine-grained adaptive strategy of epicrisis populations developing macropolymorphic structures as a basis of macroevolution but not easily splittable into well-defined species (Krassilov 1989c).

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