# CHANGES OF MESOZOIC VEGETATION AND THE EXTINCTION OF DINOSAURS

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## ABSTRACT

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The structure of Mesozoic vegetation is outlined as consisting of evergreen brachyphyllous forests, deciduous forests dominated by *Phoenicopsis* and then by *Parataxodium*, cycadophyte—sclerophyllous shrublands and fern marshes. Warm, warm-temperate and temperate zones are indicated for successive periods. Dinosaur localities are situated mostly in the warm and warm-temperate zones but a few of them fall in the temperate zone. Feeding habits of dinosaurs are inferred from combined evidence of depositional environments, surrounding vegetation and stomach contents. It is suggested that dinosaurs were associated mainly with open vegetation, such as shrublands and marshes, capable of supporting large populations of herbivores. The shrubland and marsh dinosaur communities are provisionally indicated, the latter comprising diplodocids, stegosaurs and hadrosaurids. Replacements of dinosaur communities were concomitant with major vegetational changes. Forestation at the end of Cretaceous time might have played an important role in the final extinction.

## INTRODUCTION

"We need not marvel at extinction; if we must marvel, let it be at our own presumption in imagining for a moment that we understand the many complex contingencies on which the existence of each species depends."
[Charles Darwin, *The Origin of Species.*]


Only a few introductory notes on the general causes of extinctions are needed because they have been discussed at length elsewhere (Krassilov, 1977a). Major extinctions, such as in Permian/Triassic or Cretaceous/Paleogene times affected many animal and plant taxa. Not only dinosaurs but also flying reptiles, marine reptiles, almost all Cretaceous marsupials, ammonites, innoceramids, rudistids and many less conspicuous groups of invertebrates, bennettites, nilssonialean and caytonialean plants, *Parataxodium* and *Protophyllocladus* among dominant conifers, most abundant foraminiferal and nannoplankton species disappeared at the end of Cretaceous time. Estimates

of diversity losses at the species level are hardly reliable. They are also not very instructive. What really matters is not how many species actually died out but how much the whole biota have changed. Extermination of *Homo sapiens* would amount to an ecologically meaningless figure of 0.0001% species loss. Major extinctions were not only the extinctions of many contemporaneous species but also, and more importantly, the extinctions of ecologically dominant species, those which gave a biota its aspect, the fittest organisms of their time.

Extinctions were not always preceded by gradual declines. The Campanian dinosaur fauna of Alberta was more diverse than any of the adequately studied earlier faunas (Béland and Russel, 1978). As a rule, major extinctions coincided with increased tectonic activity and climatic changes. Climax Laramid tectonism in the circum-Pacific and Alpine belts, as well as general cooling in the terminal Cretaceous (Krassilov, 1975), might have caused instability of many terrestrial and marine environments. This in turn would induce a simpler ecosystem structure, less efficient use of trophic resources, shifting $K/r$-selection pressures and diversity losses at the expense of the $K$-selected dominant species. With these general tendencies in the background, there were multiple direct causes of extinctions. Only one of them — the role of vegetational changes in dinosaur extinction — is considered in this paper.

Many authors have postulated some kind of causal relationship between vegetational changes and the extinction of dinosaurs. Because vegetational changes in the Cretaceous have been traditionally conceived as the rise of angiosperms at the expense of gymnosperms, it was suggested that angiosperms were either unpalatable or even poisonous to dinosaurs. Bakker (1978) tried to reverse this line of reasoning by arguing that dinosaurs caused the rise of angiosperms. He envisaged dinosaurs making clearings in the gymnosperm forest and the early angiosperms using these clearings according to their weedy habit (recently the "weedy" concept of early angiosperms has become widely appreciated in spite of the paucity of corroborative evidence). According to Béland and Russel (1978), the expansion of angiosperms provided an ecological basis for the Late Cretaceous radiation of ornithischian dinosaurs.

It has also been suggested that dinosaurs disturbed gymnosperm forests to such an extent that they became supersensitive to climatic fluctuations (Béland, 1976). Alternatively, the vegetational changes might have accelerated the competitive exclusion of dinosaurs by mammals. Because dinosaurs and mammals coexisted during 140 m.y., one can assume that they avoided direct competition by occupying different ecological niches. Van Valen and Sloan (1977) have viewed the mammal/dinosaur replacement as diffuse competition between two types of communities: the temperate forest with placentals and multituberculates (*Protungulatum* community) and the subtropical forest or savanna with dinosaurs, marsupials, multituberculates and insectivorans (*Triceratops* community). They have suggested that the placental mammals of the *Protungulatum* community descended from a common

ancestor which developed some kind of adaptation permitting more effective use of temperate forests. Dinosaurs might have been prevented from invading the temperate forests by trophic competition (but temperate forests are not effectively used by herbivores even now and the trophic competition is not intense there). The dietary explanation was claimed to be unlikely, because poisonous plants were more frequent in the tropical vegetation than in the temperate forest (this also can be related to the less effective exploitation of the latter). The infiltration and eventual replacement of subtropical vegetation by temperate forests might have forced dinosaur populations to shrink while the placental mammals diversified. A testable prediction of this hypothesis is that the extinction should have been delayed in tropical regions. At present, however, the latest dinosaur records are from Alberta, just above the level of the major vegetational change. Russel (1979) has provided the most comprehensive account of the latest dinosaur communities. He also has argued against dietary explanations of their extinction.

A SKETCH OF MESOZOIC VEGETATION

Early Triassic floras still contained plants of Paleozoic aspect, such as *Pleuromeia* or *Glossopteris*. Truly Mesozoic vegetation, dominated by conifers, cycadophytes and ginkgophytes, emerged in mid-Triassic time. Gradual replacements of dominant species occurred during the late Triassic, Jurassic, and Early Cretaceous, but the general structure of plant communities remained constant until the expansion of angiosperms at the expense of cycadophytes in Albian time. However, the Mesozoic genera of cycadophytes, ginkgophytes and conifers were not completely exterminated until the end of the Cretaceous. Species counts for the Triassic–Early Cretaceous floras of the U.S.S.R., comprising about half of the world's Mesozoic plant localities, will give an idea of the relative diversity of the major groups: bryophytes 22, lycopods 23, equisetaleans 98, ferns 673, pteridosperms 153, caytonialeans 20, bennettiles 291, nilssonialeans and other cycadophytes 315, ginkgophytes 231, czekanowskialeans 76, conifers 510, unassigned gymnosperms 96.

The taxonomy of some groups is debatable. Plants which produced *Classopollis* — a very peculiar and most ubiquitous Mesozoic pollen type — are conventionally placed among the conifers. However, they are distinct from normal conifers not only in their pollen grains but also in their ovuliferous organs which exhibit some angiospermous characteristics. *Nilssonia* and its allies, previously assigned to the Cycadales, differ from true cycads in both reproductive structures and general morphology of vegetative body. Their leaves were clustered on short shoots — a feature suggesting a growth form quite different from that of cycads with their thick and mostly unbranched stems. Some later representatives of the nilssonialean lineage had ovulate structures of the *Dirhopalostachys* type with the ovules enclosed in rostrate carpel-like capsules. I have included these plants in the proangiosperms — a

provisional group comprising also *Caytonia* and Czekanowskiales which had enclosed ovules and some stigma-like devices for pollination. Caytonialean plants with edible fruits (found in coprolites) were common but not dominant in many Laurasian and South American localities, while Czekanowskiales (*Czekanowskia*, *Phoenicopsis* and several other genera) were dominant in northern Asia.

The time of the first appearance of true angiosperms is uncertain. A few pollen grains with angiosperm-like exinal characteristics were reported from Barremian strata. However, similar exinal structures were described also in some Triassic pollen grains. Moreover, the distinctions between angiospermous and gymnospermous exinal structures became less clear with the progress of electron microscopic studies. A few megafossils were found in supposedly Neocomian strata of Central Asia (Lake Baykal region and Mongolia). In Aptian time angiosperms, though still rare, occurred on all continents at low and middle latitudes. Three spreading centres can be suggested: Central Asia, Central Atlantic coasts and southern Australia. Albian angiosperms were much more numerous and extended into high latitudes. The diversity of angiosperms increased steadily through the Late Cretaceous though it was considerably exaggerated by routine taxonomic treatments which ignored leaf polymorphisms. Angiosperms were subordinate to conifers in such typical Senonian floras as Mgachi in Sakhalin or Lance in North America. They probably have not achieved the status of forest-canopy trees until the terminal Cretaceous.

Life forms are well known for such Mesozoic plants as the *Cycadeoidea* whole stems of which are preserved, often in flowering state. However, in many cases they are reconstructions based on indirect evidence (Krassilov, 1972a). Discrepant interpretations of life forms, not to be discussed at length here, inevitably affect reconstructions of Mesozoic plant communities. However, at least two major vegetational types can be recognized beyond reasonable doubt. These are the evergreen brachyphyllous forests and deciduous *Phoenicopsis* forests. Brachyphyll is a collective name for taxonomically diverse conifers (and the *Classopollis*-producing plants) with convergently similar scale-like leaves. In Late Triassic—Early Cretaceous time, brachyphyllous forests were dominated by araucariaceous, taxodiaceous and cheirolepidiaceous conifers. Modern taxodiaceous genera — brachyphyllous and heterophyllous *Glyptostrobus*, *Sequoia* and also cupressaceous brachyphylls — originated from primitive taxodiaceous species in the mid-Cretaceous and then became dominant in the evergreen coniferous forests. Deciduous forests consisted mostly of ginkgophytes, czekanowskialean plants (*Phoenicopsis*, *Czekanowskia* and their allies) and primitive pinaceous conifers. All these plants had their leaves clustered on short shoots. In the Late Cretaceous they were reduced to a subordinate status by deciduous taxodiaceous conifers — *Parataxodium* and then *Metasequoia* — which probably descended from some brachyphyllous ancestors.

Ferns, cycadophytes, podozamitalean and other shrubby conifers grew

under the canopy of both brachyphyllous and *Phoenicopsis* forests. At the same time they prevailed in many localities which contained no (or only a few) macroscopic remains of arboreal species. Such localities, suggesting open vegetation, are usually described as cycadophyte beds and fern (or horse-tail) beds. Cycadophyte beds might have reflected extensive shrublands in which various bennettites grew together with nilssonias, caytonialean plants and shrubby conifers. For example, in the Far East near Vladivostok the cycadophyte beds are confined to the western part of the country covered in Early Cretaceous time by inland shrubby vegetation, sharply delimited from the coastal taxodiaceous forests to the east (Krassilov, 1967). There are several variants of the cycadophyte beds: (1) *Zamites* beds in the channel sandstones; (2) *Ctenis* beds in the floodplain deposits, containing such conifers as *Podozamites*, *Torreya*, *Cephalotaxus* and *Podocarpus*; and (3) *Nilssoniopteris* coal beds. The latter represent a swamp variant of the cycadophyte shrubland. Other edaphic variants are pachycaulous *Cycadeoidea* shrubs and coastal, presumably halophytic *Ptilophyllum* communities with *Pachypteris* and abundant *Classopollis*-producing plants. I have suggested that the first angiosperms appeared in the cycadophyte shrublands (Krassilov, 1973). Some primitive angiosperm fruits from Lower Cretaceous beds, such as *Tyrmocarpus* (Krassilov, 1973) and *Lappacarpus* (Douglas, 1969) were provided with glochidia, suggesting association with mammals. In mid-Cretaceous time angiosperms replaced cycadophytes in the shrublands and then in the forests. The first presumably shrubland angiosperms had small leathery leaves of lauraceous or proteaceous aspect. Angiosperms with broader leaf blades resembling *Magnolia*, *Ficus*, *Aralia*, *Platanus* and *Viburnum* developed concomitant with the *Sequoia* and *Parataxodium* forests.

Fern—horse-tail beds contributed about two thirds of the plant material in practically all Mesozoic localities from Madagascar (Appert, 1973) to Yorkshire (Harris, 1961) and Bureja (Krassilov, 1978a). They were most abundant in deltaic and coastal-plain facies, suggesting fern swamps or marshes. Ferns surely grew also in forests, as they do now, but they were never abundant as fossils outside the fern marsh facies. The floristic composition of the fern marshes has changed with time. In the Late Triassic—Early Jurassic they were dominated by osmundaceous ferns and *Neocalamites*, in the mid-Jurassic to Early Cretaceous by dwarf tree ferns of dicksoniaceous affinities and *Equisetum*, and in late Cretaceous time by *Anemia dicksoniana* (Heer) Krassil., *Cyathea* spp. and *Cladophlebis frigida* (Heer) Sew.

Mesozoic plant formations are distinct from any extant vegetational types. They are vaguely comparable with the araucarian forests and *Dicksonia* swamps of Queensland, Californian redwood forests and chaparral, and the Everglades of Florida. There seem to be no plant communities ecologically equivalent to the tropical rain forests or savanna.

In the 19th century Heer and Nathorst challenged the then prevalent idea of the worldwide homogeneity of Mesozoic vegetation. Valuable contributions to the geographical classification of Mesozoic floras were made by

Vakhrameev (1964), Muller (1970), Stanley (1970), Barnard (1973), Zaklinskaya (1976), and Khlonova (1980). They used ranges of selected taxa plotted on either present-day maps or on contemporary palaeomagnetic maps. Authors of palaeomagnetic maps considered them as hypothetical reassemblies of continents to be tested by biogeographical evidence (Smith et al., 1973). However, many biogeographers, instead of testing hypothetical palaeomagnetic maps, accepted them as reliable. I found some phytogeographical patterns more consistent with modern latitudes than with contemporary palaeolatitudes (Krassilov, 1977b, 1978b). In any event, a biogeographer may be interested primarily in anomalies caused by continental drift rather than by inaccuracies of the palaeomagnetic method, and the present-day map is better for this purpose.

I have studied the zonal distribution of Mesozoic vegetational types as evidenced by the ranges of their characteristic life forms, such as pachycaulous and cauliflorous *Cycadeoidea* or deciduous *Phoenicopsis* with ribbon-shaped leaves clustered on short shoots and pendulous cones. These contrasting life forms had mutually exclusive ranges (Krassilov, 1972b). I found also that plants of the *Phoenicopsis* suite did not normally occur in association with presumably mangrove bennettites with *Bucklandia*-type stems and *Ptilophyllum—Otozamites* leaves, except in a few ecotonal localities. Ecogeographical classifications of this type may better reflect climatic zonation than traditional floristic provinces. A zone of pachycaulous bennettitalean shrublands and *Ptilophyllum (Otozamites)—Pachypteris* mangroves is designated here as warm (such designations as tropical or subtropical are better to be avoided because of the reasons given above). It is characterized also by optimal development of brachyphyllous forests and cycadophyte—conifer shrubland communities. Triassic and Jurassic fern—horse-tail marshes also attained their maximum diversity in this zone. They were rich in thermophilous ferns, such as *Klukia, Stachypteris, Tempskya, Nathorstia, Weichselia, Onychiopsis*, while the horse-tails reached up to 5—6 cm in diameter. Ginkgophytes were rather uncommon, occurring mostly as upland elements in allochtonous localities.

In the ecotonal warm-temperate zone, pachycaulous bennettites were smaller, mangroves were less widespread and had smaller leaves; brachyphyllous forests were less diverse, lacking *Frenelopsis, Araucaria* was still common. Deciduous ginkgophytes, *Pseudotorellia, Czekanowskia* and *Phoenicopsis* became more conspicuous.

The temperate zone was dominated by deciduous *Phoenicopsis* forests with various ginkgophytes and pinaceous conifers which had long soft needles and *Schizolepsis*-type seed cones, resembling golden larch. There were no pachycaulous or mangrove bennettites. Cycadophyte—conifer shrublands consisted mostly of *Nilssoniopteris, Pterophyllum, Pseudocycas, Ctenis, Nilssonia* and, among conifers, *Torreya*. Fern—horse-tail marshes were extensive but their taxonomic diversity decreased at the expense of thermophilous ferns, and the horse-tails were reduced in size.

Floras of the Gondwana continents belonged in a distinct floristic realm on account of the endemic order Pentoxylales and many endemic genera. However, their ecological structure was similar to those of Laurasian floras. Brachyphyllous forests with *Araucaria*, cycadophyte shrublands and mangroves, in which pteridosperms (*Dicroidium*) were more prominent than in the northern floras, constituted major vegetational types of the warm zone while ginkgophytes and *Phoenicopsis* were more common in the southern warm-temperate zone.

Boundaries between the vegetational zones can be drawn in regions of high concentration of fossil plant localities showing climatically controlled changes along the south—north transects. For Early Jurassic time such regions are southern to central China, Central Asia from northern Iran to Kazakhstan and Western Europe from northern Italy to southern Sweden. Floras of Hupeh in central China, Hissar in Soviet Middle Asia, northern Caucasus and Rumania are strictly ecotonal, having bennettites of the *Ptilophyllum—Otozamites* group in association with *Phoenicopsis*. Thus, ecotonal zone extended across Eurasia approximately between 35°N and 45°N (Fig.1). In North America, Mexican Jurassic floras clearly belong in the warm zone. Late Triassic floras of Arizona and Virginia suggest a warm-temperate ecotone at about 40°N. On Gondwana continents, Late Triassic floras are also better represented than the Liassic. Araucariaceous brachyphylls are exceptionally abundant in the Liassic floras of southern Sakhara (Krassilov, 1978b) and araucarian cones have been reported from the Liassic dinosaur locality at Tendaguru, Tanzania (Gothan, 1927). In the Molteno flora of South Africa *Phoenicopsis* is abundant, constituting up to 90% of all specimens in certain
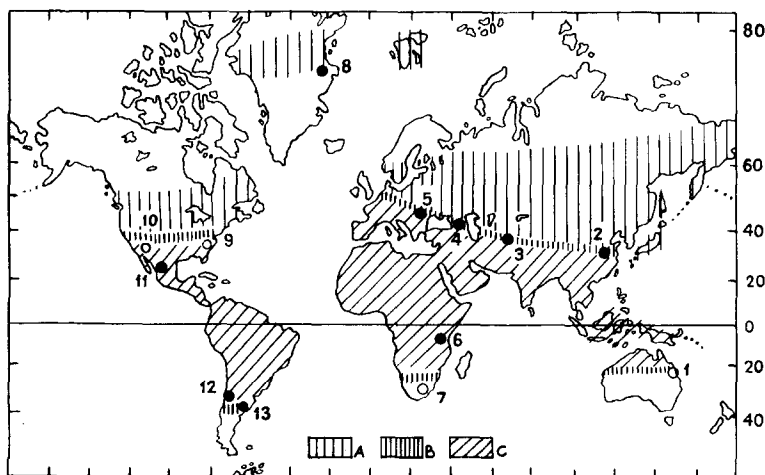


Fig.1. Early Jurassic vegetational zones: *A* = northern temperate; *B* = warm-temperate ecotone; *C* = warm. Localities defining the boundaries: *1* = Ipswich, Australia; *2* = Hupeh, China; *3* = Hissar, Soviet Middle Asia; *4* = northern Caucasus; *5* = Rumania; *6* = Tendaguru, Tanzania; *7* = Molteno; *8* = Scoresby Sound, Greenland; *9* = Virginia, U.S.A.; *10* = Chinle, Arizona, U.S.A.; *11* = Mexico; *12* = Mendoza, Argentina; *13* = Cacheuta, Argentina; open circles = Late Triassic localities.

horizons (Anderson, 1974). It is prominent also in Cacheuta (Argentina) and Ipswich (Queensland, Australia).

During the Middle and Late Jurassic, the warm-temperate ecotone moved progressively poleward. In the Early Cretaceous, it is defined in eastern Asia by the floras of the Okhotsk region and Tyrma River (Amur province). Brachyphyllous forests extended to Malacca in the south. Floras of northern Kazakhstan at about 50°N still belong in the warm zone, while a *Phoenicopsis* flora with some thermophilous ferns is known from west Siberia at 60°N. In Europe, the ecotone is to the north of Moscow and southern England, Wealden flora of which, though in the warm zone, have such temperate elements as *Pseudotorellia*. In North America, floras of western Greenland and southern Canada (Kootenay) have *Phoenicopsis* marking the southern boundary of the temperate zone (Fig.2). Early Cretaceous floras of equatorial Africa with *Frenelopsis* (see Boltenhagen, 1980), as well as those of Patagonia and Queensland with abundant *Ptilophyllum* and thermophilous fern *Nathorstia*, fall in the warm zone. In the flora of Victoria *Ptilophyllum* is also abundant but somewhat stunted in comparison with Indian or South American species (Douglas, 1969) and ginkgophytes are relatively prominent. This flora may belong in the warm-temperate ecotone.

In Late Cretaceous time, brachyphyllous communities with *Frenelopsis* and remnant cycadophyte shrublands still existed, but major parts of the warm and warm-temperate zones were occupied by *Sequoia*—laurophyllous forests. Along the Pacific coast these forests reached as far south as Thailand (Iwai et al., 1975) and probably extended across the equator into the Southern Hemisphere, as suggested by recent finds of *Austrosequoia* in Queensland
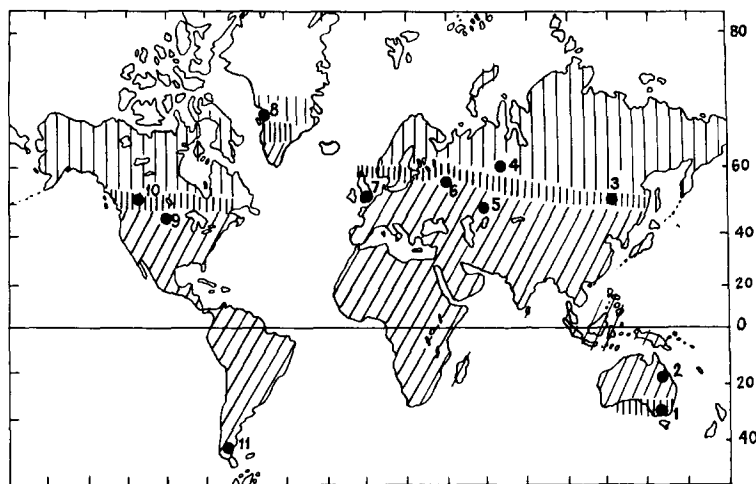


Fig.2. Early Cretaceous vegetational zones, legend as for Fig.1: *1* = Victoria, Australia; *2* = Queensland, Australia; *3* = Tyrma, Amur province; *4* = Leushy, west Siberia; *5* = northern Kazakhstan; *6* = Moscow; *7* = southern England; *8* = Kome beds, western Greenland; *9* = Black Hills, Dakota, U.S.A.; *10* = Kootenay, Alberta, Canada; *11* = Lago San Martin, Argentina.

(Peters and Christophel, 1978). Abundant small-leaved laurophyllous and pro-teophyllous angiosperms in some Central Asian, European (Bohemia) and American (Raritan) localities may evidence sclerophyllous shrublands. Late Cretaceous vegetation of equatorial Africa and America is represented mostly by spores and pollen grains, which are poor guides to life forms. Pre-valence of supposedly myrtaceous and proteaceous pollen grains in equatorial pollen floras (Boltenhagen, 1980) might have reflected widespread sclero-phyllous shrublands. A few fossil wood finds show that coniferous forests also occurred in the equatorial zone.

In the warm-temperate ecotone, broad-leaved platanophyllous angio-sperms were more abundant while laurophylls and proteophylls became less common. *Sequoia* was constantly found in association with *Araucaria, Cu-pressinocladus* and *Protophyllocladus* — a peculiar conifer with phylloclades resembling fern foliage. Ginkgophytes were widespread and *Nilssonia* was locality abundant, probably within the fern-marshes. The northern boundary of the warm-temperate zone is marked by the northernmost occurrences of *Debeya* (proteophyllous angiosperm) in northern Sakhalin, Amur province, Altai, western Greenland and Vancouver Island and palms in Japan and Vancouver (Fig.3). These northern outposts at 50° have been reached by thermophilous plants during the climatic optimum of Campanian age. Further north, *Sequoia* was gradually replaced by deciduous *Parataxodium* and *Metasequoia* and platanophyllous angiosperms prevailed over laurophylls. *Phoenicopsis* still survived in these temperate forests and *Nilssonia* was com-mon except in Chukotka and northern Alaska. The southern temperate zone was marked by the first appearance of *Nothofagus*-like fossil woods (Gothan,
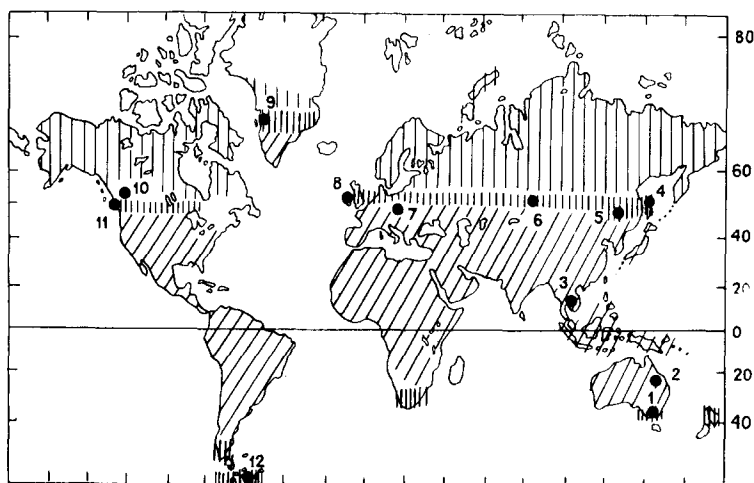


Fig.3. Late Cretaceous vegetational zones. Legend as for Fig.1: *1* = Victoria, Australia; *2* = Queensland, Australia; *3* = Thailand; *4* = Sakhalin; *5* = Amur province; *6* = Altai; *7* = Czechoslovakia; *8* = Ireland; *9* = western Greenland; *10* = Edmonton, Canada; *11* = Vancouver, Canada; *12* = Snow Hill, Antarctica. Southern warm-temperate zone is marked by *Nothofagus* pollen occurrences reviewed in Mildenhall (1980).

1908). *Ginkgoites* seems to be common in the Late Cretaceous of Victoria (Douglas, 1969).

It is interesting to note in relation to the palaeolatitude problem that the Liassic and Early Cretaceous ecotones are more oblique to modern latitudes than the Late Cretaceous ecotone. Vegetational zonation does not support a northward drift of North America in relation to Asia implied by palaeomagnetic maps (Smith et al., 1973). On the other hand, the ecotonal aspect of the Mesozoic floras of Greenland and southern Australia is more consistent with their position in the contemporary reassemblies.

Most dinosaur localities are situated within the warm and warm-temperate zones (Colbert, 1964). However, the northernmost occurrences of ceratopsids in central Alberta, *Psittacosaurus* in southern Siberia at about 55°N and dinosaurian footprints in the Lower Cretaceous of Spitsbergen fall in the temperate zone. These latter finds may suggest that cooling alone would have been not enough for extermination of dinosaurs.

DINOSAUR HABITATS AND FEEDING HABITS

As a student I was told that giant Jurassic dinosaurs fed on soft aquatic plants. Later I found this inconsistent with the fact that soft floating plants (aquatic ferns and angiosperms) first appeared in the mid-Cretaceous. In recent studies of dinosaur palaeoecology, giant dinosaurs are usually conceived of as terrestrial elephant-like animals feeding on conifers and other woody plants. Yet little use is made of the available fossil plant data.

What dinosaurs actually ate can be inferred from (1) the general character of the surrounding vegetation, (2) determinable plant remains in the stomach contents, (3) fossil plants found together with dinosaurs, (4) functional interpretations of the dinosaur morphology, (5) depositional environments of skeletal remains and other taphonomic evidence, and (6) comparisons with ecologically similar living animals. Each of these sources provides fragmental but complementary meaningful evidence. It was concluded from skeletal assemblages and trackway studies that at least some large herbivorous dinosaurs were gregarious (Bakker, 1971). It was suggested by trackway evidence that a herd of more than 130 coelurosaurs and ornithopods stampeded before an approaching carnosaur (Thulborn and Wade, 1979). Mixed herds of this size are formed today in steppes, savannas and adjacent shrublands or parklands, while closed forests support relatively small populations of large herbivores. One can surmise that a similar situation existed in the past, that is, most large dinosaurs inhabited open landscapes.

It follows from the above survey of the Mesozoic vegetation that cycadophyte—conifer shrublands (with sclerophyllous angiosperms in the Late Cretaceous) were widespread in the warm and warm-temperate zones while neocalamitalean and fern—horse-tail marshes were of cosmopolitan distribution. Dental characteristics of herbivorous dinosaurs agree with their feeding either in the cycadophyte and sclerophyll shrublands (camarasaurids, iguano-

dons, ceratopsids and some other groups with strong slicing teeth) or in the fern—horse-tail swamps and marshes (diplodocids, stegosaurs and some ankylosaurians with weaker teeth). The Jurassic and Early Cretaceous bipedal herbivores are usually considered as low-browsers which again is consistent with the idea of their predominantly shrubland habitats. Thorny cycadophytes (*Withamia*) are known from the Wealden iguanodon environments. Feeding habits of the giant quadrupedal herbivores are more debatable. Comparatively weak teeth and posteriorly placed nostrils were previously interpreted as adaptations to feeding on submerged plants. In the recent literature they are more often related to feeding on conifer branchlets while the head was thrust deep into the crown. Russel et al. (1980) consider brachiosaurs and other giant sauropods which dominated many Jurassic assemblages as "curious Mesozoic elephants" with grinding mills — gastroliths — in their stomachs. Their nostrils were placed posteriorly on the skull to avoid damage from branches. An ectothermic brachiosaur weighing 15 tons would consume nearly as much food as an elephant, that is about 60 kg of fresh vegetation daily. Bakker (1978) has suggested that feeding diplodocids assumed a tripodal posture, that is resting on their hind legs and tail.

They were curious indeed these "Mesozoic elephants", squatting before conifers, and so sensitive to damage from branches. But is it not simpler to conceive of them as feeding on the delicate foliage of dicksoniaceous ferns in the fern marshes? They might have kept on feeding when the marshes were flooded at high tides, hence the posterior position of their nostrils. Frequent finds of mired diplodocids seem to support this suggestion.

A tripodal feeding posture was suggested also for stegosaurs (Bakker, 1978). However, Russel et al. (1980) have concluded from their taphonomic observations in the Middle Saurian bed of Tendaguru (Tanzania) that stegosaurs fed on herbs. Together with other low-browsers they gathered in restricted areas of plentiful herbaceous vegetation during periodic droughts. These areas might be fern marshes on coastal plains.

Feeding habits of the large Late Cretaceous herbivores — ceratopsids, ankylosaurians and hadrosaurids — arouse much interest due to their peculiar feeding organs — the hook-shaped and duck-like beaks. All ceratopsian dinosaurs and their psittacosaurian relatives had strong beaks comparable to those of turtles but laterally compressed as in birds. According to Ostrom (1966), the ceratopsian beaks appear too narrow for biting off sizeable pieces of food, as turtles do. They lack sharp edges which also suggests grasping or plucking rather than biting or cutting. The beaks are separated by an edentulous region from the powerful dental batteries specialized (especially in the advanced ceratopsids) for cutting. Ostrom (1966) wrote: "It is quite evident that a wide variety of ceratopsian species were highly specialized for feeding on specific and unusual plant food". The ceratopsian food might have been unusually resistant and unpalatable to other animals. He further suggested that cycads and palms meet these requirements. *Cycas* and palmettos have been reported from several Late Cretaceous floras but they were relatively

uncommon. Cycadeoid bennettites with their short barrel-shaped trunks, about 0.5 m (up to 3 m) high and encased in the armour of persistent petiole bases and topped by a crown of large fronds, appear to be a better choice. A ceratopsian dinosaur can be conceived of as grasping at the frond base buried in a thick mass of ramental scales with its hooked beak and tearing it up by a movement of its heavy head. The beak could also be useful in plucking out cauliflorous strobili from between the leaf bases (there were as many as 500 strobili per stem, 0.5 m long). Alternatively, the parrot-beaked psittacosaurs and at least some ceratopsids might have been fruit-eaters. Recently large fruits of *Nyssoidea* type were found in several dinosaur beds in Mongolia (unpublished). They are so abundant that they might have served as a food source even for very large animals. Much smaller fruits of the extant *Nyssa* are eaten by birds and rodents (Eyde, 1963). Hard putamens of *Nyssoidea* surely demanded strong dentition. Upper Cretaceous dinosaur beds of North America contain fig-like objects (fruits or tubers) which Berry (1924) considered as possible dinosaur food. Schoemaker (1977) has shown that these objects were fruits rather than tubers.

Ankylosaurians, another group of heavily armoured Late Cretaceous dinosaurs, might have also lived in shrublands, browsing at about 1 m above the ground (Béland and Russel, 1978). Most of the Late Cretaceous dinosaurian faunas were dominated by hadrosaurids (Brett-Surman, 1979). These large bipedal herbivores, weighing up to 11 tons, are characterized by the stout duck-like bills, paddle-like fore feet and large laterally compressed tail. They lacked any special organs of defence. Because of these characteristics hadrosaurids have for a long time been considered either aquatic or amphibious, feeding on submerged plants. Ostrom (1964) has challenged this view in an impressive paper in which he revised all aspects of the hadrosaurian functional morphology and also discussed their putative habitats and surrounding vegetation. He has shown that depositional environments of the hadrosaurian fossils were much alike from central Alberta to northern Mexico. Skeletal remains came from alluvial and lacustrine deposits often with lignitic seams, regularly interbedding with marine facies. Hadrosaurids apparently lived on coastal plains. Aquatic plants constituted only a minor component of the surrounding vegetation, while large populations of hadrosaurs must have depended upon abundant plant sources. Their solid dental batteries were adapted for efficient grinding, the tooth replacement mechanism and the high degree of tooth wear indicated coarse food. From these dental characteristics and the hind limb anatomy, Ostrom has concluded that hadrosaurids were terrestrial animals feeding on woody plants. The bills might have served for stripping shoots and leaves. The webbed manus and flattened tail probably helped in swimming across rivers or lakes in the course of migration or as an escape from carnosaurian predators. As a final proof of such a mode of life, Ostrom cited data on the stomach content of a mummified hadrosaur, *Annatosaurus annectens* (*"Trachodon"*), studied by Kräusel (1922). As a preliminary result of his studies (which to my knowledge, were

never completed), Kräusel reported shoots of conifers and hardwoods, needles of *Cunninghamites elegans* (this name was previously applied mostly to fossil *Araucaria* shoots, but occasionally also to those of *Sequoia*) as well as abundant small fruits and seeds obtained by maceration of the dark-brown thready stomach content. In an ensuing discussion (published in the same issue of *Palaeontologische Zeitschrift*), Abel suggested that the stomach infilling was secondary. However, Dreverman asserted that the peat-like material represented original stomach content. In Ostrom's words, Kräusel underrated his discovery, being reluctant "to accept at face value what must have seemed startling evidence in view of ideas on hadrosaurian ecology then prevalent". Actually Kräusel wrote that *"Trachodon* weidend ans Land ging und sich dabei Keineswegs aus die Bodenvegetation beschränkte".

In recent reviews of the dinosaur ecology, Bakker (1978) suggested that hadrosaurian beaks were adapted for browsing close to the ground, while Béland and Russel (1978) considered hadrosaurids as unspecialized browsers with tooth batteries like those of elephants, feeding on trees up to 3—4 m above the ground. According to the latter authors, hadrosaurids, ceratosaurids and ankylosaurians might have fed on the same vegetation, utilizing different plant strata. They supposedly perceived their environment as fine-grained, migrating freely across the mosaic of plant communities. However, there are significant preservational differences between three major groups of herbivorous dinosaurs. Complete specimens of hadrosaurids are much more frequent than those of ceratopsids and ankylosaurians, which are often represented by isolated skulls and tail clubs, suggesting predepositional transport and sorting. Hadrosaurids apparently lived at or near the site of deposition while ceratopsids and akylosaurians lived further inland. Frequency analysis of dinosaur remains in marine facies (Horner, 1979) has shown that hadrosaurids actually dwelt on coastal plains, presumably in the fern marshes.

The comparison of hadrosaurs with elephants can be misleading. It is difficult to reconcile characteristic hadrosaurian bills with an assumption of the elephant-like feeding habits. Nor is this comparison very enlightening because while the extant elephants are high-browsers, the Pleistocene species of the *meridionalis-trogontherii* group were grazers. Kräusel (1922) has described the hadrosaur stomach content as peat-like "faulende Pflanzenmassen" with abundant fruits and seeds. If this hadrosaur were an unspecialized browser consuming fruits occasionally together with twigs and leaves, it hardly could eat such a great number of various small fruits and seeds at a time even in the fruiting season (and mummified remains suggest fast burial under sediments, which is more probable in spring than in autumn). On the other hand, small fruits and seeds as well as isolated conifer needles are common in many kinds of peat. It is tempting to suggest that the peat-like stomach content was actually peat or gyttja. The waterside habitats of hadrosaurids, their duck-like bills, strong shearing dentition and aquatic adaptations are consistent with their feeding mostly on drifted plant material or even peat.

To summarize, two major kinds of dinosaurian habitats can be inferred

from their distribution, taphonomic evidence and putative feeding habits (Fig.4): shrublands dominated by cycadophytes and later by sclerophyllous angiosperms and fern-marshes or swamps. Giant diplodocids, stegosaurs and hadrosaurids can be provisionally assigned to the marsh group while the shrubland communities probably included Jurassic and Early Cretaceous ornithopods, Late Cretaceous ceratopsids and some ankylosaurians. It seems unlikely that any of these dinosaurs were high-browsers. More specific dinosaur—plant relations remain conjectural. Peculiar feeding structures imply an unusual diet as suggested above for ceratopsids and hadrosaurids.

It is generally assumed that Mesozoic carnivores preyed on the herbivorous dinosaurs. However, Freeman (1979) has shown that the Middle Jurassic mammal beds are mostly coprocoenoses, the mammal bones coming from faeces of small dinosaurs. To form rather extensive coprocoenoses, the dinosaurs — supposedly smaller species or juveniles — must have preyed regularly on mammals. This suggestion puts the dinosaur—mammal relations in a different light: they might have coexisted on the prey—predator basis and not as competitors. Feeding on mammals can also explain an excess diversity of carnivores in relation to herbivorous dinosaurs in many Mesozoic faunas.

## CONCURRENT EVOLUTION OF DINOSAUR AND PLANT COMMUNITIES

Let us now compare major events in the history of the Mesozoic vegetation and dinosaur communities. If my previous suggestion that dinosaurs lived mostly in shrublands and fern-marshes were correct, then there should



Fig.4. A diplodocian dinosaur in the fern-marshes (above) and a ceratopsian dinosaur in the shrubland.

be a significant time correlation between the evolution of these plant communities and the replacements and extinctions of dinosaurian faunas.

Diverse dinosaur communities appeared in mid-Triassic time simultaneously with cycadophyte shrublands and fern-marshes. In Early Jurassic time, the dicksoniaceous ferns and *Equisetum* had gradually replaced the camptopteridaceous ferns and *Neocalamites* in the marshes. This was accompanied by the similarly gradual replacements of tetrapods (Olson and Galton, 1977). Dominant mid-Jurassic herbivores, diplodocids and stegosaurs had perished at the Jurassic—Cretaceous boundary and were replaced by new groups of ornitischian dinosaurs. Bakker (1978) has related this replacement to putative degradation of conifer forests and the rise of angiosperms which was favorable for low-browsers. However, at this time the brachyphyllous conifer forests were hardly disturbed and angiosperms were far too scanty to affect the supposed replacement of high-browsers by low-browsers. In fact, both brachyphyllous forests and cycadophyte shrublands have expanded while the fern marshes have been drastically reduced in Mongolia (Krassilov, in press) and possibly in other regions. This situation might have been to the advantage of shrubland dinosaurs, such as iguanodons, while marsh dwellers, especially the larger species, had to decline because of the reduced food supply.

The next major dinosaur replacement in the Middle Cretaceous was clearly correlated with world-wide vegetational changes. Microphyllous angiosperms replaced megaphyllous cycadophytes in the shrubland plant communities. This might have caused considerable reduction of the leaf mass available for shrubland browsers. Consequently, dominant Early Cretaceous groups of the shrubland ornithischians declined or changed their habitats. Some of them probably penetrated marsh communities (which remained undersaturated after the extinction of giant sauropods) and there gave rise to new adaptive types, such as hadrosaurids. Their place in the shrublands was filled by ceratopsids and other groups which could cope with vegetational changes. Mass production of fruits in the shrublands might have induced new feeding habits, and ceratopsids with their hooked beaks were probably preadapted for utilizing this new food source by feeding on cauliflorous bennettitalean strobili (see above).

Marsh habitats were affected by nearly complete elimination of dicksoniaceous ferns and partial forestation by redwoods. The appearance of abundant water ferns and angiosperms can be related to eutrophication of lakes. Hadrosaurs, like hippopotamuses, might have been responsible for eutrophication and increased productivity of aquatic vegetation.

At the end of the Cretaceous period, characteristic Mesozoic genera of ferns and gymnosperms perished together with the dinosaurs. The Danian floras of Amurland and Mongolia as well as the Fort Union and Edmonton floras of North America show that the deciduous forests with *Metasequoia* and *Trochodendroides* expanded over the area of the richest Cretaceous dinosaurian faunas. Fern-marshes and remnant cycadophyte shrubs were eli-

minated and the sclerophyllous shrubland formations much reduced. Evidence from other countries (see Krassilov, 1975) seems to suggest that the widespread forestation in the terminal Cretaceous left no extensive areas of open vegetation to support large populations of herbivores. Insects and insectivorous species among reptiles, birds and mammals might have also been affected by these vegetational changes, and predatory dinosaurs depended either on dinosaurian herbivores or on mammals.

Sclerophyllous shrublands, though of different floristic composition, reappeared in Late Paleocene time and new communities of large herbivores were formed. But a mangrove fern, *Acrosticum aureum*, is the only reminder of the Mesozoic fern-marsh formations.

## CONCLUSIONS

It is suggested that dinosaur communities have been associated with extensive shrublands and fern-marshes. Changes in these plant formations probably induced dinosaur replacements. Eventual elimination of the fern-marshes and reduction of the shrubland formations in the terminal Cretaceous coincided with the extinction of dinosaurs. While ad hoc suggestions for particular dinosaur groups remain speculative, close correlation between vegetational events and dinosaur evolution leaves little doubt in their causal relationships. Much is still to be learned of these relations to obtain a more convincing model. At present it appears most plausible that dinosaurian shrubland and marsh habitats have been severely disrupted and eventually lost due to the widespread forestation which in turn was induced by climatic changes. Similarly, Pleistocene megafaunas might have been affected by the post-glacial forestation of their tundra-steppe habitats. In both cases biotic changes triggered by climatic events progressed from the lower trophic levels to the higher. Dinosaurs could cope with environmental changes during 150 m.y., but they evidently became less resistant to adverse conditions when their food resources were undermined.

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