Saint Petersburg University

Institute of Earth Crust

L[ev] A[lexandrovitch] Nessov

DINOSAURS OF NORTHERN EURASIA: NEW DATA ABOUT ASSEMBLAGES, ECOLOGY, AND PALEOBIOGEOGRAPHY

Reviewers:

Corresponding Member of the Russian Academy of Sciences I. S. Darevsky

Doctor of Geological and Mathematical Sciences V. A. Prozorovsky

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Translator: Tatayana Platonova, Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia

Translation editor: Hans-Dieter Sues, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A.

NOTE ON TRANSLATION: This work, originally published in Russian in 1995, has been translated into English to introduce Nessov's research on dinosaurs from the former Soviet Union to specialists worldwide. It contains important primary descriptions for a number of new dinosaurian taxa from the Cretaceous of Uzbekistan as well as a comprehensive synopsis of localities with dinosaurian remains on the territory of the former Soviet Union. Some of the paleobiological speculations will strike western readers as idiosyncratic, but we tried to retain the original character of Nessov's work as much as possible in this translation. Throughout the text, pagination for the Russian original is indicated by bold-face numbers in brackets to facilitate cross-referencing. This translation should be used in conjunction with the original work to view the illustrations (which are not reproduced here). The transliteration used by the translator differs in some respects from that commonly used in the United States so that the spelling of certain names of authors and places differ (e.g., "Yefremov" rather than "Efremov"). Ms. Platonova's translation effort was supported by National Science Foundation grant EAR-9804771.

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INTRODUCTION

The present work is devoted to the dinosaurs of northern Eurasia within the boundaries of the former Soviet Union. Remains and tracks of dinosaurs are known from Uzbekistan, Kazakhstan, Tadzhikistan, Kirghizia, Turkmenistan, Russia, Armenia, and Georgia.

Existing reviews of localities of dinosaurian remains discovered in the former Soviet Union (Tolmachev, 1926; Yuryev, 1954a) as well as specialized bibliographical selections of discoveries of these animals in that country (Riabinin, 1931a, 1939; Rozhdestvensky, 1964; Rozhdestvensky and Tatarinov, 1964: p. 647, 648) usually include, in addition to dinosaurs, other ancient reptiles from either particular regions or from all of Asia (Yefremov, 1944; Rozhdestvensky, 1964, 1974; Rozhdestvensky, 1977; Rozhdestvensky and Khozatsky, 1967). Some reviews are incomplete (Rozhdestvensky and Tatarinov, 1964; Paleozoology of the USSR). All have become obsolete.

If considered from the perspective of cladistic systematics, dinosaurs are a paraphyletic group because they do not include the ancestor of the group nor all its descendants (as birds are the descendants of theropod dinosaurs). Dinosaurs, whether they represent one, two, or possibly several lineages, take their origin from pseudosuchians. Therefore, it would be more natural, from the cladistic point of view, to establish a group including various pseudosuchians, pterosaurs(?), as well as crocodylians, ornithischians, and saurischians, and also birds or a group including only several evolutionarily derived theropods and birds. It would nevertheless be reasonable to preserve the term "dinosaur" in order to be free to use it in the future.

The first discoveries and/or identifications of dinosaurian remains in the European part of the Commonwealth of Independent States (CIS) were made by Kiprianov prior to 1883, K. F. Egorov in 1912 and P. M. Klevensky in 1931, by A. D. Arkhangelsky in Transbaikalia in 1910, by V. T. Surgai and A. F. Sosedko in the Kyzylkum in 1930, by E. V. Ivanov in 1923 and V. D. Prinada in Tashkent Chul' [chul' = hilly plain; Tashkent Chul' is a hilly plain located north of Tashkent in southern Kazakhstan] in 1924-1925, by P. D. Trusov in 1928 and O. S. Vyalov in the Fergana region in the 1930's, by G. V. Mukhin in 1925, A. N. Kirikov in 1926, E. I. Belyaeva and M. G. Prokhorov in 1927 and D. I. Yakovlev in the basin of the Il River, and by I. I. Krom in the basin of the Emba River in 1926. Shell of dinosaurian eggs was found for the first time in the former Soviet Union by V. S. Erofeyev and L. D. Kudina in the Zaisan Basin in 1959. Tracks of dinosaurs were first discovered on the conterminous territory of the CIS by G. D. Romanovsky and P. A. Chuenko in 1882, and tracks of dinosaurs were found by Chabukiani in Georgia in 1933.

Citizens of Russia (inhabitants of the Kasatkina stanitsa [stanitsa = large cossack village], now the village of Kasatkino) and later Colonel Manakin discovered, for the first time for science, a locality with dinosaurian remains on Chinese territory (1900-1902) (Manakin, 1902; Riabinin, 1925). This find was made long before the discovery of Central Asian localities (in Mongolia and also the Chinese provinces of Gansu and Inner Mongolia).

Over the past 15 to 20 years, the amount of data on the composition of dinosaurian faunas in this country [Commonwealth of Independent States, abbreviated as CIS] and the list of localities have increased several times. **[4/5]** Therefore, a new review of the evidence is needed. Ichnological research on dinosaurs is proceeding vigorously, with studies being carried out by V. V. Kurbatov, V. P. Novikov, K. N. Amanniyazov, V. I. Sedletsky, and L. K. Gabuniya. These efforts have also been guided by results of paleoichnology abroad (Lockley, 1991; Lockley et al., 1991).

A great body of new data was obtained by teams of the Stratigraphic Party headed by I. M. Abduazimova (Tashkent) and Leningrad (St. Petersburg) University. It was not uncommon that localities, where previously only fragmentary remains of one or two dinosaurian forms had been recorded, appeared to contain rich assemblages of these animals after several years of work. The Appendix to the present work lists all known localities, including even those that contain few dinosaurian remains that cannot be identified even to the level of order. Several of these localities may represent the first evidence of rich and previously unknown dinosaurian faunal complexes. Thus, for instance, even after dedicated paleontological exploration at Dzharakuduk, the fauna from this locality was regarded as relatively impoverished (Rozhdestvensky, 1964). Now, however, the locality is known to contain the most diverse fauna of aquatic and terrestrial vertebrates from the Cretaceous of Eurasia.

It should be noted that very little is known in the world as a whole and in Eurasia in particular about the dinosaurs during the period from the end of the Middle Jurassic to the beginning of the Late Jurassic (Bathonian-Callovian; Oxford Clay) and particularly about the faunas of these animals during the first half of the Late Cretaceous (Cenomanian - Santonian) (Steel, 1969, 1970; Haubold, 1979; Steel and Haubold, 1979; Norman, 1985; Czerkas and Olson, 1987; Chure and McIntosh, 1989; Russell and Weishampel, 1989; Norman, 1989; Weishampel et al., 1990b; Britt et al., 1990). Even already available data on the dinosaurs of that time given in the literature are very incomplete (Charig, 1993: fig. 3). Even fewer data on dinosaurs are available for the Aalenian stage (at the beginning of the Middle Jurassic). No significant remains of these animals are known worldwide for this age interval.

During the past few years, remains of dinosaurs have been found on the territory of the former Soviet Union that belong to taxa previously unknown for this region: Segnosauria and Oviraptorosauria in the Cretaceous, Stegosauria in the Jurassic, and also true horned dinosaurs, Ceratopsidae, for which no significant records had been known for the Cretaceous of Eurasia and which had long been considered endemic to North America (Rozhdestvensky, 1977; Coombs, 1984; Russell, 1991). The world's oldest, or at least very early, representatives of several taxa were found: Hadrosauridae in the late Albian, Protoceratopsidae in the late Albian and early Cenomanian, Ceratopsidae in the late Turonian and Coniacian, Segnosauria in the Albian, early Cenomanian, and possibly late Barremian - middle Aptian, Caenagnathidae in the late Turonian, the genus *Troodon* in the early Cenomanian, and Stegosauria at the boundary between the Middle and Late Jurassic. All these data as well as other new evidence significantly clarify possible dispersal routes, evolutionary histories of taxa, and the evolutionary history of some dinosaurian assemblages from the Central Asian part of the CIS, Kazakhstan, Transbaikalia, the Far East and North-East of Russia, and also China, Mongolia, and western North America.

Unfortunately, only a few complete skeletons of dinosaurs have been found on the territory of the former Soviet Union. **[5/6]** The reason is that the taphonomic situation in the coastal plains often favored protracted maceration of skeletons and their disintegration into separate elements (Nessov, 1990: fig. 1, 1991; Ro_ek and Nessov, 1993: fig. 2). Along with the known negative aspects, the discovery of fragmentary bones and teeth of dinosaurs also has many advantages. On the basis of fragmentary bones, rather than complete skulls, it is easier to study important features of the structure of the internal parts of the braincase (canals for cranial nerves and blood vessels, parts of the inner ear), which are invaluable for establishing the phylogenetic relationships between taxa. Series of similar bones belonging to individuals of different ages, but of the same species, permit study of ontogenetic variation. Based on isolated bones and teeth mixed by currents in the straits between basins and in channels in the river deltas and forming apparent natural samples, one could relatively easily and quickly obtain quantitative data on preponderance of certain groups and their actual occurrence in the localities (see Part 1). This allows us to obtain relatively sound if approximate information concerning, for example, the ratio of biomasses of carnivorous theropods and herbivorous dinosaurs. Complete skeletons of dinosaurs of closely related species, genera, and subfamilies recovered during the long-term studies conducted by paleontologists in North

America, Mongolia, and China are invaluable for the reconstruction of these animals known from fragmentary elements.

1. REVIEW OF MAJOR DINOSAURIAN TAXA OF THE MIDDLE JURASSIC TO CRETACEOUS OF NORTHERN EURASIA

For the review, it is expedient to list the Latin names of the dinosaurian groups mentioned throughout the text: Acanthopholids – Acanthopholidae, ankylosaurids – Ankylosauridae, ankylosaurs – Ankylosauria, armatosaurs – Armatosauria (Stegosauria + Ankylosauria + (?)Pachycephalosauria), baryonychids – Baryonychidae, hadrosaurs – Hadrosauridae, hadrosaurines – Hadrosaurinae, deinodontids – Deinodontidae, deinonychosaurs – Deinonychosauria, dryptosaurids – Dryptosauridae, dromaeosaurids – Dromaeosauridae, sauropods – Sauropoda, iguanodontids – Iguanodontidae, camptosaurs – Camptosauridae, carnosaurs – Carnosauria, lambeosaurines – Lambeosaurinae, megalosaurids – Megalosauridae, oviraptorosaurs – Oviraptorosauria, ornithomimids – Ornithomimidae, ornithopods – Ornithopoda, prosauropods – Prosauropoda, protoceratopsids – Protoceratopsidae, psittacosaurids – Psittacosauridae, segnosaurs – Segnosauria, spinosaurids – Spinosauridae, stegosaurs – Stegosauria, tarbosaurs – *Tarbosaurus*, titanosaurids – Titanosauridae, torvosaurids – Torvosauridae, triceratopses – *Triceratops*, coelurosaurids – Coelurosauridae, ceratosaurs – Ceratosauria, ceratopsids – Ceratopsidae, ceratopses – Ceratopsia.

1.1. Segnosaurs

This peculiar group of dinosaurs was established for the first time on the basis of specimens from Mongolia (Barsbold and Perle, 1980; Perle, 1979, 1991). According to various hypotheses, it was already a relict group when it appeared in the fossil record during the Cretaceous; it evolved since the time of divergence of the theropod and sauropod lineages (Late Triassic), or the segnosaurs took their origin as a separate branch from early Prosauropoda (Weishampel et al., 1990a). Segnosaurs, judging from a number of features that changed little compared to those of their supposed ancestors among the prosauropods (shape of the skull and its details, character of cheek dentition, considerable length of the neck with two pleurocoels on each side of the cervical vertebrae, short metatarsals appressed to one another, etc.), should be placed closer to the beginning than to the end of the system of the saurischian dinosaurs. The specimens discovered in the Commonwealth of Independent States suggest that segnosaurs were characterized by extraordinarily strongly pneumatized neck vertebrae (with numerous internal cavities) and strongly oblique articular surfaces on the vertebral centra. The humeri had much expanded distal ends; the ungual phalanges were large, similar to each other in size, relatively strongly curved, sharp, and strongly compressed from side to side. The other phalanges, as well as the metacarpals and metatarsals, had almost no distinct collateral ligament pits on their distal articular ends. Teeth of segnosaurs from the Late Cretaceous in Middle Asia were relatively tall, sharp towards the apex, and numerous small serrations were present along the blade-like anterior and posterior margins at the apex of the tooth crown (Nessov, 1981: fig X, 10, pl. II, fig. 4) **[7/8]**

Judging from discoveries in the CIS, Mongolia, and China, segnosaurs already included relatively large forms during the late Barremian - Albian. During the first half of the Late Cretaceous (Cenomanian - Santonian), segnosaurs were relatively small in size. During the second half of the Late Cretaceous, relatively large forms existed along with forms of moderate size. In one late Campanian - early Maastrichtian group (family Therizinosauridae), the ungual phalanges became elongated and more or less straight. The relatively straight, long unguals of the therizinosaurs were probably used by adult individuals for defense against predators (Paul, 1984) and in young individuals for holding onto branches. In segnosaurs (Segnosauria indet.) from the early - middle Albian in Khodzhakul (Karakalpakstan), Coniacian of Dzharakuduk (Uzbekistan), Turonian - Coniacian of Iren Dabasu (China) and from the Santonian of Shakh-Shakh (Kazakhstan), the thick, mediolaterally compressed, and strongly curved ungual phalanges (Pl. II, figs. 1-3, 6) could have been used for both defense and for locomotion along the trunks and in the crowns of trees (Fig. 1).

In island forests dominated by sycamores on the coastal plains during the Coniacian, these dinosaurs, given their strongly pneumatized, lightly built skeleton, could probably swim across the parts of basins that separated islands and peninsulas covered by forest. This could have been particularly common and necessary during rising water levels as a result of wind tide and after heavy rains. A. K. Rozhdestvensky (1970, 1976) assumed that these large forms could have fed on ants and termites. This is difficult to accept considering the ecological limitations on energy flow through this kind of insect and also in view of the abundance of segnosaurian remains, for instance, near sycamore forests situated along channels at Dzharakuduk during the Coniacian.

The features listed below, such as the strongly arched curvature of the neck, extraordinary lightness of strongly pneumatized cervical vertebrae and probably the base of the skull, small size of the head, very weak teeth (Pl. II, fig. 4) without apical wear but usually polished on the lingual and labial sides (retaining a sharp edge at the apex), "similarity to sloths" in the structure of the preungual and ungual phalanges (Coombs, 1983), uniformity in size of the latter within the hands (Perle, 1981), deep vertical grooves on the distal articular surfaces of the phalanges permitting interphalangeal motion in only one plane, retroversion of the pubis and eversion of the anterior pelvic bones (supporting the sides of the abdominal wall), great width of sacrum (particularly in its posterior portion), and transversely expanded sacral centra and sacral ribs suggest that movement along large branches of trees, with the back down, the anterior part of the head in front of the hands, but not far from these was a normal position for the relatively small segnosaurs (of the type known from Middle Asia) (Fig. 1) and that the animals fed on soft food.

The backward displacement of the distal ends of the pubic bones in ancestors of the known segnosaurs to the opisthopubic state could have been selected, as in dromaeosaurids among theropods, for more efficient climbing along vertical stems. With the opisthopubic pelvis, the abdomen could have evolved from a sharply keeled (particularly in its posteroventral portion) to a more flat one. Naturally, a question arises whether similar processes **[8/9]** could have occurred for the same reason in the early ornithischians as at the first stages of evolution in birds.

It should be noted that the distinction between segnosaurs and large-clawed theropods based only on the discoveries of isolated ungual phalanges, which are large and strongly flattened from side to side (see figures in Hu [1964] and Rozhdestvensky [1976]), presents considerable difficulties. If such specimens are of Turonian - Maastrichtian age, they can probably be placed among segnosaurs. During the Late Jurassic and Early Cretaceous, there existed large-clawed theropods that were phylogenetically distant from segnosaurs. In the fossil record, remains of segnosaurs first appear in the Aptian - Albian (Russell and Dong, 1994; Part 4.1.2.29 of this work); tracks of segnosaurs are apparently known from the Albian and the Late Jurassic (see Parts 4.4.2.194 and 4.4.1.187).

[FIGURE 1 HERE]

Fig. 1. Reconstruction of a young segnosaur in its natural environment, in the crown of a sycamore tree with nests of *Desertiana* built by wasps of the genus *Polystiane* (Late Cretaceous, Coniacian; Central Kyzylkum, Uzbekistan). **[9/10]**

Comparison of segnosaurian bones with the skeleton of the modern three-fingered sloth, *Bradypus tridactylus* (No. 321, Department of Vertebrate Zoology, St. Petersburg University), reveals similarity in a number of characters - distal expansion of the humerus, the long and (in cross-section) rounded diaphysis of this bone, the low height of the spinous processes on the dorsolumbar and sacral vertebrae - and in several other characters noted above. In view of the currently known features of segnosaurs, it is certainly possible to assume that they could have fed on fish among other things (Barsbold and Perle, 1979: 43; Barsbold and Perle, 1980), but it is difficult to imagine how they could have caught them. We cannot exclude, therefore, the possibility that segnosaurs could have fed on dead fishes.

It seems more probable, however, that these animals, judging from their relatively weak dentition, could have fed in part on very soft vegetation, but also possibly on nests of *Desertiana* (Nessov, 1985: pl. II, fig. 18; Nessov, 1988b: fig. 1, 14), which were built by social hymenopterans, most likely primitive wasps closely related to the Polystinae. These flat nests with cells turned to one side, probably the shade side, were hung below branches (Fig. 1). Cells of nests of these insects were slightly turned upwards, as is the case in evolutionarily advanced bees (but, unlike in the latter, the cells were not organized on both sides of the vertical plane, and probably were protected from overheating by the sun by the bodies of the adult inhabitants). Adult insects were located on the bottom side of the cells, which were built using soft, phosphate-containing mud. Evidently such nests contained larvae and food reserves. Phosphatized parts of such nests belonging to less than 5 to 7 species (only two of which have been formally described; Nessov, 1988b) are quite common in the Coniacian deposits of Dzharakuduk, in exactly the same levels where remains of segnosaurs occur most frequently. A nearly complete nest has been found, which eliminates the possibility that these structures could have been compound fruits of aracean plants. The same type of fossil, although with cells in a more irregular arrangement, is known from the Upper Cretaceous of southwestern Utah, USA (Brown, 1941; Zeuner and Manning, 1976; Wentzel, 1990). Judging from the coordinates given for this discovery (Hintze, 1982), it most probably originated from the Wahweap Formation, which belongs to the lower (but not lowermost) Campanian (Eaton and Cifelli, 1988). It was argued that this fossil, called *Celliforma favosites* (not the type species of this genus), which probably should be called *Desertiana favosites* (Brown), belonged to wasps of the subfamilies Vespinae or Polystinae. The basis of each cell in the specimen from Utah, as in the nests from the Coniacian of Dzharakuduk, was made of mud. The openings of the cells of the fossil from Utah are spaced at a greater distance from each other than their bases, whereas the axes of cells extend parallel to each other in the nests from Uzbekistan. All this suggests that, during the Campanian in western North America and during the Coniacian in western Asia, nests were built by different species (genera?) of wasps. Filled by larvae, pupae, and food reserves, these nests could have been a food resource for Cretaceous vertebrates. As such nests were abundant and permanent, there may have existed vertebrates that specialized to a certain extent on feeding on such nests, as, for example, the modern Honey Buzzard, *Pernis apivorus* - a relatively large bird from the order of diurnal raptors. **[10/11]**

Discoveries of three-dimensionally preserved remains of bodies of adults of presumed Hymenoptera in the Coniacian of Dzharakuduk (Nessov, 1992: pl. III, fig. 7) and in the Maastrichtian of Bug Creek, Montana, USA (material in the Royal Ontario Museum) indicate the possibility of associating the nests (as traces of vital activity) with particular insect species. Considering the frequently occurring carnivory of wasps, their ability (at least in some forms) to process even relatively large carrion of vertebrates (particularly fishes) by means of their large mandibles and also feed their larvae on carrion, and considering the frequent mass deaths of fishes, amphibians, and other aquatic vertebrates in the zone of interbasin channels (regarding the mechanism responsible for their death see Ro_ek and Nessov [1993] and Part 3 of this volume), one could assume that the segnosaurs from the Coniacian of Dzharakuduk, like many other terrestrial vertebrates at that time, could have become part of food chains tied to the nutrient-rich aquatic ecosystems. Segnosaurs, however, could have done this indirectly, obtaining part of the energy flow through wasps and wasp-like Hymenoptera, whereas large pterosaurs (Pl. I, fig. 18) collected food from the surface of open areas of basins.

Therefore, Rozhdestvensky (1970, 1976) may at least be partially correct in his assumption that segnosaurs possessing huge claws fed on social insects. It should be noted at the same time that A. K. Rozhdestvensky was one of the first who was aware that the curious reconstruction of therizinosaur (Malyeyev, 1959) [which, as is clear now, is erroneous in most details] anticipated the existence of a saurischian group in the Cretaceous in Asia, a group later called Segnosauria, combining *Alectrosaurus olseni* (?=*Chilantaisaurus tashuikouensis*) and *Therizinosaurus cheloniformis* within Therizinosauridae (Rozhdestvensky, 1976; Rozhdestvensky, 1977: 112). This inaccuracy, excusable at the time when the two cited works were written, was due to the fact that, following the original description of *Alectrosaurus olseni* (Gilmore, 1933), A. K. Rozhdestvensky apparently did not think that mixing of remains of organisms of quite remote phylogenetic branches had occurred when the genus was established. Thus Gilmore (1933) referred the humerus, proximal phalanx, and ungual phalanx (specimen AMNH 6368) as well as the incomplete femur, tibia and fibula, astragalus, tibiotarsus with a set of phalanges, three separate metatarsals, two incomplete ungual phalanges attributed to the forelimb, and a fragment of the distal part of the pubis (referred to AMNH 6554) to the theropod *Alectrosaurus* from the Iren Dabasu Formation (China). Mader and Bradley (1989) showed that the bones included in AMNH 6368 belong to Segnosauridae, although it is not certain that these three remains belong to a single specimen. The majority of bones initially referred to AMNH 6554 appeared to belong to one individual of the relatively small carnosaur *Alectrosaurus olseni* (Mader and Bradley, 1989). In our opinion, the two fragments of strongly curved, mediolaterally flattened ungual phalanges attributed to AMNH 6554 may also belong to the segnosaurs; they were only provisionally included with the bones of *Alectrosaurus olseni* (Mader and Bradley, 1989). From the locality that produced the segnosaurian remains (AMNH 6368), a group of platycoelous caudal vertebrae is known (AMNH 21784), which possess slightly dorsoventrally flattened centra and long, thick prezygapophyses. These vertebrae, as well as possibly vertebrae from our material (Pl. III, fig. 6), may also belong to segnosaurs. **[11/12]** The humerus of the segnosaur from the Iren Dabasu Formation has a knob on the posterior side of the diaphysis (Mader and Bradley, 1989: fig. 8; cf. Perle, 1979: fig. 2), and the distal part of the bone is wide. The proximal phalanx (AMNH 6368) has almost no distinct collateral ligament pits distally.

Having originated among Late Triassic prosauropods, segnosaurs could have survived until the end of the Cretaceous only because of the relatively strict specialization in both feeding and association with habitats where the biotic environment was not very demanding. This means that competition was weak and directional selection had slowed down. It is unlikely that segnosaurs are descendants of forms intermediate between prosauropods and ornithischians (Paul, 1984), particularly if we take into account the fact that species at the base of these lineages could have not even belonged to the dinosaurs, but to the lower grade (stage) of pseudosuchians.

The fact that there was already a notable increase among prosauropods in the size of ungual phalanges, particularly on the manual digits, situated close to the midline of the body (convergence with dromaeosaurids and troodontids) has attracted our attention. In prosauropods, this could have been related to the ability of adult individuals to pull down branches or very large leaves using forelimbs (to be more exact, using the "hook" of the inverted first digit) and also to the ability of very young individuals of prosauropods to climb vertical trunks. The latter was probably very important for reaching those areas that were difficult to access for predators, and also for using soft young leaves near the apical bud of cycadophytes and tree ferns as well as young cones of cycadophytes with insects on the surface of the latter that were not accessible to adult prosauropods. Early segnosaurs could have arisen from prosauropods by fetalization and decrease in body size in adult individuals and by a relative increase in and equalization of the size of three ungual phalanges of the forelimbs and four unguals of the hindlimbs. The diversity of segnosaurs in Asia suggests that much of their history unfolded on its territory.

Whereas the aforementioned nature of feeding in association with trees had been really typical of segnosaurs and the latter were a group of Asian origin, segnosaurs could have had to endure considerable difficulties in their migration across Beringia into North America. This is possibly the reason why there is little evidence concerning finds of segnosaurian remains in North America (Currie, 1987), and they are known only from the middle Campanian (the interval immediately following the main Late Cretaceous thermal maximum at higher latitudes [German, 1988]) when the Bering Land Bridge was most passable for warmth-loving forms.

Some discoveries beyond the boundaries of Asia may also belong to segnosaurs or to groups most closely related to them. They include an incomplete ungual phalanx from the Lower Cretaceous (?Berriasian - Barremian) of the Sundays River Formation in the Republic of South Africa (Mateer, 1987: fig. 3a-b) and the giant ungual phalanx (with a very thick base) from the Lower

Cretaceous of Niger (Rozhdestvensky, 1970, 1976; references in these works). Quite large, but only slightly mediolaterally flattened ungual phalanges (up to 31 cm long along the upper edge) were noted for the long-snouted, awl-toothed *Baryonyx* (Baryonychidae) (Charig and Milner, 1986) from the Lower Cretaceous (Berriasian) of England. **[12/13]** Similar to the latter genus is also the long-snouted, sharply cone-toothed *Spinosaurus* (Spinosauridae) from the Cenomanian (beginning of the Late Cretaceous) of North Africa (Buffetaut, 1989), and *Dryptosaurus* (Dryptosauridae), which has sharp teeth, large unguals, and a strong, distally extending deltopectoral crest (Russell, 1984) and is known from the Maastrichtian (end of the Late Cretaceous) of eastern North America (Russell, 1984; Schwimmer, 1988; Denton, 1990; Gallagher, 1990). All these forms could have formed a sister-group, more derived in relation to known segnosaurs. One cannot exclude that one or two family names given above are junior synonyms of Spinosauridae Stromer, 1915, and that the giant unguals from the Lower Cretaceous of Niger also belonged to a spinosaurid (or baryonychid, which is less likely). A close relationship between at least the type genera of spinosaurids and baryonychids is supported by the discovery of long spinous processes on the back not only of *Spinosaurus* but also *Baryonyx* (Charig and Milner, 1990: 133 and legend to fig. 9.7). Nevertheless, the presence of long spinous processes in spinosaurids and baryonychids is hardly essential for the assessment of their distant rather than close phylogenetic relationships, because development of such crests could have been determined by the character of climate and function of the dorsal crest as a heat exchanger (Norman, 1985). Such a crest is known, for instance, in the African iguanodontid *Ouranosaurus* that existed at the same time as the spinosaurids (or baryonychids), but it is absent in the currently known non-African iguanodontids.

Considering that the ungual phalanges found with the skull of *Baryonyx* differed in size (Charig and Milner, 1990: fig. 9.6), it is highly probable that only the middle digits of these animals had disproportionately large unguals. A similar state can also be observed in the closely related African spinosaurids. The body sizes of *Baryonyx* and *Spinosaurus* are such that it is impossible to assume tree climbing for adult individuals. This, however, does not exclude this ability in young individuals of these animals, similar to prosauropods, who were their ancestors.

The Early Jurassic theropod *Dilophosaurus* in the western USA, which is usually attributed to the ceratosaurs, the Late Jurassic *Ceratosaurus* (the nominal genus of Ceratosauria; Weishampel et al. [1990a] and references therein), and the Cretaceous *Baryonyx* and *Spinosaurus* (Buffetaut, 1989) have apparent similarities in the more or less pronounced awl-shaped teeth and their arrangement in a single groove (Elzanowski and Wellnhofer, 1993: 247), in the presence of a relatively pronounced notch near the contact between the premaxilla and maxilla (and also in the weakness of the contact between the latter two bones, at least in some of the aforementioned forms), in the longitudinal elongation of nostrils, in the presence of the dorsomedial crest or crests of the skull in those of the cited genera for which the skull roof is known, and in a number of other features (Charig and Milner, 1990). This, in combination with data on a number of characters in the aforementioned forms and with information on other saurischians, shows the reduction of the dentition from primitive prosauropods to segnosaurs. On the other hand, the number of evolutionarily advanced features increased from prosauropods to spinosaurids + baryonychids (+ ?dryptosaurids) and ceratosaurs (Weishampel et al., 1990a: 151-168), allosaurids, and possibly further in a number of more advanced theropods. Beginning with the baryonychids, this advanced state can be related to carnivory (predation or scavenging). **[13/14]**

These characters appear in the initial increase of tooth height and then in the acquisition of blade-like appearance, shortened skull, and decrease in the number of teeth. Torvosauridae (Galton and Jensen, 1979: fig. 1) from the Late Jurassic of the USA are one of the early groups that attained notable shortening of the snout and tooth row, and flattening of teeth, but retained large unguals on at least some digits. In segnosaurs, the loss of premaxillary teeth, strong development of ungual phalanges that are similar to each other in size in both the pes and manus, the structure of the anterior part of the ilium, and the position of the pubic bones are autapomorphies for the group. This group is a peculiar branch in the evolution that diverged from the theropod and sauropod lineages. Nevertheless, both segnosaurs and ceratosaurs retained two pairs of pleurocoels on either side of the centra of cervical vertebrae.

Theropods could have taken their origin from early sauropodomorphs of the prosauropod type, from which one can observe an obvious trend at least towards ceratosaurians. Some of the early small, aberrant theropods could have independently originated from some pseudosuchians. Ancestors of Late Triassic *Coelophysis* could have undergone "theropodization" much faster than, for instance, the ancestors of the Cretaceous baryonychids. One cannot exclude that theropods had multiple origins and that formation of a number of carnivorous and scavenging forms proceeded independently and at different rates.

In the structure of the teeth, skull, neck, trunk vertebrae, and tail, as well as in the shoulder girdle, humerus, and femur, segnosaurs retained more similarities with prosauropods than with theropods and sauropods. Therefore, in this work, segnosaurs are placed at the beginning of the system of the Cretaceous saurischians.

One cannot exclude the possibility that the segnosaurs of the same type as those known from Dzharakuduk were in part ecologically analogous to tree sloths among modern mammals. The therizinosaurids from Mongolia with their huge, considerably straightened ungual phalanges (see Barsbold, 1983) could have been comparable to some extent to the large terrestrial extinct forms of sloths and used their unguals mainly for defense against large theropods and possibly partially for procuring food. Considering the weak initial curvature of the ungual phalanges in the sloth *Bradypus tridactylus* it is feasible to infer an arboreal mode of life for young *Therizinosaurus*.

Apparently the forms intermediate in structure and time of existence between the small and relatively generalized Early Jurassic prosauropods (probably Anchisauridae) and the Cretaceous segnosaurs inhabited woody areas not affected by aridization at the beginning of the Early Cretaceous (which reached its peak probably during the Hauterivian stage during the maximum marine regression in the mid-latitudes). In Asia, stable humid conditions could have existed (based on the characteristics of atmospheric circulation), for instance, in southeastern Indochina (Sinitsin, 1966) (See also Parts 4.4.1.187 and 4.4.2.194).

[14/15]

1.2. Theropods

In many of the localities studied (see Part 4.1), a relatively large portion of finds comprises remains of carnivorous dinosaurs, particularly teeth with resorbed roots. This is evidently determined by the relatively common accumulation of remains of predators and scavengers under conditions when herbivorous prey is consumed in large numbers. Under these conditions, accumulation of permanently shed teeth of theropods in the sediments will be inevitable, and the proportion of their remains in the locality will be much higher than in the former "living" community of organisms. In this connection, it should be noted that calculation of the ratio of remains of the herbivorous and carnivorous dinosaurs in fossil associations cannot provide information about poikilothermy, heterothermy, or homoiothermy in dinosaurs. Such estimates are usually based on the assumption that poikilothermic predators need less food per unit of time, and that a larger number of poikilothermic predators can feed on the same biomass of herbivorous prey than homoiothermic ones. Such questions of dinosaurian bioenergetics are difficult to resolve because carnivorous dinosaurs, even the large ones, could fed not only on other dinosaurs, but also on other vertebrates and even invertebrates and on both living and dead animals. Eventually, they could eat dead individuals of their own species. The latter appears to be quite possible; in fossil associations, teeth are numerous, whereas parts of braincases and relatively complete jaws of theropods are very rare.

Many teeth of carnosaurs (considered within the limits of the group assumed by Weishampel et al. [1990a]) in the localities studied by us have tracks of split-off enamel and wear facets not only near the apex of the crown, but immediately in front of it, along the anterior edge. Because the tooth in the jaw usually had a slightly recurved apex, the area situated slightly anterior to the apex of the tooth (Pl. I, fig. 5) was the first place that contacted food, and also the bones inside the body of the animals to be consumed. A study of a dozen of such teeth with wear marks at the apex shows that, apart from cutting through meat, such mediolaterally flattened teeth of Turonian-Coniacian carnosaurs, as in the Jurassic torvosaurids (Britt, 1991) or in the Late Cretaceous (middle Campanian) "*Laelaps*" *explanatus* Cope (Lambe, 1902; Osborn, 1924b), were used also for splitting bones. Such considerably flattened teeth in Dzharakuduk (Pl. I, figs. 5-6, 8) probably belong to *Alectrosaurus* - the largest theropod in the assemblage. At least some of the sharply angled fragments of tubular bones in late Barremian - middle Aptian strata in Transbaikalia, the late Barremian - Santonian of Middle Asia, and the Maastrichtian of the Amur Region and Chukot Peninsula could have been the result of destruction of bones by the teeth of various large theropods that played the roles of predators and scavengers. These fragments, together with meat, could remain in the stomach for some time and later, after the initial stages of **[15/16]** digestion, could have been ejected as pellets (Fedorov and Nessov, 1990; Parts 4.1.2.15 and 4.1.3.151).

In the Coniacian of Dzharakuduk (Site CBI), rod-like small ossified ligaments of dinosaurs have been found (Yuryev, 1954b). Bone "shavings" were taken from one of the sides of the bones; as a result, a flat surface was formed along the ossified ligament. Long grooves situated parallel to each other extend over this surface at an angle of several degrees to the long axis of the bone. The distance between these grooves correlates with the distances between the denticles along the posterior edge of teeth of a species of large theropod dominant in the assemblage. Evidently the predator tearing flesh that contained ligamentous bones from a dinosaur (most probably from the dorsal part of the sacral regions or at the basis of the tail) moved the head slightly sideways or upwards with a very strong effort sufficient for taking "bone shavings" from one of the sides of the long ligament bone. It is unclear whether the food was taken from live prey or a dead animal.

An important replacement among the dominant carnosaurs took place in Middle Asia between the Coniacian and Santonian. Up to this boundary (at least since the end of the Albian) there existed carnosaurs with relatively strongly mediolaterally flattened teeth (of the *Alectrosaurus* type) and, from the beginning of the Santonian at least to the early Campanian, there were other theropods that had notably (labiolingually) thicker teeth more typical of tyrannosaurids (Currie et al., 1990: fig. 8.5 K,N), but nevertheless less thick than in *Tarbosaurus bataar*.

Troodontids, a family of relatively small theropods, is found in the CIS in the early Cenomanian (Pl. I, fig. 23), probably in the Santonian (Pl. III, fig. 12), and significantly in the middle Campanian (Kyrkkuduk II). Whereas the most archaic of the forms discovered in the Cenomanian of Sheikhdzheili generally possesses features apparently acquired by its ancestors in Asia, the larger *Troodon* cf. *T. formosus* from the Kakanaut locality (Magadan Region) is probably a reverse invader from North America (Nessov and Golovneva, 1990). One should bear in mind that the oldest troodontids are first known in Asia in the late Aptian (Khovboor, Mongolia) and, in North America, the family is first recorded from the late Albian of Utah (Parrish and Eaton, 1991).

Oviraptorosauria were reported by A. N. Riabinin (1939) with some doubt for the fauna from the Late Cretaceous of Tashkent Chul'. Now actual jaws of dinosaurs of this group have become known from the upper Turonian of Dzharakuduk (Pl. II, fig. 16). They belong to the family Caenagnathidae (Currie et al., 1994 [“1993”]) (Pl. II, fig. 16) and represent an additional link between faunas from the coastal plains of the first half of the Late Cretaceous in western Asia and the second half of the Later Cretaceous in western North America. According to one hypothesis (Weishampel et al., 1990a), these toothless dinosaurs crushed shells of pelecypods on the anterior specialized portions of the jaws. Opponents of this idea note the possibility that oviraptorosaurs could have eaten leaves or thick seeds and collected fruit. It should be noted that in the upper Turonian of Dzharakuduk, at the level with the caenagnathid jaws, remains of relatively small pelecypods, in particular of the genus *Sainshandia* (Martinson et al., 1986), are rather numerous and typically preserved in the form of phosphatized gills, mantle, foot, or siphons. **[16/17]** If at least a few oviraptorosaurs did feed on mollusks this could have taken place during low tides resulting from wind action in temporarily drying shallow water areas of the basins.

Oviraptorosauria had a slightly enlarged ungual on the first digit of the forelimb; the manus of these dinosaurs was obviously grasping (Barsbold, 1986; Weishampel et al., 1990a: figs. 10.3-10.4). This could have been related to procurement of food such as pelecypod shells (Weishampel et al., 1990a: 258). It is more probable that this was associated (at least for some Oviraptorosauria) with utilizing seeds of cycadophytes, *Gingko*, and possibly some angiosperms. The majority of modern representatives of cycadophytes is associated with oceanic coastal regions of the continents; some species occur in the typical sea coast formation in the sublittoral zone and on coral-reef islands where salinization of soils is possible. Large, brightly colored seeds of cycadophytes (frequently 3x2 or 4x3 cm and sometimes up to 8 cm in length) are sometimes arranged into solid cones, which reach tens of centimeters in length (Grushvitsky and Chavchavadze, 1978). Many present-day wild animals (bears, monkeys, rodents, etc.) willingly consume the soft external covering without damaging the harder inner one containing the seed with its toxic content. These animals also spread seeds. The edible part of the seeds is covered by a thick rind. The jaws in the earliest known oviraptorosaur, *Caenagnathasia* (Pl. II, fig. 16) (Currie et al., 1994), and in more recent and more derived forms could have been quite suitable for "gnawing out" of seeds firmly appressed to each other within the cones, all the more so, because trunks of many cycadophytes were not tall and their cones would have been accessible to oviraptorosaurs. If the sharpened edges of the toothless jaws had been able to extract seeds, the system of complex ridges and knobs on the alveolar surfaces probably permitted separation of the edible portion of the seeds from the inedible part. Oviraptorosaurs, if they fed on seeds of cycadophytes by "gnawing” them out of large cones, obtained energy through the terrestrial vegetation fertilized during tides of waters rich in organic material from the sea or liman basin. However, if all or some oviraptorosaurs had been sclerophages adapted to locomotion in water they could have obtained energy from the food web through plankton and suspended detritus from bivalves (see Weishampel et al. [1990a: 258] and references in that work). Many other small theropods probably collected dead fishes and amphibians near the coast, and thus could also have fed on aquatic inhabitants.

It should be noted in this context that theropods of different species relatively frequently left their tracks in coastal shallow areas. Possibly the dominance of tracks of theropods in many footprint assemblages (Part 4.4) points to a general collecting strategy in different-sized species of these animals.

One cannot rule out that theropods of the genus *Troodon* with its short teeth with inflated crowns and few denticles oriented towards the apex and somewhat towards the sides were also adapted to feeding on seeds of cycadophytes. The genus *Troodon* was particularly widespread during the development of the Kakanaut Formation in the northeast of the Koryak Highlands (middle Maastrichtian). A monodominant plant **[17/18]** community consisting only of cycadophytes of the genus *Encephalartopsis*, with a short trunk, was frequently noted for that period (Nessov and Golovneva, 1990; Krassilov et al., 1990).

The external layer of the cover of the ovule in present-day *Gingko* (Samylina, 1978) is juicy, amber-yellow in color, and 5-6 mm thick. It, however, has the smell of rancid butter and causes allergic reaction in humans (Coe et al., 1987). Inside the deeper denser cover (looking like the "stone" of a relatively small apricot), there is a structure used by people for food after heat treatment, the ovule, which in time develops into a seed. One such "stone," approximately two times smaller and slightly more flattened on the sides than in the Recent species, has been found in the Coniacian of Dzharakuduk. Such structures could have been among the food objects of oviraptorosaurs and troodontids. Known from the second half of the Late Cretaceous in Mongolia are very firm fruits or compound fruits of angiosperms (which were studied by V. A. Krassilov and Martinson [1982]). We cannot exclude that they also could have been consumed by oviraptorosaurs and troodontids.

As noted, segnosaurs probably had large ungual phalanges on all digits (Perle, 1981). However, troodontids and dromaeosaurids had large unguals on the first digit of the forelimb and the second digit of the hindlimb. We can suppose that these large ungual phalanges situated close to the midline of the body could have been used not only for attack and defense (see Barsbold and Perle [1983]), but also, like an electrician's climbing-irons, for climbing trees with vertical trunks. It is possible that the downward or even slightly backward turn of the pubis in segnosaurs and in the dromaeosaurids *Adasaurus* and *Deinonychus* (Barsbold and Perle, 1979: fig. 1; cf. Weishampel et al., 1990a; Barsbold, 1983) - i.e., transformation to the opisthopubic state – represented a specialization for quadrupedal climbing, the rearrangement transforming the pronounced keel-shaped abdomen into a flattened abdomen, which facilitated climbing along vertical trunks. The analogous development of the opisthopubic state in birds such as *Archaeopteryx* was possibly also connected with a certain specialization in climbing vertical trunks to escape from ground predators.

If dromaeosaurids truly were predators capable of climbing trees, considering the presence of their remains in the late Turonian and Coniacian of Dzharakuduk (Pl. II, fig. 11), we can assume that tree canopies did not provide absolute protection for segnosaurs hiding there. It is important to note that pelvic structure is known only for one troodontid specimen, where it was still of the propubic type (Weishampel et al., 1990a: 265); thus specialization for climbing in representatives of the genus *Troodon* was not as advanced as in dromaeosaurids.

The scope of the present work does not permit us to dwell on the ecological characterization of other theropod groups. It can be noted, however, that remains of very young individuals of large theropod species and of small carnivorous dinosaurian species are very common in the sediments of channels situated between basins. **[18/19]**

1.3. Sauropods

Sauropods are dinosaurs of medium to large size. Known among sauropods are more or less terrestrial forms with broad and short teeth and also species with thin and long, pencil-like teeth. The majority of the latter was amphibious and mostly fed on soft aquatic vegetation. One can assume for terrestrial sauropod forms an ability to stand on their hindlimbs to obtain green fodder from the high parts of the canopies. Development towards elongation of the neck ("giraffe-like state") at different stages in the (Jurassic) evolution of the group was related to obtaining food. The aquatic and amphibious forms of sauropods could swim in the basins with the neck held on the water surface.

Apparently its was quite common for sauropods to use gastroliths (stones in the muscular part of the stomach), which functioned based on the principle of a ball mill for grinding the material of food boli. Considering that gastroliths, which are here attributed to sauropods (Stokes, 1982; Whittle, 1988; Gillette, 1990), in the Turonian-Coniacian of Dzharakuduk consist mostly of brightly colored (red, pink, brown and also white and striped) jaspers, flints, and quarzites, one can infer that the sauropods could at least distinguish red color.

It is likely that sauropods, like other herbivorous dinosaurs, used unicellular intestinal symbionts, which were capable of breaking down cellulose (Coe et al., 1987). We cannot exclude that the first herbivorous mammals (closely related to Condylartha) that existed in the Coniacian age in the Dzharakuduk region obtained intestinal symbionts for breaking down cellulose from herbivorous dinosaurs, in particular from sauropods.

At the boundary between the Middle and Late Jurassic (Bathonian - Callovian), sauropods dominated among the herbivorous forms of dinosaurs. The same pattern was noted for the late Barremian - middle Aptian (Transbaikalia). These were forms with short thick teeth (Cetiosauridae or Camarasauridae). However, from the end of the Aptian (Clansayesian) to the early Campanian, only sauropods with long neck vertebrae and thin, pencil-like teeth with a nearly smooth enamel surface are known from Uzbekistan (Nessov, 1985: pl. III, fig. 7) (Pl. III, figs. 9-11). They belonged to the Diplodocidae or Titanosauridae (McIntosh, 1990), but differed notably from the North American *Alamosaurus* (Kues, 1980: figs. 3-5) in the relief of the tooth enamel and the much narrower teeth, and also in the relatively lightly built skeleton. Possibly replacement of short-toothed sauropods by long-toothed sauropods occurred over large areas of Asia. Neck vertebrae of long-toothed sauropods of the late Turonian - Coniacian of Dzharakuduk (Uzbekistan) were long, abruptly opisthocoelous, with strongly protruding external stiffening ribs and large internal cavities. In the Coniacian of Dzharakuduk (upper part of site CBI-14), centra of various vertebrae of this type reached a length of 38 to 40 cm, which is relatively large, compared to sauropod giants of the Jurassic of North America (Jensen, 1985a,b), but small teeth of sauropods, remains of their young, occur here much more frequently. **[19/20]** Sauropod teeth with resorbed root are relatively common in the upper Turonian and Coniacian (Pl. III, fig. 9); their skeletal remains (Pl. X, fig. 24) are exceedingly rare. Therefore, in the interbasin channels, near which localities of the Dzharakuduk type were formed, sauropods lived for a long time, but rarely died. Overall, sauropods from the Aptian-Santonian to early Campanian were still uncommon, and apparently their diversity was extremely low. Considerable differences in the structure of teeth and vertebrae between the Late Cretaceous sauropods of Uzbekistan and the somewhat later *Alamosaurus* from the southern part of North America (Kues, 1980; Lucas and Hunt, 1982), as well the thermophilic nature of the sauropods, which extended in the northern direction no further than England and the Amur Region, permit us to assume that there was no exchange of sauropods between America and Asia (across Beringia) at least during the second half of the Cretaceous.

1.4. Stegosaurs and ankylosaurs

The dinosaurs from these two groups are sometimes combined in a single group (including some groupings closely related to them or without such affinities) under the name armatosaurs (A. K. Rozhdestvensky, pers. comm., 1978; Zhao, 1983) or thyreophorans (Sereno, 1986). Their remains are usually rare in localities in the CIS. Based on scant teeth, the presence of stegosaurs was established near the boundary between the Middle and Late Jurassic (Kirghizia). Remains of ankylosaurs have long been known from the Cretaceous of the CIS. At the site CBI-14 in the Coniacian of Dzharakuduk, single teeth of ankylosaurs, unlike their pre-Turonian discoveries (Nessov, 1985b: pl. I, fig. 9) (Pl. IV, figs. 10-11), usually do not have a distinct constriction at the boundary between the root and crown. The teeth of ankylosaurs that lived before and after the Cenomanian - Turonian boundary usually do not show traces of wear by food, but sometimes they have facets that formed as a result of contact with teeth of the opposing tooth row. Such teeth occur in strata with approximately the same frequency as mammal teeth of this age (in the richest areas, approximately one specimen per 600-1,000 kg of matrix). The frequency of occurrence for remains of ankylosaurs is dozens of times lower than that for remains of hadrosaurids and theropods (this applies not only to one locality, but to a number of localities with several Late Cretaceous associations). This suggests that, in the semihumid conditions of the coastal plains, a relatively small current of energy flowed through ankylosaurs during the Cretaceous (as through the stegosaurs during the Jurassic), and they probably had a relatively limited, non-constant food source. The powerful protective armor of ankylosaurs, up to an ossification in the eyelid capable of protecting the eye like the visor of a knight's armor (Coombs, 1972), the huge amount of phosphate, which had to be consumed with food to build the powerful exoskeleton, the very large and complex nasal cavity, which apparently housed an efficient olfactory organ, extremely weak tooth wear, and a number of other morphological details of these animals suggest that these armored dinosaurs were not exclusively herbivorous forms, but were facultative consumers of egg clutches of other dinosaurs (Rozhdestvensky et al., 1987). **[20/21]** As is known (Weishampel et al., 1990a) for at least in some species of the ornithopods, and possibly also a number of other groups of dinosaurs (see analogues among extant crocodylians; Coombs, 1989), the clutches were protected by parents and the diverse impact of such adult individuals (protecting eggs) on ankylosaurs stealing the eggs could have been a selective factor in the development and strengthening of the armor of the latter. During times other than the reproductive periods of other dinosaurs, ankylosaurs could have been coprophagous or omnivorous forms. However, the relatively long incubation period of large dinosaur eggs could have provided ankylosaurs with food for a large part of the annual cycle. Such a hypothesis explains the paradoxically weak tooth wear by food in ankylosaurs, and the presence of a huge amount of phosphates accumulated in the body of these animals in the form of hypertrophied defensive bony structures. It should be noted that advanced stegosaurs as well as ankylosaurs had inside the front of the snout inside a spoon-shaped toothless space suitable in shape and position for crushing relatively fragile eggs. Weak wear by food is noted also for the stegosaurs of the Jurassic of the Fergana region. It is possible, therefore, that the first stages of using mass clutches of dinosaur eggs for food could have started as early as the Jurassic, and these stages were present in stegosaurs. At the same time, there is a fact that can be interpreted as contradicting the presented hypothesis for ovophagy in ankylosaurs. It is known that the content of the nitrogen isotope ^{15}N in organic matter increases, although insignificantly, from one trophic level to another. Preliminary results of analysis of this isotope content of bones of several dinosaurs from North America (Ostrom and Macko, 1991) showed that its amount in the ankylosaur *Panoplosaurus* was much lower than in the hadrosaur; in the latter, it was lower than in the ceratopsid, and the highest amount was found in the tyrannosaurid. If the results of the cited isotopic analysis are correct and the isotope content in the eggs correlates with that in the body of the female that laid them, this fact would indicate a different nature of feeding of armored dinosaurs than is proposed above in this chapter.

In the Cretaceous of Uzbekistan, a replacement of ankylosaurs is noted at the Cenomanian - Turonian boundary. Quite common in localities of Albian-Cenomanian age are nearly flat, small, and polygonal plates of dermal armor (Shamosauridae); common in Turonian - Santonian strata are large, longitudinally elongated, and boat-shaped osteoderms with a cavity inside (Ankylosauridae). This replacement is associated with the largest rearrangement during the Cretaceous of the faunal assemblages on land and in the sea, climatic pattern, and atmospheric and oceanic circulation.

1.5. Ornithopods

Remains of Hypsilophodontidae are known from the Jurassic of Africa, Asia, and North America and the Early Cretaceous of Africa, Australia, Europe, and North America. They survived in the form of relicts in North America until the end of the Cretaceous (Maastrichtian) and at least until the end of the early Campanian in southern Sweden. **[21/22]** Despite the similarity between the Campanian - Maastrichtian dinosaurian faunas of western North America and the coastal plains along the southwestern edge of the former Asian landmass, no bones or teeth of hypsilophodontids have been reported in the literature from the Cretaceous of Asia. However, eggshell is known from China, which in details of its structure is similar to that attributed to hypsilophodontids in North America (Zhao and Li, 1993). Moreover, in the upper Albian of Khodzhakul (Karakalpakistan) and in the upper Turonian - Coniacian of Dzharakuduk (Uzbekistan), teeth are known with two deep grooves on either side of the pronounced crest (Nessov, 1981: fig. X, 13) (Pl. X, figs. 19-23). These teeth, although problematic and possibly belonging to young hadrosaurids (Currie, 1987; Hall, 1993: fig. 2A), still resemble teeth of hypsilophodontids. They differ from some hypsilophodontid teeth (Galton and Taquet, 1982), but in some details are similar even to teeth of dinosaurs more archaic than the hypsilophodontids. In any case, one apparently should not assume that hypsilophodontids were found in the Late Cretaceous in Asia. The teeth noted bear resemblance in the development of the median crest on the crown and the depth of the grooves on either side of the crest to the teeth of some iguanodontids (Weishampel and Bjork, 1989: figs. 6-7). From the latter, the teeth from Uzbekistan differ in the absence of additional crests parallel to the main one.

Representatives of the family Hadrosauridae (duck-billed dinosaurs) from the late Albian and Cenomanian of the Kyzylkum were, for the most part, small (height of body approximately 2 m and weight approximately 100-200 kg, rarely heavier). At that time, their remains (Pl. IX, fig. 1) occurred quite infrequently in localities. For the beginning of the Cenomanian, this may be accounted for by the abundance of primitive small, herbivorous Protoceratopsidae (*Asiaceratops*), which "took" a considerable part of the energy from the vegetation. At the boundary between the Cenomanian and Turonian, hadrosaurids (Pl. VIII, figs. 1-10; Pl. IX, figs. 2-21; Pl. X, figs. 3, 4, 11-14; Pl. XI, figs. 1, 2, 4) became completely dominant among the dinosaurs of the coastal plains of southwestern Asia.

This apparently may be characteristic of dinosaurian faunas of Asiatic origin in the coastal plains of the entire large area of Asiamerica. The Ayat island (Fig. 2), situated west of the major, southern part of Turgai Strait (northwestern Kazakhstan), was inhabited by a fauna dominated by hadrosaurids, whereas these dinosaurs were quite rare in Europe (Buffetaut [1983] and references in that work). In Europe, for instance, in southern France, sauropods continued to be dominant nearly until the very end of the Cretaceous.

In the upper Turonian - Coniacian of Dzharakuduk (Uzbekistan), representatives of the hadrosaurine subfamily (comprising flat-headed forms, the lower stage in the family of duck-billed dinosaurs) were dominant. But at that time, at least in the Coniacian, representatives of a higher evolutionary stage, the lambeosaurine subfamily (helmet-headed forms) already existed, but were rare (Pl. IX, figs. 13, 16; Pl. XI, fig. 4). **[22/23]**

[FIGURE 2 HERE]

Fig. 2. Dispersal routes of South Asian dinosaurian fauna to the Middle Asian region west of North America and reverse shift of American forms into Asia.

[23/24]

During the evolution from hadrosaurines (Pl. VII, fig. 1) to lambeosaurines, the depth of the hypophyseal region of the braincase, particularly the basisphenoid, increased considerably, which was probably related to an increase in the size of the hypophysis and changes in position and diameter of the cerebral branches of the internal carotid artery, some veins, and the abducent nerve. Bones of young hadrosaurids (with a reconstructed total body length of approximately 40 cm) are observed relatively frequently in the sediments of interbasin, liman-lake channels with directionally variable, bidirectional currents as a result of wind-tide action (Ro_ek and Nessov, 1993: fig. 3). The most numerous remains here are teeth of hadrosaurids, worn and shed during life, that had undergone also chemical action in the intestine (Pl. VIII, fig. 10). This suggests that hadrosaurids, including their young, were a relatively permanent presence in the area of the aforementioned channels. The egg-laying places could have been located not far from the places of deposition of the hadrosaurid bony remains. However, there is almost no hope to discover eggshell of hadrosaurids or other dinosaurs in such liman areas: Dzharakuduk, Tyulkeli, and other localities of the Turonian - Coniacian. In this area, in the localities with dinosaurian remains, bivalve shells as well as eggshell consisting of calcium carbonate were completely dissolved; remains of mollusks consist only of sandstone steinkerns, or phosphatized soft tissues including gills, mantle, siphons, and ligaments. The cement of the rock matrix contains little or no calcium carbonate. All this indicates a relatively low pH of the ancient interstitial waters in the soils, and also in the ground at the bottom of the water bodies. Under such conditions, only very small fragments of eggshell can be preserved in rare instances. This cannot happen, however, unless the shell is subject to phosphatization. Shell is only preserved in rocks with carbonate cement.

It should be noted that the portion of hadrosaurid remains in fossil assemblages increases from the late Turonian through the Coniacian to the Santonian and early Campanian. A great abundance of bony remains of hadrosaurids is noted for the Yalovach Formation in the northeastern Fergana Valley and remains of crest-knobbed, considerably elongated eggs in the same formation literally a few kilometers westwards (in the north and northeast of the Fergana Depression). This permits classifying the remains of elongated eggs with crest-knobbed relief and angusticanaliculate type of perforation, which are dominant in the Yalovach Formation and in the lower Nichkesai subformation of the Fergana and in the North Zaisan Formation of the Zaisan Basin, as hadrosaurid (Nessov and Kaznyshkin, 1986) rather than carnosaurian (Mikhailov, 1991) or protoceratopsid (Rozhdestvensky, 1971: 30). Referring the eggs to carnivorous dinosaurs, the abundance of such eggshell in the localities from the Upper Cretaceous in the CIS (up to 95-100% of collections from the Fergana and Zaisan areas) contradicts the ecologically determined low reproduction rates of carnivorous forms and scavengers. It is more likely that these eggs could have belonged to herbivorous hadrosaurids, which are dominant in the assemblages.

[24/25]

1.6. Ceratopsia

The small protoceratopsids (Protoceratopsidae) of the early Cenomanian of the southwestern Kyzylkum, belonging to the genus *Asiaceratops* (Nessov et al., 1989), have only been found in the form of isolated bones (except for groups of bony elements of braincases). The common occurrence and dominance of their remains among other dinosaurian bones and teeth suggest a possible gregarious mode of life and former abundance of these animals. Hundreds of fragmentary remains belonging to different individuals provide sufficiently significant evidence for very small body size in *Asiaceratops* (Pl. IV, figs. 13-16; Pl. V, figs. 1-19; Pl. VI, figs. 1-15, 19-37; Fig. 3); because of the mixing of the macerated remains in the interbasin channels (Nessov, 1990; Ro_ek and Nessov, 1993), we can assume that almost every bone of these dinosaurs found belonged to a separate individual. Therefore, such characters of *Asiaceratops* as small size (the centrum of the largest vertebra among the more than one hundred discovered is only 16 mm in length) and the small number of teeth in jaws, the abundance of folds on the crowns (Nessov, 1981: fig. VIII, 7; Nessov et al., 1987, 1989) are not juvenile features (Kurzanov, 1992) but rather characters of adult individuals of *Asiaceratops*. These characters are among other features diagnostic for the genus (which is one of the oldest in its family). This genus existed some 18 million years before *Protoceratops*. Until quite recently the latter genus and *Bagaceratops* (Maryanska and Osmolska, 1975) were regarded as the most primitive in the family and in the entire suborder Neoceratopsia. Apparently the oldest known protoceratopsid in the Central Asian part of the CIS existed during the late Albian of Karakalpakistan (genus *Kulceratops*) (Pl. IV, fig. 12). Only two problematic teeth of primitive protoceratopsids, which, like *Asiaceratops*, show similarities to teeth of psittacosaurids (Rozhdestvensky, 1978: 68; Chure and McIntosh, 1989: 26), have been found during more than 8,000 man-hours of prospecting in Coniacian-age localities. In the Santonian - early Campanian of Middle Asia, remains of protoceratopsids have not been discovered, whereas in Mongolia and in Northern China (Inner Mongolia), protoceratopsids were among the dominant forms during this time interval. It should be generally assumed that there were three episodes of change among dinosaurian faunas in Asia: the first one with dominance of sauropods, the second with dominance of protoceratopsids, and the third with dominance of hadrosaurids. In the southwest of the Asiamerican landmass (Fig. 2), the first stage ended in the late Aptian (or slightly earlier), the second at the beginning of the Turonian, and the third possibly in the late Campanian and Maastrichtian. For Mongolia, these episodes occurred in pre-Aptian times, at the end of the Campanian, and in the middle Maastrichtian. Thus the rate of replacement of dominant forms in Middle Asia was greater, and there was particularly notable heterochrony in the disappearance of protoceratopsids and establishment of the dominance of hadrosaurs.

The discovery of true Ceratopsidae (Pl. VII, figs. 1-8, 15-21) in the Cretaceous of Uzbekistan (Dzharakuduk II) came as a surprise, despite the relatively secure identifications of these dinosaurs by A. N. Riabinin and A. P. Gartman-Veinberg already in the 1930s [see Appendix and also L. I. Khozatsky (1949)].

[25/26]

[FIGURE 3 HERE]

Fig. 3. Reconstruction of the skull of the protoceratopsid *Asiaceratops salsopaludalis* Ness. et L. Kazn. (early Cenomanian, Karakalpakistan): a, left lateral view; b, dorsal view.

The first ceratopsid species formally described from the CIS was *Arstanosaurus akkurganensis* Suslov et Shilin from the locality Akkurgan (Kazakstan). In the initial description, it was, however, not referred to ceratopsids but to hadrosaurids (Shilin and Suslov, 1982). Nevertheless, this dinosaur, like all ceratopsids, had teeth with bifurcated roots, and the replacement tooth had its apex situated in the space between the two roots of its predecessor (Shilin and Suslov, 1982: fig. 1c). The ceratopsid nature of the jaw was established by J. Horner and confirmed by D. A. Russell (pers. comm., 1989) (Nessov et al., 1989). However, this species is still classified as a hadrosaurid (Weishampel et al. 1990a: 129, 558). It is paradoxical that even a colored reconstruction of *Arstanosaurus* (Britt et al., 1990) was that of a hadrosaur.

Ceratopsids of the late Turonian - Coniacian of Dzharakuduk (genus *Turanoceratops*) had typical, distinctly bifurcated tooth roots (Nessov, 1986: figs. 2, 4) (Pl. VII, fig. 1). **[26/27]** However, unlike the advanced forms that lived 10-20 million years later in North America, these ceratopsids from southwestern Asia had only two teeth in each vertical row [one functional and one replacement (Nessov et al., 1989: pl. I, fig. 19b) (Pl. VII, fig. 21)]. The maxilla of the holotype contained a total of approximately 20 vertical tooth series (which is few when compared to ceratopsids of North America). The arstanosaur is a much more advanced representative of the family; it had a larger number of teeth (about four) in each vertical series (Shilin and Suslov, 1982: fig. 1), whereas North American forms of ceratopsids had 3-5 teeth per vertical series in the jaw bone. Ceratopsids of the genus *Turanoceratops* had one large, forward-bent, and symmetrical nasal horn (Pl. VII, fig. 15; Fig. 4) and small, horn-like projections above the eyes, a moderately posteriorly elongated squamosal (which is slightly serrated or unserrated along the posterolateral margin), and the medial bridge of the frill slightly decreases in width upwards and backwards. The animal resembled the most primitive representatives of North American Centrosaurinae such as *Eucentrosaurus* and *Avaceratops* (Dodson, 1990).

Wherever bones and teeth of ceratopsids are found in Middle Asia, they are two or more times less common than remains of hadrosaurids, which is usually also the case in North America (Dodson, 1987: 71). *Turanoceratops*, like its North American relatives, lived under conditions of a semihumid climate, apparently in the platane forests along interbasin channels and in adjacent marshes. The nature of the dentition, allowing cutting rather than grinding, permitted ceratopsids to use coarse foods. Such foods could apparently be ground up further in the stomach.

[FIGURE 4 HERE]

Fig. 4. Schematic reconstruction of the skull of the ceratopsid *Turanoceratops tardabilis* Ness. et L. Kazn. (late Turonian, Uzbekistan), in lateral view. Dotted areas indicate parts preserved in the material.

In the southwest of the Asian landmass, ceratopsids evidently existed from the beginning of the late Turonian (*Turanoceratops*) up to the Santonian - **[27/28]** early Campanian (*Arstanosaurus*), i.e., for at least 7.5-12 million years. In Mongolia and China, ceratopsids have not yet been found; the only fragment attributed to this group allows other interpretations (Gilmore, 1933; Steel, 1969: fig. 23, 3), such as attribution to ankylosaurs (Coombs, 1987). It is interesting that protoceratopsids, like ceratopsids, demonstrated increase in body size in their phylogenetic lineage (Kurzanov, 1992). A probable region of ceratopsid origin were the coastal plains in the south of Asia. A possible time of origin for the group was the early Turonian; the climate was semihumid or humid.

The evidence for *Turanoceratops* indicates that, in the early stages of the evolution of ceratopsids, the development of a strong nasal horn, horn-like supraorbital projections, and strong flattening and growth of the squamosal (i.e., tournament armament) left behind the process of increase from 2 or 3 or 4 teeth in the vertical series. But these teeth were already quite typical of ceratopsids (Marsh, 1896: pl. LXVII, fig. 2; Hatcher et al., 1907: fig. 43); they had lateral and medial projections of the root. However, the first and last teeth in the tooth row in *Turanoceratops* almost surely were single-rooted teeth. It is not known whether such teeth existed in North American ceratopsids.

The ceratopsid genus *Turanoceratops* is the oldest in the family. Comparison of details of the braincase in *Turanoceratops* (Fig. 5) with illustrations of braincases of North American ceratopsids explicitly shows that the general evolutionary trend in the family could have been from forms with a short braincase, with weak crests for the attachment of muscles and ligaments for lifting the head (as in *Turanoceratops*), to forms with a longer braincase, sharp crests for ligaments and muscles above the foramen magnum (Hatcher et al., 1907: figs. 6, 8, 107; Lull, 1907: pl. XLIX; Weishampel et al., 1990a: 602).

[FIGURE 5 HERE]

Fig. 5. Braincase of ceratopsid *Turanoceratops tardabilis* Ness. et L. Kazn.: a - posterior view, b - view from the left.

[28/29]

One can see also that, from the Turonian to the Campanian - Maastrichtian, the dorsal and lateral (and somewhat posterior) orientation of the axes of the paroccipital processes shifted to a lateral position, the bases of these processes shifting ventrally, closer to the base of the occipital condyle. At the same time, a lateral move (and possibly decrease in height) of the basioccipital tubera took place. All this could have been related to the increasing role of muscle efforts of ceratopsids required not only to support the thick skull in its usual stationary position or for lifting it up, but also to increase efforts for lateral shift of the entire skull or for counteracting such lateral shifts.

It is difficult to understand that the increase in the length of the frill in ceratopsids, particularly of its squamosal part, was connected only with the development of the external adductor muscles of the lower jaws (Ostrom, 1966), because increasing muscle length is not an efficient way to increase muscle strength. Moreover, the frill of ceratopsids increased allometrically with age

(Farlow and Dodson, 1975). One probably has to agree with the opinion that the most elevated, posteromedial part of the frill in protoceratopsids and ceratopsids was used mostly as a signalling structure (Farlow and Dodson, 1975; Davitashvili, 1976).

North American ceratopsids of the Campanian - Maastrichtian had the occipital condyle moved far back, with a spherical shape of its articular surface, and the four anterior cervical vertebrae were fused. These data, as well as evidence on the structure of the squamosal and maxilla of *Turanoceratops* and skulls of other ceratopsids (Hatcher et al., 1907; Lull 1907, 1933; Ostrom and Wellnhofer 1986; Weishampel et al., 1990a; references in these works), and also for the protoceratopsids from the Cenomanian and psittacosaurids from the Aptian, permit us to assume that the ritual of tournaments between males, by pushing the opponent back by means of lateral blows and pushing with the forehead, was established relatively early in the evolution of the suborder Ceratopsia. This concept differs essentially from the one assuming tournaments of *Monoclonius* with strong maneuvering, as in present-day rhinoceroses. It differs also from the idea that tournaments in *Protoceratops* were similar to those observed in the relatively short-horned mountain goats of the genus *Oreamnos* in North America (Farlow and Dodson, 1975). The latter, however, cannot be suitable biomechanical models, because they have neither the median crest on the top of the head nor lateral flattening of the snout. According to the concept presented here, the foreshortening and rough bony structure of the antorbital region as well as the jugal and surangular bones in *Protoceratops* were related to lateral and anterolateral pressure applied to the jugal and antorbital region of the rival during tournaments (Fig. 6a). Selection proceeded to strengthen certain parts of the skull for pushing forward and to the side, and counteracting the competitor's pushing. In the early, small protoceratopsids of the genus *Asiaceratops* (Nessov et al., 1987: 148) the maxilla was lightly built and relatively much longer (Pl. V, fig. 2) than in *Protoceratops*. However, judging from the hypertrophy of the jugal and surangular bones in *Asiaceratops* (Pl. VI, fig. 1; Fig. 3), forceful cheek contacts between competitors were quite common and important. **[29/30]**

The extraordinarily rough detailed structure of the maxilla in the Early Cretaceous *Kulceratops* (Pl. IV, fig. 12) could have been related to particularly large lateral loads during tournaments. The relatively late representatives of the genus *Protoceratops* (Weishampel et al., 1990a: fig. 29.1) had the most specialized state for the tournaments. Their squamosal still occupied a very small area; the frill probably served only as a display structure (Farlow and Dodson, 1975), significantly increasing the area of the head visible from the front, which could have affected competitors prior to actual physical contact.

[FIGURE 6 HERE]

Fig. 6. Correlation (relative position) of heads of combating males of the protoceratopsid *Protoceratops andrewsi* Granger et Gregory (a) and the ceratopsid *Turanoceratops tardabilis* Ness. et L. Kazn. (b). Outlines of the skull of *P. andrewsi* simplified from Brown and Schlaikjer (1940) and Rozhdestvensky (1965).

[30/31]

Superimposing a drawing of a *Protoceratops* skull in lateral view on a mirror image of the same drawing made on transparent tracing paper would show (Fig. 6a) that the anterior end of the rostral bone was placed opposite the posterior end of the jugal of another specimen and would provide coincidence of the rudimentary nasal horns in both combatants and the most convenient position during tournament pushes. The surface of contact between the rivals would be reminiscent of a triangle (Fig. 6a).

The medial nasal crest and the small horn on this crest in protoceratopsids during the first stages of evolution apparently increased the area of contact with the rival's snout and mechanically strengthened the anterodorsal edge of the skull. The trend toward fusion of the anterior cervical vertebrae into a single unit arose relatively early because of the large loads on the neck region in Ceratopsia.

Beginning as early as the late Turonian, the area of the squamosal in ceratopsids increased considerably (Fig. 4). This was apparently related to the change in the nature of the tournaments, when the contact between rivals' heads was not only in the region of the cheek and snout, but also along the entire length of the skull (Fig. 6b). The pressure on the rival was to a larger extent towards the side. This occurred probably because of the evolutionary replacement of the inborn stereotypes, which was determined by the notable increase in body mass among ceratopsids as compared to the majority of protoceratopsids. In ceratopsids, axial loads combined with the lateral ones in the cervical vertebral column could have become harmful for participants of the tournaments. It is possible to assume for psittacosaurs and the small early protoceratopsids a short run before contact (mutual blow) between rivals. In ceratopsids, however, the tournament probably began with a relatively slow approach, a complete lateral contact of heads, and only afterwards lateral pressure of the rivals on one another took place. Spassov (1979) indicated the possibility of lateral rather than direct frontal contact between the rivals in ceratopsids. Among Centrosaurinae of the *Eucentrosaurus* type (Lambe, 1915: fig. XI; Weishampel et al., 1990a), in our opinion, there should have been a slight turn of the head along the axis during the contact of heads during tournament, with a turn of the cheek towards the rival's cheek. As this occurred, the nasal horn of each individual was situated lateral from the parietal shield of the rival. It is possible that the nasal horn of the eucentrosaur was situated near the parietal hook that projects forwards and downwards from the upper margin of the parietal "frame". Apparently the spherical shape of the occipital condyle in ceratopsids was an adaptation facilitating contact between the heads. The anterior part of the maxilla was supported by a concave or flat area on the rival's squamosal. The basal part of the larger squamosal in centrosaurines transmitted considerable forces to the braincase. The latter had posteriorly situated "power" crests for that purpose. These forces were also transmitted to the occipital condyle, to the quadrate, and, through it, to the mandible. Part of the forces was transmitted to the projection of the pterygoid. During the tournament contact between ceratopsid species with a short frill (Fig. 6b), the posterointernal part of the squamosal was most likely adjacent to the posterior part of the neck. A strong posterior elongation of the lateral (squamosal) part of the frill (as in *Styracosaurus* among centrosaurines and in *Chasmosaurus* and *Pentaceratops* among chasmosaurines) could have permitted leaning its posterior part on the region of the shoulder girdle and to push the rival with the entire mass of its body **[31/32]** through the region of the "shoulder", leaning from the inside on the squamosal part of the frill.

Long, posteriorly directed horns on the frill of *Styracosaurus* could have played a role not only for display, but also for defense of the anterior part of the trunk when gliding to the posterior part of the rival's head. Direct interaction with the posterior frill horns in the rival assumed by Spassov (1979: fig. 3) is unlikely, because strong skin injuries in the anterior part of the trunk would have been common in that case. Stops and fixators precluding such gliding in *Styracosaurus* were weak and were formed only by a small knob or by a short, anteroventrally directed hook at the apex of the frill.

At a certain axial inclination of the head towards a competitor, the basis of the long nasal horn of centrosaurines of the *Eucentrosaurus* type was situated approximately in the plane of the squamosal part of the frill and the short supraorbital horn of the side turned towards the competitor could have been used as a support and a fixator limiting the forward gliding of the head. In *Pachyrhinosaurus,* which lacks supraorbital horns, the height of horn growth above the bony nasal knob (probably inclined forwards, like the bony nasal horn in *Eucentrosaurus*) was probably sufficient to be fixed (against gliding) on the medial spine near the middle of the frill, when pushing the competitor with the "cheek". One can assume that there were two horny projections on the nose of the pachyrhinosaur; they could have been inclined not only anteriorly, but also laterally. In this case, the trunk could have been protected from gliding of the competitor by the posterolateral spine of the frill. The function of the supraorbital horns and fixators could have been strengthened with time, which had to determine the increase of their power and height (see specimens referred to different species of *Chasmosaurus*; Weishampel et al., 1990a: fig. 29.3b-d). In chasmosaurines like *Anchiceratops*, *Arrhinoceratops*, and *Pentaceratops*, the competitors probably "crossed" the supraorbital horns and, as a result, could have created considerable longitudinal loads on each other, but also retained the ability to push the competitor aside because of the support of their maxillary region on the concave or relatively flat squamosal area of the competitor's skull. Support of the maxillary area on the squamosal of the competitor apparently became unnecessary because the basis of each somewhat anteriorly inclined supraorbital horn became so strong that, when the supraorbital horns crossed (Farlow and Dodson, 1975), considerable turns of competitors' heads were possible around the longitudinal axis as well as in the vertical and horizontal planes. Probably contact of the horns occurred above the dorsal edge of the orbit. In some cases the tip of the supraorbital horn of one individual could "draw" on the surface of the rival's frill. This could have caused considerable posterior closure of the frill fenestrae in *Triceratops* during the course of evolution; their slit-like rudiments in the anteriormost part of the frill, out of the reach of the end of a rival's horn, were retained. It should be noted that the squamosal of *Triceratops* was externally devoid of the concavity for contact with the competitor's maxilla. The display and support function of the frill in *Triceratops* decreased, and the frill could have become shorter. Therefore, the course of evolution of the "armament" and protection against it from the evolutionary **[32/33]** level of ancestors of the psittacosaurs to primitive protoceratopsids to ceratopsids proper was apparently rigidly determined and carried out through a succession of stages.

The tournament combat of reptiles and other higher vertebrates is frequently strictly ritualized. Control of the ritual is commonly determined by the instinct and features of animal's structure. If we compare lateral images of skulls of different ceratopsids with their mirror images on transparent tracing paper, it can be seen (Fig. 6b) that in the ceratopsids, unlike in *Protoceratops* (Fig. 6a), the features of the skull contact noted above the eyes of the competitors were situated at a different distance from each other. One cannot rule out that the spatial correlation of competitors' eyes was specific to each of the two families. If we assume the aforementioned hypothesis about the peculiar features of the interaction between ceratopsid male competitors' heads during tournaments, the question arises what the development of nasal and supraorbital horns, projections of the frill and lateral parts of the squamosals in females was and whether the specimens with weak tournament abilities were females. However, distinguishing skulls of females within the already published material is difficult primarily because traditionally the differences in the degree of development of horns were frequently used for the corroboration of new species of one or another genus (e.g., see the history of this question for *Triceratops*; Ostrom and Wellnhofer, 1986). It should be noted that the material reported in the literature for the majority of species is not sufficiently large to permit separation of adult females from young individuals. Nevertheless, dimorphism has been established for some species (Weishampel et al., 1990a: fig. 29.3b,d), and may represent sexual dimorphism. It appears possible that the task of discerning of sexes in ceratopsids may be complicated if gender in these animals had been determined not by the XY chromosome system, which is the case in birds and mammals, but rather by the differences in the temperature for egg incubation, which is now known for many turtles and crocodylians (Paladino et al., 1989). With this mechanism of sex determination, it is quite difficult to maintain a relatively high degree of sexual dimorphism (in evolutionary terms). It is known that adult ceratopsids can be readily distinguished based on those features of the structure of horns and frills that may be related to the sex of the animals (e.g., Tanke, 1988; Sampson and Tanke, 1990). It should be noted that even in those forms that possess the XY system, such as reindeer (with antlers in both males and females), weak sexual dimorphism may develop during evolution. It is possible that part of the "armament" of ceratopsid females was excessive in terms of tournaments. However, we cannot exclude that the horns and frill in females could have been useful for defending themselves and possibly also their progeny against predators. Those phylogenetic lines of ceratopsids, which (for accidental reasons in evolution) acquired tournament armament that was also efficient for defense against enemies (of other species), could have enjoyed an advantage over those in which the tournament function of the "armament" prevailed over the defensive function. This was probably the cause of survival in representatives of the genera *Torosaurus* and *Triceratops* among ceratopsids from the very end of the Cretaceous (Maastrichtian).

All sizes of bones available for different individuals of the late Turonian - Coniacian ceratopsids from Dzharakuduk show that their skull **[33/34]** was small (length including frill approximately 60-100 cm). This correlates with the small size of the body, the length of which was smaller in these ceratopsids than in the majority of ceratopsid species from North America. The ceratopsid from Dzharakuduk had approximately the size of *Avaceratops* and small specimens of *Eucentrosaurus*, but it was still larger than *Brachyceratops*. The body size of *Turanoceratops* was, however, at least eight times larger than in the late Albian and early Cenomanian protoceratopsids *Kulceratops* and *Asiaceratops*.

The position of the squamosals in *Turanoceratops* (judging from their contacts with the quadrates and the high paroccipital processes set apart at a short distance) indicates that this form (Figs. 4, 6b) was characterized by a relatively short frill, and that the distance between the lateral sides of the squamosals was short (i.e., the skull was relatively narrow posteriorly). The outline of the interfontanelle bridge of the frill in dorsal view and the fenestrae of the latter was apparently similar to that of *Eucentrosaurus* (Lehman, 1990: fig. 16, 1).

The first find from the Upper Cretaceous of Dzharakuduk that was referred to ceratopsids (Riabinin, 1931a: pl. III, fig. 7; Steel, 1969: fig. 23, 6) should not only be compared to ceratopsids (e.g., Marsh, 1896: pl. LXVI; Hatcher et al., 1907: fig. 65; Lull, 1907; Weishampel et al., 1990b: fig. 29.7g-k), but also to ankylosaurids (Coombs, 1978: fig. 6A).

It appears quite doubtful that a long, weakly bent, and hollow bone, almost without narrowing towards either end, discovered in inter-trappean deposits (Maastrichtian - Danian) of Gudzharat, India (Dwivedi and Ghevariya, 1984), belongs to ceratopsids. The doubts are based on the more pronounced, cone-like shape of the horns in ceratopsids; the horns are not as long and are not hollow (in the unweathered state; the inside is composed of dense, small-celled, spongy osseous bony tissue with relatively thick cell walls). Judging from the microstructure of the bony tissue and the general shape, the fragment of the bone from India could be a relatively strongly eroded (or with its surface pathologically modified) diaphysis of the tubular limb-bone of a large vertebrate.

New discoveries of ceratopsid remains in Asia can also be expected in other localities of the upper Turonian - Coniacian of the Kyzylkum, the Turonian - Campanian of the northeastern Aral region and Tashkent Chul', and also in the Iren Dabasu Formation and its analogues in northern China (Gilmore, 1933; Steel, 1969: fig. 23.3) and in the upper part of the Bainshirein Formation of eastern Mongolia, in association with turtles of the genus *Lindholmemys*.

Ceratopsids, which existed before the late Santonian - early Campanian temperature maximum at high latitudes or during the last temperature maximum, inhabiting coastal plains along the dispersal route to North America, can be found at their presumed center of origin (in South Asia) and in eastern China, in the Far East of Russia, and in the far North-East of Russia.

The comparison of morphology and time of existence of the various Asian and North American ceratopsids suggests that the early stages of evolution of the family, with differentiation into the centrosaurine (monocloniine) and chasmosaurine lineages, took place in Asia.

[34/35]

2. DESCRIPTIONS OF NEW DISCOVERIES

Order Saurischia

Suborder Segnosauria

Notes. Segnosaurs (Segnosauria), at the rank of an infraorder of theropods, were recognized 15 years ago (Barsbold and Perle, 1980). After that time, the group was usually included in Theropoda. However, segnosaurs do not share evolutionarily derived characters with the latter and therefore cannot be referred to theropods (Paul, 1984). Thus, for example, segnosaurs do not have important features of Theropoda such as the presence of a tarsometatarsus (Weishampel et al., 1990a: 149) that is compact, relatively compressed side-to-side, and relatively elongated; the length of the tarsometatarsus in segnosaurs is only approximately 30% of the length of the tibia (Perle, 1979: 51). The phylogenetic relations between theropods and segnosaurs have been clarified by the remains of *Alxasaurus elesitaiensis* (Russell and Dong, 1994) from the upper Aptian of the Alashan Desert, Inner Mongolia, China. *Alxasaurus* has an important complex of features typical of Late Cretaceous segnosaurs, but not all features of those animals were present in *Alxasaurus*. Its dentary is low, with approximately 40 very small teeth, which is much less than in *Segnosaurus* and *Erlikosaurus* among segnosaurids (Perle, 1979, 1981). The tooth roots are tapered. The tooth crowns are similar in the general shape and in the rough serration to those in prosauropods. The ligament pits on the distal parts of phalanges of the forelimb are moderately well developed on one side and weak on the other. The ungual phalanges of digits I and II of the forelimb are relatively similar in size and moderately large (34% of length of the humerus). The proximal end of metatarsal III is wide as in *Segnosaurus*, rather than compressed from side to side as in Tetanurae. The phalanges of the hindlimb are much longer than in Late Cretaceous segnosaurids. At least on the known phalanges, ligament pits are absent. Instead there are only weakly sloping hollows. The ungual phalanges of digits II-IV of the hindlimb are relatively strongly flattened from side to side, but they are relatively short and weakly curved.

Therefore, *Alxasaurus*, unlike Late Cretaceous segnosaurids, has ligament pits at least on one side of phalanges of the forelimb. The ungual phalanges of digits II-IV of the hindlimb had not increased in size as in the Late Cretaceous segnosaurids. Because *Alxasaurus* already shows a tendency towards disappearance of the ligament pits on the phalanges, which is an evolutionarily derived feature of the known segnosaurids, this genus is placed here among the segnosaurs, but not in the Tetanurae as in the original description. If we do not include segnosaurs among theropods, there are two possibilities: to group them with prosauropods or to regard them as a separate group among Saurischia. As prosauropods do not possess their own evolutionarily derived features they are here considered a paraphyletic group. Therefore, combining segnosaurs with prosauropods is not reasonable. This leaves placing segnosaurs as a separate group of saurischians. The apomorphic features of this group are reduction of ligament pits, subequal size of the large ungual phalanges of the hindlimb, and loss of teeth on the premaxilla. **[35/36]** Adopting this scheme assumes a trichotomy among saurischians, exclusion of segnosaurs from the taxon Sauropodomorpha, and consideration of prosauropods as a paraphyletic group. Apomorphic features have not been identified for the family Alxasauridae; therefore, it could be a paraphyletic taxon (lower grade) related to Segnosauridae and Therizinosauridae.

Segnosauria indet.

Pl. I, fig. 13, Pl. II, figs. 1-6, 127

"Large-clawed deinonychosaurs": Nessov, 1989: 174

Material. Teeth, ungual phalanges and other phalanges, proximal and distal parts of humeri, vertebrae, possible basisphenoid and frontal.

Description. Teeth of segnosaurs, which are very diverse in shape, are found in the upper Turonian - Coniacian of Dzharakuduk. Sometimes they are strongly thickened labiolingually, their crowns are not inflated, gradually tapering towards the apex and with relatively large denticles along the edges. There are also teeth that are somewhat flattened labiolingually, with short worn edges (Pl. II, fig. 4) or with a spatulate, flattened, and posteriorly expanded area near the apex, as in the lower jaw of *Erlikosaurus*; there is not a single ungual phalanx of the same type as in *Erlikosaurus*, with grooves for the horny sheath extending onto the dorsal edge of the phalanx and a weak knob for the flexor ligament located ventrally and relatively distally. Teeth with a considerably recurved apex, as in the genus *Segnosaurus* from Mongolia (Perle, 1979, 1981; Barsbold and Perle, 1980; Weishampel et al., 1990a), have also not been found. A basisphenoid (No. 719 from site CBI-14), possibly belonging to a segnosaur, is wide and strongly pneumatized.

The ungual phalanges (Pl. II, figs. 1-3) are large, considerably compressed from side to side, strongly bent with a knob, which is considerably shifted backwards and very thick, for the digital flexor ligament. Grooves for the horny claw sheath (in lateral view) usually approach the dorsal edge at a very low angle. These grooves, unlike those in *Erlikosaurus* (Perle, 1981), almost reach the apex of the ungual phalanx. Preungual phalanges (Nos. 699-702) have only small, sloping hollows on the sides distally. (P. Currie drew the author's attention to this feature.) In lateral view, the ventral surface is distinctly concave.

All vertebrae are highly pneumatized, particularly the cervical vertebrae with long centra. Such vertebrae have a very low neural arch, moderately deep pleurocoels (with two pleurocoels on either side of the vertebra). The centra of these vertebrae show a slightly opisthocoelous condition. They are strongly expanded anteroventrally, where, on either side, there is a relatively large area for the cervical rib, which was probably fairly well developed and long. The anterior articular surface of such cervical vertebrae (Nos. 704-710) is strongly inclined ventrally and only slightly anteriorly, and the posterior surface is inclined mainly posteriorly but only slightly dorsally. This in all likelihood indicates that, in normal articulation in the living animal, the relatively long neck curved sharply in the form of a downward arch. **[36/37]** On some short vertebrae (possibly anterior cervical or the anteriormost thoracic; Nos. 711-712) a very large, slightly concave anterior articular surface faces sharply ventrally (at an angle of approximately 35º to the long axis of the centrum), whereas the posterior articular surface is inclined dorsally (at an angle of 60º to the long axis).

One anterior trunk vertebra (No. 713) is high with a relatively strong and long hypapophysis, large and nearly flat prezygapophyseal facets, and postzygapophyseal facets that are smaller in area and concave transversely. The weakly concave plane of the anterior articular surface of the centrum is only slightly inclined ventrally.

One posterior thoracic vertebra attributed to a segnosaur (No. 714) has a centrum that is constricted at mid-length and ventrally concave in an anteroposterior direction. A pleurocoel is absent. The anterior articular surface of the centrum is inclined slightly dorsally, and the posterior one is inclined slightly ventrally. The spinous process is of moderate height.

All vertebrae have narrow, very deep vertical slits for longitudinal interspinous ligaments. The axial space between the ligament grooves inside the spinous processes has very dense bony tissue and frequently it is the only part that remains intact when the walls of large pneumatic chambers inside the vertebra have been destroyed.

The distal portions of humeri (Nos. 715, 716) are very strongly expanded transversely, but apparently not as strongly as in *Erlikosaurus* (Perle, 1981). The proximal parts of these bones (Nos. 721, 722) have smooth margins, and the proximal head extends along the proximal edge.

Comparison. The segnosaur from the late Turonian-Coniacian of Uzbekistan that existed during the deposition of the Bissekty Formation of Dzharakuduk differs from an older segnosaur (Segnosauria indet.) from the early-middle Albian of Karakalpakistan (Khodzhakul) in the notably smaller size of the ungual phalanges and apparently in relatively smaller vertical size of their articular surfaces for the preungual phalanges. The Dzharakuduk segnosaur is close to an older, early Cenomanian form (Pl. II, fig. 6) from Sheikhdzheili and to a Turonian-Coniacian form from the Iren Dabasu Formation, Inner Mongolia, China (Gilmore, 1933; Mader and Bradley, 1989); specific identity with the latter can probably not yet be excluded.

Notes. The segnosaur from Dzharakuduk differs from *Segnosaurus galbiensis* (Perle, 1981) and *Erlikosaurus andrewsi* (Barsbold and Perle, 1980) in the relatively greater length of all preungual phalanges and from *S*. *galbiensis* by even less pronounced recurved apices of the teeth (Perle, 1979: fig. 1).

Probably an incomplete, average-sized ungual phalanx attributed to a carnosaur from the Cretaceous in the vicinity of Chiangchunting, Shandong Province, China (Young, 1958) belongs to a segnosaur.

Because the lower part of the Bainshirein Formation (with remains of the turtle *Kyzylkumemys*, which is also known from the Cenomanian of Karakalpakistan) is represented at the localities Amtgai and Khara-Khutul in eastern Mongolia, the segnosaurs of the genera *Enigmosaurus* and *Segnosaurus* (Barsbold, 1983) most likely are Cenomanian rather than

Turonian in age. Remains of *Erlikosaurus* (Barsbold, 1983), if they come from layers 3 and 4 at the locality Baishin-Tsav **[37/38]** (Tsybin and Kurzanov, 1979), may date from the late Cenomanian, but if they come from layers 5-7 (9) they may possibly be early Turonian in age.

Distribution. Late Turonian - Coniacian (Late Cretaceous) of the Central Kyzylkum, possibly early Turonian - Coniacian of Inner Mongolia (China).

Suborder Theropoda

Family Tyrannosauridae Osborn, 1905

Genus *Alectrosaurus* Gilmore, 1933

Type species - *A. olseni* Gilmore, 1933, early Turonian - Coniacian, Iren Dabasu Formation, Inner Mongolia, China.

Notes. Among the material from the Bissekty Formation, a carnosaur is represented along with small theropods (see below). The carnosaur, the largest theropod in the assemblage from the late Turonian - Coniacian of the Middle Asian region, is still much smaller than *Tarbosaurus bataar* from the Upper Cretaceous of Mongolia (Malyeyev, 1974) and smaller than the tarbosaurs from the North-Eastern Aral region (e.g., Pl. X, fig. 1). The carnosaur from Dzharakuduk had a more lightly built skeleton than later representatives of this group. However, it was apparently larger than the late Albian and early Cenomanian carnosaurs that possibly also belonged to the genus *Alectrosaurus*. Using available bones in the material (including femur, tibia, and metatarsal III), the carnosaur from Dzharakuduk can be readily compared with *Alectrosaurus* from the Upper Cretaceous of Inner Mongolia (Gilmore, 1933; Perle, 1977; Mader and Bradley, 1989).

Alectrosaurus sp.

Pl. I, figs. 1, 3, 5-6, 7?, 8, 10, 11?, 16?; Pl. II, figs. 13-14; Pl. X, figs. 9-10.

Material. Fragment of maxilla, teeth, femora, vertebrae, tarsus, ungual phalanges.

Description. The posterior area of a maxilla (No. 600) is 152 mm long, has a height approximately 50 mm anteriorly, and a thickness in this region of 23 mm; six complete alveoli and one incomplete one are present. The posterior end is broken, but the place of breakage is situated near the anatomical end of the bone. The preserved area of the bone is extremely low compared to the corresponding region in later tyrannosaurids (Malyeyev, 1974). Judging from the preserved fragment, the number of teeth in the theropod from Dzharakuduk was larger than in *Tyrannosaurus* and *Tarbosaurus*, but was comparable to that noted in primitive megalosaurids (Weishampel et al., 1990a: fig. 6, 29A-B). Evidently the posterior antorbital opening extended anteriorly much farther than the sixth tooth counting from the posterior end. A deep groove for contact with the anterior process of the jugal extends approximately up to this level and almost along the middle of the dorsal edge. The fourth alveolus has dimensions of approximately 16 x 9 mm posteriorly. On the lingual side, not far above the alveolar margin there is a 1.5 mm wide groove, in which replacement teeth developed. The relief of this area is **[38/39]** much smoother than in *Tarbosaurus* (Malyeyev, 1974: fig. 4); the crest for contact with the posterior part of the palatine also has a much smoother relief.

Teeth (Pl. I, figs. 5-6, 8) are considerably flattened from side to side in approximately the same fashion as in "*Dryptosaurus*" *medius* (Marsh) (Gilmore, 1920: pl. 34, fig. 1); the blade-like, flattened condition is much more pronounced than in tarbosaurs, and more so than in tyrannosaurs (Malyeyev, 1974; Hu, 1964: figs. 8, 11). The denticles along the edges of the crown are small (approximately 12-16 per 5 mm), with short, weakly developed notches of enamel forming their boundaries.

Femora (No. 724) presumably belonging to the alectrosaur have the head of the femur moderately elevated inwards. The ventromedial part of the head has a hemispherical shape; in the lowest part, the articular surface of the joint is separated from the remainder of the bone by a relatively low step. The lesser trochanter has a shape rather typical of carnosaurs in the form of a subvertical crest that weakly projects forward from the surface of the bone. In anterior view, the trochanter has the appearance of a sharply pointed triangle, with its apex oriented upwards. The fourth trochanter has the shape of a narrow crest that protrudes more strongly than in *Tarbosaurus* (Malyeyev, 1974; Weishampel et al., 1990a) (Pl. X, fig. 1). The distal end of the femur has an only slightly visible extensor groove.

The pleurocoel is weakly developed on the vertebra (Pl. I, fig. 2).

The tarsus (Pl. I, figs. 19, 20, etc.) is similar to that of the holotype of *Alectrosaurus olseni*. Ungual phalanges of the fore- and hindlimbs (Pl. I, fig. 14; Pl. II, figs. 13-14; Pl. V, figs. 9-10) are relatively short and small.

Notes. Apparently the laterally flattened condition of the teeth attributed to the Late Cretaceous theropod of the genus *Alectrosaurus* and teeth in the Late Jurassic *Torvosaurus* (Galton and Jensen, 1979) is not determined by evolutionary relationship but rather by a similar nature of feeding. The narrow, blade-shaped teeth could have been used for cutting soft tissues from bones, whereas Campanian-Maastrichtian tyrannosaurids could tear, by means of their much thicker teeth, large pieces of prey even with relatively small bones. One can assume that the theropods from Dzharakuduk and *Torvosaurus* were scavengers to a larger extent than the tyrannosaurids of the second half of the Late Cretaceous, which were capable of dealing with live prey of much larger size.

According to S. M. Kurzanov (1989), the alectrosaur is the most generalized tyrannosaurid, but not an ancestor of later representatives of the family. If this is true, and if alectrosaurs are represented in Dzharakuduk, it can be assumed that the replacement of alectrosaurs by tarbosaurs at the boundary between the Coniacian and Santonian (see below) in the coastal plains (see Malyeyev, 1955; Rozhdestvensky, 1965) could have taken place not because of the origin of the latter genus in the currently known range of alectrosaurs, but because of migration of the tarbosaurs (capable of competition) from another area of origin.

New collections would be very important for establishing the phylogenetic relationships of the moderately large tyrannosaurids of late Albian, early Cenomanian, and early Turonian age.

Distribution. Late Turonian - Coniacian (Late Cretaceous) of the Central Kyzylkum.

[39/40]

Genus *Tarbosaurus* Malyeyev, 1955

Tarbosaurus sp.

Pl. X, fig. 1

Material. Femur.

Description. The relatively small femur, which has a length of 530 mm, has a small, weakly projecting but high trochanter. The extensor groove is weakly pronounced.

Notes. The largest carnosaurs in the assemblages of the Albian - Cenomanian and even the Turonian - early Campanian of Middle Asia are much smaller than their middle Campanian - Maastrichtian relatives in Mongolia and North America. It is possible that the increase in body size during the evolution of Late Cretaceous tyrannosaurids and the replacement of *Alectrosaurus* by *Tarbosaurus* in Asia (at the boundary between the Coniacian and Santonian or during the early Santonian?) were determined not only by selection for survival of the largest individuals of predators as prey evolved towards increased size (as one of the fastest ways for prey to avoid predators), but also by competition among large theropod predators for carrion of large dinosaurs. It could have been quite common for large theropods to consume carrion of their species and to compete for it. Apparently for this particular reason, the majority of localities in Khodzhakul and the Yalovach and Bostobin formations, whatever collection methods have been used, display a pronounced abundance of theropod teeth and an obvious absence of their bony remains, even in the contrast with the ratios of teeth and bony remains of hadrosaurids in the same localities.

Distribution. Santonian - early Campanian (Late Cretaceous) of the North-Eastern Aral Sea region.

Family Ornithomimidae Marsh, 1890

Genus *Archaeornithomimus* Russell, 1972

Archaeornithomimus(?) *bissektensis*, sp. n.

Pl. III, fig. 7.

Named for the Bissekty Well.

Holotype - CCMGE No. 479/12457, right femur; Uzbekistan, Dzharakuduk; Upper Cretaceous, Coniacian, middle part of the Bissekty Formation, site CBI-14

Material. Femur.

Notes. The bone has a relatively thin diaphysis and is S-shaped. The proximal head is moderately expanded and turned slightly upwards. The distal end is relatively narrow in the mediolateral direction. The greater trochanter is weakly protruding upwards, the lesser trochanter has the shape of an arc-like, narrow crest and is separated by a relatively shallow notch from, but placed quite high relative to the greater trochanter. The fourth trochanter is situated above the middle of the bone; it has the appearance of a narrow vertical crest.

Comparison. It differs from *A*. *asiaticus* (Gilmore) from the Turonian - Coniacian (Iren Dabasu Formation) of Inner Mongolia, China (Gilmore, 1933; **[40/41]** Smith and Galton, 1990: fig. 3G-L – left rather than right bone shown) in the pronounced curvature of the diaphysis, the slightly narrower region of the head of the greater trochanter (even in proximal view), less protruding lesser trochanter, and the medial condyle of the distal articular end apparently somewhat more strongly protruding downwards.

Notes. In repose, the distal end of the femur appears to be placed further anteriorly and more laterally from the medial plane than in *A. asiaticus*. In the curvature of the diaphysis and the greater difference in the downward projection of the distal condyles, the dinosaur resembles some oviraptorosaurs; however, the new species differs from oviraptorosaurs in the non-inflated crest of the lesser trochanter extending not as far proximally and in the much more pronounced groove between the two distal condyles.

Distribution. Coniacian (Late Cretaceous) of the Central Kyzylkum.

THEROPODA indet.

Material. Two femora.

Description. The collections contain remains of moderately large theropods (smaller than *Alectrosaurus*, but larger than all other theropods of the assemblage), which are characterized by an anteroposteriorly narrow articular surface of the head of the femur, which is moderately elevated in the medial direction, and also by the crest of the lesser trochanter, which strongly projects forward, is high, and very sharp from above. The general appearance of the proximal portion of the femur of these animals is reminiscent of the pattern typical of ornithomimids. Relatively common in the material are long, anteroposteriorly narrow teeth of theropods (Pl. I, figs. 3, 7, 10-11) with (labiolingually) somewhat more thickened bases than in the typical teeth of *Alectrosaurus*. This theropod was smaller than *Alectrosaurus* sp. The femora noted above approximately correspond in size to the theropod to which these teeth could have belonged. It would be convenient to suggest that both belong to the same species. However, known ornithomimids (if the femora of the type described here belong to them) have no teeth or only greatly reduced teeth. In this connection, the question of classification of the aforementioned femora and teeth remains unresolved.

Unranked taxon BULLATOSAURIA Holtz, 1994

Family TROODONTIDAE Gilmore, 1924 (=SAURORNITHOIDIDAE Barsbold, 1974)

Genus *Troodon* Leidy, 1856 (=*Stenonychosaurus* Sternberg, 1932; =*Pectinodon* Carpenter, 1982)

Troodon asiamericanus, sp. n.

Pl. I, fig. 23

Pectinodon asiamericanus: Nessov, 1985b: pl. III, 16 [nomen nudum]

[41/42]

The name is given in reference to the distribution of the genus in Asiamerica.

Holotype. CCMGE No. 49/12176, tooth; Uzbekistan, northern edge of the Sheikhdzheili Mountains; Upper Cretaceous, lower Cenomanian, upper part of the Khodzhakul Formation, site SSHD-8 .

Material. Six teeth.

Description. The teeth are small and considerably flattened along the sides. The height of the crown is approximately 5 mm, usually less. Serrations are present only along the posterior edge of the crown; they are relatively large (compared to the size of the crowns) with relatively narrow bases. The serrations of the crown are situated relatively close to each other and are oriented backwards towards the apex. One of the sides of the crown (probably the lingual one) is usually more flattened, and a shallow groove extends across it, parallel and close to the anterior edge of the crown.

Comparison. It differs from *Troodon formosus* Cope from the Campanian - Maastrichtian of North America and *Troodon* sp. cf. *T. formosus* from the middle Maastrichtian of the Koryak Highlands (Estes, 1964: fig. 69; Carpenter, 1982; Currie, 1987a; Currie et al., 1990; Nessov and Golovneva, 1990) at least in the more pronounced serration of the crowns, the more strongly flattened sides, their smaller size, and the narrow bases of the serrations.

Notes. It differs from *Saurornithoides mongoliensis* from the Campanian of Mongolia (Osborn, 1924c: fig. 4) in the smaller and relatively stable size of teeth, the (anteroposteriorly) longer bases of the crowns, and the more regular serration pattern extending up to the apices of the crowns. In the nature of the crown serrations, the new species is reminiscent of *Saurornitholestes langstoni* from the Campanian of Canada (Currie et al., 1990), but differs in the much smaller height of the teeth and their greater flattening. It differs from *Richardoestesia* from the Campanian of Canada (Currie et al., 1990) in the relatively smaller height and relatively stronger lateral flattening of the crowns. It differs from teeth of a probable troodontid, possibly already described from bony remains and teeth (Barsbold et al., 1987: pl. 49, fig. 2) and doubtfully classified as a bird (Kurochkin, 1988:

pl. VII, figs. 5-6; compare with Howgate, 1984: fig. 2), from the upper Aptian of Mongolia in the more arc-shaped (rather than straight or bluntly recurved) profile of the anterior edge of the tooth.

In general, one cannot exclude that the peculiarity of teeth in *Troodon* (short crown, constriction between crown and root, similar to the condition in a number of ornithischians, large serrations along the edges of the crown with strong distal inclination of the serrations) could have been related to partial herbivory. The latter could have taken place when large seeds of Cycadales, which are tightly packed in large cones, were gnawed out (see Chapter 1). In the aforementioned tooth characters, *Troodon formosus* is quite similar to *Lesothosaurus diagnosticus* (Sereno, 1991: figs. 1-2) among the primitive ornithischians of the Early Jurassic, which, because of the extension of the edge of the crown of one tooth behind the edge of the crown of another has a continuous serration of the tooth row in the cheek region, with hook-shaped, relatively sparsely arranged premaxillary teeth. Considering the fusion of the alveoli in the posterior region of the jaws in *Troodon* (Currie, 1987a), one can assume a similar arrangement of teeth and similar adaptations in this theropod, which probably was capable of facultative herbivory, procuring and consuming seeds. Possibly this is the reason why teeth of *Troodon* were long attributed to ornithischians and referred to pachycephalosaurs, which have teeth of a relatively primitive type among ornithischians. **[42/43]** With regard to pachycephalosaurs proper, they have not yet been found anywhere in the coastal plains of the western and southwestern regions of the Asian land mass (now Middle Asia, southern and western Kazakhstan). These dinosaurs, however, were relatively common in the Campanian - Maastrichtian of Mongolia and North America. In the early-middle Maastrichtian assemblages of Mongolia, pachycephalosaurs are one of the three most common groups. The only tooth attributed with some doubt to pachycephalosaurs (Nessov, 1981: fig. X, 14) appears to belong to a segnosaur, a group that was unknown to science until 1979-1981. Pachycephalosaurs are known from the Barremian (Early Cretaceous) of England to the Maastrichtian (Late Cretaceous) of Mongolia and North America. Their absence in the Albian - early Campanian of

Middle Asia is an enigma, which can probably be explained by biogeographic differences between the faunas.

Distribution. Early Cenomanian coastal plains of southwestern Asia (see Fig. 2).

Troodon isfarensis, sp. n.

Pl. III, fig. 12

The name of species is given in reference to the Isfara River.

Holotype. - CCMGE No. 484/12457, incomplete left frontal; Tadzhikistan, Kyzylpilyal (locality Isfara II); Upper Cretaceous, lower Santonian, lower part of the Yalovach Formation, site FIS-2.

Material. Frontal.

Description. The frontal has a posterolateral projection that descends considerably downwards and should have considerable size (measured anteroposteriorly). The dorsal margin of the orbit bears small, densely located knobs. A bony crest passing along the boundary between the orbit and the brain cavity protrudes very weakly ventromedially. A series of weak, arc-shaped folds extends anteriorly from this crest. Medial to the crest there is a second, weaker and short crest, which turns toward the middle line more abruptly than the first one.

Comparison. Differs from *Troodon formosus* Cope from the Campanian - Maastrichtian of North America and Beringia (Currie, 1987b) in a relatively weaker crest on the boundary between the bony orbit and brain cavity and in the presence of a second crest that curves more abruptly medially. The principal difference is the (anteroposteriorly) wider base of the posterolateral projection.

Notes. Teeth characteristic of the genus *Troodon* have not been found at the locality to date. The genus *Troodon*, with representatives from Karakalpakistan, Tadzhikistan, and northeastern Russia (Kakanaut locality), as well as possibly some other localities of the CIS, is one of the few found in the Late Cretaceous of both North America and Asia [another one is *Saurolophus*, possibly also *Tyrannosaurus* (Maryanska and Osmolska, 1984)].

Distribution. Sea coast (liman) plains of the early Santonian at the southwestern extremity of Asia (see Fig. 2).

[43/44]

THEROPODA incertae sedis

Genus *Euronychodon* Antunes et Sigogneau-Russell, 1991

Euronychodon asiaticus, sp. n.

Paronychodon cf. *lacustris*: Nessov, 1985b: pl. III, 16; Nessov, 1986: figs. 2-3.

The name of the species comes from its occurrence in Asia.

Holotype. - CCMGE No. 9/12454, tooth; Uzbekistan, Dzharakuduk; Upper Cretaceous, middle part of the Bissekty Formation, lower part of the site CBI-14.

Material. Seven teeth.

Description. The teeth are small, recurved, differing in the degree of elongation (they are frequently much shorter, less frequently longer than the specimen shown before) with relatively numerous longitudinal enamel striae of the labial side of the crown (up to 14 and more striae; the anterior striae are slightly more recurved than the anterior edge of the tooth). The lingual side of the crown is most frequently flattened, sometimes weakly concave with a few striae.

Comparison. The species is similar to *Euronychodon portucalensis* Antunes and Sigogoneau-Russell, 1991 from the Maastrichtian of Portugal in the lack of serrations on the anterior and posterior edges of the crown, but differs in the presence of numerous grooves on the side usually interpreted as the labial side on such teeth.

Notes. Marsh (Marsh, 1889: pl. III, figs. 18, 22) placed teeth of this unusual type near the symphyseal part of the jaws, although he attributed them not to dinosaurs, but to multituberculate mammals. This error occurred because the dentition of multituberculates was, for the most part, unknown at that time.

North American discoveries of *Paronychodon*, as noted by Estes (1964: 143 and references), are characterized by serration of the posterior edge (see also Currie et al. [1990]). Teeth of the *Paronychodon* and *Euronychodon* types may represent anterior maxillary teeth of theropods (adjoining each other with flattened sides) that differ from the typical teeth of the maxilla in those theropods to which they belonged. Such teeth could have been formed beginning at those ontogenetic stages when the nasal labial slit of embryos was largely closing. The rudiment of such slit in adult theropods could have been responsible for the formation of small teeth of atypical shape. The flattened side of such teeth faced towards the mid-line.

The new species (or new morphotype of teeth) differs from teeth of *Siamosaurus suteethorni* from the Upper Jurassic of Thailand (Buffetaut and Ingavat, 1986) in the flattening of one of the sides.

Distribution. Coniacian (Late Cretaceous) of the Central Kyzylkum.

[44/45]

SAURISCHIA incertae sedis (THEROPODA?: SPINOSAURIDAE?)
or PISCES: OSTEICHTHYES: TELEOSTEI: SAURODONTIDAE
Genus *Asiamericana*, gen. n.

Named after the continent Asiamerica.

Type species. - *A. asiatica*, sp. n., Coniacian of Uzbekistan.

Diagnosis. The teeth are straight and, unlike those of the majority of other theropods, have a plane of symmetry perpendicular to the one passing through the apex of the crown and its two cutting edges.

Composition of the genus. Type species from the Coniacian of Uzbekistan and undescribed species from the Santonian - early Campanian of Kazakhstan (see Part 4.1.3.99) and Maastrichtian of North America (Estes, 1964: fig. 69).

Asiamericana asiatica, sp. n.

Pl. II, fig. 9

Spinosauridae?: Nessov, 1989: 174

Name of the species from the occurrence in the Asian part of the ancient continent Asiamerica.

Material. Three teeth.

Description. The teeth are thecodont, differing from each other in size two- or threefold, and considerably flattened in the portion near the root. They usually have a weakly sloping vertical groove; sometimes, in place of this groove, there is a nearly flat surface extending along the long axis of the tooth. This surface occupies approximately one third or one half of the anteroposterior width of the tooth. There are no serrations along the anterior and posterior edges.

Comparison. In the absence of serration along the edges of the teeth the form differs from the undescribed species from the Maastrichtian of the USA, referred to theropods (Estes, 1964: fig. 69b), and also from another undescribed species from the Santonian - lower Campanian of Syuk-Syuk, Kazakhstan (Yu. V. Suslov, oral communication).

Notes. The lack of serrations along the tooth edges is also known for spinosaurids from the Cenomanian of Africa (Weishampel et al., 1990a). However, teeth of spinosaurids are much thicker labiolingually. The structure of slit-like pulp cavity of and the near-root part of the thecodont teeth from the Coniacian of Dzharakuduk in general seems to suggest their dinosaurian nature. The notable differences in size of the Asian discoveries and the lack of morphological transitions to the larger teeth of other theropods with recurved crown apices militates against the assumption that these may be teeth of young rather than adult theropods (Estes, 1964: 143).

The teeth described here differ from the somewhat similar crowns of Cretaceous bony fishes of the family Saurodontidae in the lack of inflation of the near-root part of the crown and in the lack of an increase in enamel thickness along the edges. Farlow and co-authors (Farlow et al., 1991) noted that the genes responsible for the formation of tooth-edge serrations in theropods could have been suppressed in small forms. **[45/46]** In this connection, and if *A. asiatica* is a theropod, it cannot be excluded that ancestors of this species were characterized by small body size and a certain level of fetalization.

Distribution. Coniacian (Late Cretaceous) of the Central Kyzylkum.

Order ORNITHISCHIA

Suborder ORNITHOPODA

In the recent years, it has been discovered that hadrosaurids and hypsilophodontids were characterized by complex social behavior, cared for their progeny, and had the ability to reach extremely high latitudes due to homeostatic mechanisms that have yet to be understood. The latter has also been shown for iguanodontids (Weishampel et al., 1990a; Nessov and Golovneva, 1990; references in these works). All this suggests that ornithopods, rather than ceratopsids, should be placed at the upper stage of ornithischian evolution, and therefore at the end of the classification for this order. In this work, however, the traditional sequence of ornithischian suborders has been retained.

Family HADROSAURIDAE Cope, 1869

The lowest stage within HADROSAURIDAE, below HADROSAURINAE

Genus *Gilmoreosaurus* Brett-Surman, 1979

Type species. *Manchurosaurus mongoliensis* Gilmore, 1933, early Turonian - Coniacian, Iren Dabasu Formation, Inner Mongolia, China.

Notes. The genus *Gilmoreosaurus*, situated at the base of the hadrosaurine lineage, was established (Brett-Surman, 1979) based on materials described earlier (Gilmore, 1933) from the upper third of the Iren Dabasu Formation (see Weishampel and Horner [1986]) in the region of a geographic locality by the same name in Inner Mongolia, China. Some vertebrates represented in these strata (at least the relatively small carnosaur *Alectrosaurus olseni* with its relatively lightly built skeleton, the ornithomimid *Archaeornithomimus*(?) *asiaticus*, a segnosaur, hadrosaurids [see below] as well as the shark *Hybodus* and skate *Myledaphus* (D. Russell, in litt., 1989; Currie and Eberth, 1993) are, to a certain extent, similar to those known from the Bissekty Formation at Dzharakuduk. On this basis, a correlation can be made between the aforementioned deposits in China and Uzbekistan. The Bissekty Formation at Dzharakuduk contains in its upper part Coniacian sharks and skates that predated closely related Santonian cartilaginous fishes. Underlying the Bissekty Formation is a marine stratum with remains of early Turonian foraminiferans. In a thin, red-colored bed underlying this marine horizon, a faunal complex somewhat similar to the one known for the Bissekty Formation is known; it contains remains of the skate *Myledaphus* and the turtle *Lindholmemys*. However, this layer also contains remains of turtles of the family Carettochelyidae (cf. *Anosteira*) that differ from the Cenomanian ones. It is referred here to the lower Turonian. It is situated above the reliably dated Cenomanian deposits (Dzharakuduk locality) containing a typically **[46/47]** Cenomanian assemblage and occurs in the interval between the levels with teeth of late Albian sharks and with the early Turonian ammonite *Mammites nodosoides* in the southwestern Kyzylkum. Therefore, the fauna of dinosaurs and other vertebrates from Iren Dabasu (Gilmore, 1933) and also the fauna from a nearby or identical locality named Iren Nor (Rozhdestvensky, 1966) are dated as early Turonian - Coniacian. Apparently a Turonian - Coniacian date should be assumed for assemblages with remains of the theropods *Alectrosaurus* sp. and *Archaeornithomimus* sp., hadrosaurids closely related to *Bactrosaurus johnsoni*, and the turtle *Adocus* sp. from the middle and upper parts of the Bainshire Formation at the Baishin-Tsav locality in eastern Mongolia (Kurzanov and Trusova, 1979; Tsybin and Kurzanov, 1979). Remains of *Adocus* in the Upper Cretaceous of Uzbekistan are noted in the entire Bissekty Formation of Kyzylkum and in the younger Yalovach Formation (Santonian) of the Fergana Depression as well as in the Bostobin Formation (Santonian - early Campanian) of the North-Eastern Aral region; they occur in association with *Lindholmemys*. However, in the latter two formations, remains of carnosaurs, hadrosaurids, skates, and bony fishes other than those indicated above have been observed. This corroborates a Turonian - Coniacian age for the fauna of the dinosaurs and other vertebrates at Iren Dabasu in northern China.

Remains of hadrosaurids from the Bissekty Formation are rather similar to those known from the Iren Dabasu Formation. At the same time, the hadrosaurids of the Bissekty time interval differ from those known in the Cenomanian and late Albian of Karakalpakistan (Pl. IX, fig. 13) in larger body size and details of tooth serration. In this connection, the hadrosaurids from Iren Dabasu cannot be dated as Cenomanian (Rozhdestvensky, 1966). They can be regarded only as early Turonian (Steel, 1969) or pre-Turonian (Weishampel and Horner, 1986).

A. N. Riabinin (1931a) named the new species of hadrosaurid, *Cionodon*(?) *kysylkumense*, based on a small number of bones collected by A. D. Arkhangelsky at Dzharakuduk in the early 1900s. This species has been regarded in recent years as a nomen dubium, i.e., a doubtful name (Rozhdestvensky, 1977; Weishampel et al., 1990a). Although a holotype for this species was not designated, the original placement in *Cionodon* was based on comparison of one of the vertebrae (Riabinin, 1931a: pl. I, fig. 1) with North American material. This vertebra has a pronounced ventromedial crest (the transverse section at mid-length of the centrum is similar to a slightly inflated triangle with its apex pointing downwards). This feature, along with the typically anteroposteriorly concave shape of the lateral surfaces of the centrum, indicates that the vertebra belongs to the Saurolophinae or Lambeosaurinae (see Maryanska and Osmolska [1981]). It is apparently a trunk vertebra. Judging from the large foramina for vessels situated on either side, it belonged to a young individual. Here this vertebra is designated the lectotype of the species named *Cionodon*(?) *kysylkumense* by Riabinin and, based on its characters, is referred by us to a grade (evolutionary stage) above the lower Hadrosauridae (i.e., saurolophines + lambeosaurines). We place in the same species large vertebrae with ventral crests from Dzharakuduk (Pl. IX, fig. 13, etc.) and possibly some other relatively large vertebrae (Pl. IX, figs. 11?, 14?), tall teeth with a relatively narrow crown (e.g., Pl. IX, fig. 16), and also a maxilla (Pl. XI, fig. 4), permitting attribution of the remains listed above, including the lectotype of *Cionodon*(?) *kysylkumense* Riabinin, to the genus **[47/48]** *Bactrosaurus* among the lambeosaurines, and naming this species *B. kysylkumensis* (Riab.) rather than *Thespesius kysylkumensis* (Riab.) (Steel, 1969). Among the other specimens attributed to hadrosaurids by A. N. Riabinin (1931a), we cannot find subfamilial characters (Riabinin, 1931a: pl. II, figs. 3-4) or their hadrosaurid identity is doubtful.

Distribution. Late Albian(?), Cenomanian-Coniacian of Asia.

Described below are the remains of hadrosaurids that are older than those from the Bissekty Formation. (Probably they represent some of the oldest ones known.)

Gilmoreosaurus (?) *atavus*, sp. n.

Pl. IX, fig. 1

The name of the species is derived from *atavus* (Latin) -- great great grandfather.

Holotype. - CCMGE No. 576/12457, tooth; Karakalpakistan, Khodzhakul; Lower Cretaceous, upper Albian, lower or middle part of the Khodzhakul Formation, site SH-20.

Material. About 10 teeth.

Description. The teeth are very small for hadrosaurids (Pl. IX, fig. 1). The figured specimen is one of the largest (judging from the size of crown) among approximately 10 teeth, which are, for the most part, strongly worn and were found at the aforementioned locality. The edges of the crown weakly diverge from the apex towards the middle of the distance between the apex and root; when viewed from the enamel-covered side, the part of the crown with serrations along the anterior and posterior edges is smoothly rounded in the form of a vertically elongated semioval. The latter has no straight edges as in Turonian and Coniacian hadrosaurids (Pl. IX, figs. 17, 20). The serrations along the upper edge are simple, continuing as smooth riblets along the enamel-covered side of the tooth, but do not form short chains of knobs (cf. Pl. IX, fig. 17). The riblets on the enamel-covered side connected with the serrations along the edge are very long, up to one fourth of the total height of the crown, as measured from the apex to the pockets situated on either side of the median crest in the near-root part of the tooth. The riblets extend towards the root, parallel to the median crest (rather than obliquely to this crest as in later hadrosaurids).

Comparison. The new species differs from later hadrosaurids in its very small size, the simplicity of the serrations along the edges, the direction and great length of the enamel riblets associated with the serrations, and the greater depth of the pockets on either side of the median crest.

Notes. All the aforementioned features that distinguish the new species from known hadrosaurids are primitive, because they are similar to features characteristic of the teeth in primitive ornithischians (Weishampel et al., 1990a: fig. 19.2), which possess simple serrations, long riblets associated with the serrations, and deep pockets on either side of the median crest.

Isolated teeth of hadrosaurids from the Campanian - Maastrichtian cannot be used for taxonomic identification to genus and species because of the low taxonomic significance of their details (when evolutionary development of separate teeth was already completed) (Coombs, 1988). However, in the initial, unknown evolutionary stages of hadrosaurids, the details of their teeth had a higher taxonomic value. **[48/49]** It was at that time that the rapid, stepwise change of the principal details of crowns took place. It was accompanied by consecutive loss of their primitive features and acquisition of derived features, but not simply by an increase in the number of teeth.

Remains (teeth and bones) of hadrosaurids are known in North America since the late Albian (Russell, 1984; Haubold, 1990; Parrish and Eaton, 1991). Tracks referred to the ichnofamily Hadrosauripodidae and identified as those of hadrosaurids are known from the late Albian of Tadzhikistan (see Parts 4.4.2.195 and 4.4.2.196). Hadrosaur tracks of *Amblydactylus* are supposedly known in the undivided Aptian - Albian of Canada (Currie, 1983).

Distribution. Late Albian (Early Cretaceous) of Karakalpakistan.

Gilmoreosaurus arkhangelskyi Nessov et L. Kaznyshkina, sp. n.

Pl. VIII, figs. 1-2, 3?, 4-7, 8?-10?; Pl. IX, figs. 2-10, 12?, 14?, 17; Pl. X, figs. 3?, 4?, 5, 11?-14?, 17; Pl. XI, figs. 1-2.

Gilmoreosaurus kysylkumense (Riabinin): Nessov, 1989: 173.

The species is named after the geologist A. D. Arkhangelsky.

Holotype. - CCMGE No. 664/12457, left frontal; Uzbekistan, Dzharakuduk; Upper Cretaceous, upper Turonian, lower part of the Bissekty Formation, site CDZH-16.

Material. Frontals and parietals, braincase, maxillae and dentaries, surangular, atlas and axis, vertebrae, sacrum, and humeri.

Description. The frontals (Pl. VIII, figs. 6-7; Pl. XI, figs. 1-2) are foreshortened and enter the margin of the orbit. The sutural contact area with the nasal is oriented towards the midline and gently backwards. In subadult specimens, the edge of the frontal is thin; a fontanelle was retained between the frontal and nasal bones for a long time during ontogeny. The anterior process of the frontal is situated medial to the contact with the prefrontal. This process is spinous (rather than lamellar) and oriented almost precisely anteriorly. In dorsal view, it has a narrow base. The suture with the parietal is shifted anteriorly in the direction of the midline, which indicates the characteristic medial anterior projection on the parietal (Pl. VIII, figs. 1, 2, 4, 5). The parietal surface, which is fairly large in size, weakly concave or flat, subrhombic in outline, extends onto the dorsal surface of the skull. The posterior process of the parietal is not long, which suggests a moderate length for the upper temporal fenestrae. Posteriorly and dorsally on the supraoccipital, crest-shaped, knobbed areas for contact with the squamosals diverge toward the sides and downwards. The supraoccipital proper extends onto the posterior surface of the skull in the form of a relatively high and moderately wide triangle (cf. Rozhdestvensky, 1968a: figs. 3, 9). The arrangement and diameter of the anterior openings of canals for the cerebral arteries and abducent nerves in the basisphenoid (Pl. VIII, fig. 1b) are quite typical for hadrosaurines, as are apparently features of details of the lateral wall and base of the braincase (Pl. VIII, fig. 1). The latter is not yet involved in **[49/50]** the "verticalization" process (Ostrom, 1961: fig. 12 and references). The opening for cranial nerve V is large and rounded. The postorbital (Pl. IX, figs. 9-10) has a very short posterior root with a "pocket" (Pl. IX, figs. 9b, 10b) for the tapered anterior process of the squamosal. The suture of the postorbital with the frontal is relatively long. There is a pit for contact with the anteroventrolateral process of the parietal.

The most complete maxilla (Pl. IX, fig. 4) only lacks a small part of the anterior process (Pl. IX, fig. 4a). The reconstructed total length of this bone is about 210 mm. In the figured specimen, 18 alveoli have been preserved; this nearly adult individual could have had a total of 23-24 tooth series. The most elevated part is situated at approximately 45% of the bone's length, measured from the posterior end. The dorsal process is complete; but, as erosion of the bone has occurred, the upwards protruding process could have slightly shifted forwards, even closer to the anatomical middle of the bone, as is the case in the type specimen of *Gilmoreosaurus mongoliensis* (Weishampel and Horner, 1986). The posteroventral part of the suture with the jugal has only slight posterodorsal projections; the bone is low in this region, and apparently only one or two teeth in each vertical series could fit in the posterior part of the tooth row.

The dentary (Pl. IX, figs. 5-8; Pl. XI, fig. 3) has a (in lateral view) straight or weakly concave ventral edge; anterior to the tooth row, the dorsal edge descends gently and the anterior process considerably projects anteriorly. Apparently adult individuals had 22 to 24 tooth series in the dentary.

The surangular (Pl. X, figs. 13, 14?) is tall, occupying a relatively large area on the external surface of the mandible. Teeth attributed here to this species (e.g., Pl. IX, fig. 17) are characterized by numerous rough serrations along the edges of unworn teeth and by short crests (of chains of knobs) extending from these serrations. These crests extend obliquely towards the median crest and the root; the crowns are of moderate height.

The atlas-axis complex (Pl. IX, fig. 3) referred to this species is relatively long.

The sacrum (Pl. IX, fig. 2, and other specimens) has a ventral surface that shows relatively smooth areas alternating with areas bearing a medial groove.

Caudal vertebrae (Pl. X, fig. 5) have a relatively short, notably posteriorly inclined spinous process.

Humeri (Pl. X, figs. 3-4) have a weakly protruding proximal portion of the deltopectoral crest.

Comparison. The new species differs from *Gilmoreosaurus mongoliensis* (Gilmore) in the anterior process of the frontal, which is short and awl-shaped, rather than double (i.e., not separated into a deep and a surficial portion), more lamellar and longer, mostly oriented anteriorly, but not dorsally and laterally. The frontal of the new species has a more pronounced posteromedial notch (for the anterior projection of the parietal), but a shallower anterior notch near the midline. The maxilla of the new species, unlike that of *G. mongoliensis,* has a slightly less symmetrical outline of the dorsal edge in lateral view; this in part results from the fact that in the holotype of *G. mongoliensis* all projections of the dorsal edge are **[50/51]** eroded (Weishampel and Horner, 1986: fig. 1A). The latter could have had a slightly less symmetrical outline (in lateral view) if it had been better preserved. A distinctive feature of the new species is the anterior process of the dentary, which protrudes further forwards and descends more smoothly in this direction. The new species from Dzharakuduk differs from *G.*(?) *atavus* sp. n. in the more complex structure of the denticles on the tooth crown (each denticle seems to be formed by a series of knobs arranged in a row, having the appearance of a short, arc-shaped crest that is oriented towards the midline and root).

Notes. The new species slightly resembles in some details, such as the long anterior part of the dentary, which gradually decreases in height, the short processes of the postorbital, and the contacts of the maxilla, representatives of the North American genus *Prosaurolophus* Brown from the middle Campanian of North America, which belongs to the most primitive saurolophines (Brown, 1916a; Brett-Surman, 1979; Weishampel et al., 1990a). However, *G. arkhangelskyi* sp. n. is still notably more primitive than *P. maximus* in the manifestation of these features. It has not attained the level of saurolophines but remains at the hadrosaurine level. Moreover, in the Bissekty gilmoreosaur, the frontal extends into the margin of the orbit as a relatively long rather than strongly shortened process. In features such as the large area of the surangular on the external side of the mandible and considerable length of this bone the new species is slightly reminiscent of *Gryposaurus* from the middle Campanian of Canada and *Telmatosaurus* from the latter half of the Late Cretaceous of Hungary and Romania, which is one of the most primitive known hadrosaurids.

The braincase from Iren Dabasu (Gilmore, 1933: figs. 21-22, 24-25) in all likelihood does not belong to a lambeosaurine; therefore, it should be identified as *G. mongoliensis* rather than *B. johnsoni*.

The new species was without doubt dominant among dinosaurs of the late Turonian - Coniacian of Dzharakuduk and possibly the entire Kyzylkum - Aral region.

Distribution. Late Turonian - Coniacian of Dzharakuduk (Uzbekistan) and Tyulkeli (Kazakhstan).

Subfamily LAMBEOSAURIDAE Parks, 1923

Genus *Bactrosaurus* Gilmore, 1923

Bactrosaurus kysylkumensis (Riabinin) 1931

Pl. IX, figs. 13, 16; Pl. XI, fig. 4

Cionodon? kysylkumense (part.): Riabinin, 1931a: 116 and pl. II, fig. 1.

Thespesius (=*Cionodon*) *kysylkumense*: Rozhdestvensky, 1977: 113.

Cionodon kysylkumense: Weishampel et al., 1990a: 558.

Lectotype. - CCMGE No. 1/3760, trunk vertebra; Uzbekistan, Dzharakuduk; upper Turonian - Coniacian, Bissekty Formation.

Material. Maxilla, vertebrae, tooth.

Description. The right maxilla (Pl. XI, fig. 4) reaches considerable depth posteriorly, accommodating two or three teeth in each vertical series. Near the mid-length of the bone, the number of teeth in each series could have reached a minimum of three. **[51/52]** Immediately above the posterior end of the tooth row there is a typical relatively short, posteriorly oriented process of moderate height, which has also been noted in *B. johnsoni* (Weishampel et al., 1990a: fig. 26.6a).

The described jaw bone could have accommodated a total of 23 vertical series, based on the preserved proportions. The dorsal edge and the anterior part of the bone were damaged.

The trunk vertebra (Pl. IX, fig. 13) has a pronounced ventromedial crest.

The tooth (Pl. IX, fig. 16) has a relatively high and narrow crown, which is rather large.

Notes. Distribution of remains of this species, uppermost in the section, may be restricted to the upper part of site CBI-14. However, remains of notably larger hadrosaurids than those described above occur 8-12 m higher in the section, closer to the top of the Bissekty Formation, in yellow, unconsolidated sands.

The hadrosaurids of the late Albian - Coniacian of Uzbekistan differ distinctly from iguanodontids in bone and tooth morphology (Norman, 1987; Norman et al., 1987). Therefore, divergence of these two families occurred not at the boundary between the Early and Late Cretaceous (Rozhdestvensky, 1966; Verzilin et al., 1970), but somewhat earlier, probably at the end of the Berriasian - Barremian interval and during the Aptian.

Suborder CERATOPSIA

Family PROTOCERATOPSIDAE Granger et Gregory, 1923

Subfamily ASIACERATOPSINAE Nessov et L. Kaznyshkina, 1989

Genus *Asiaceratops* Nessov et L. Kaznyshkina, 1989

Asiaceratops salsopaludalis Nessov et L. Kaznyshkina, 1989

Pl. V, figs. 1-19; Pl. VI, figs. 1-37.

Holotype. - CCMGE No. 9/12457, left maxilla; Karakalpakistan, Khodzhakulsai; Upper Cretaceous, lower Cenomanian, site SH-25.

Material. Isolated skull bones, parts of two braincases, vertebrae, bones of girdles and limbs.

Description. In addition to the already published description (Nessov et al., 1989) it should be noted (Fig. 3) that the postorbital region of the skull (particularly the squamosal) is long, the nasal opening is not very high, the dorsomedial projection formed by the nasals is weak, and the frontals enter the margins of the orbits to a considerable extent not only in young but also in adult specimens.

PROTOCERATOPSIDAE incertae sedis

Genus *Kulceratops*, gen. n.

The name comes from the words "kul" (Uzbek), lake (after Lake Khodzhakul) and "ceratops", commonly used ending for generic names of ceratopsians.

Type species. - *K. kulensis*, sp. n., late Albian (end of the Early Cretaceous), Karakalpakistan.

[52/53]

Diagnosis. The maxilla is short, moderately high, very roughly built with a very thick suture with the jugal. This suture is formed by a wide external crest and a narrower internal one, which are partially divided by a deep groove. The ascending plate of the maxilla not far from the contact with the premaxilla is very thick mediolaterally. The notch for the anterior part of the coronoid process of the mandible between the posteroventrolateral process and the ascending jugal process of the maxilla is shallow; anterior to it, there is a large opening above.

Comparison. The new genus differs from *Asiaceratops* from the Cenomanian of the same region (Nessov et al., 1989) and from other more recent protoceratopsids, mostly from the Campanian of Mongolia and China (Granger and Gregory, 1923; Brown and Schlaikjer, 1940b; Maryanska and Osmolska, 1975; Osmolska, 1986; Weishampel et al., 1990a; Kurzanov, 1992), in its small size, the unusual thickness of the maxilla, which has rough features and appears inflated. It also differs from *Asiaceratops* in the much shorter length of the maxilla (considering the position of the tooth row) and its much greater height, in the presence of only one rather than several openings above in the posterior part of the bone under consideration, in the shallow depth of its posterior notch (when viewed from above), and the less protruding suture with the pterygoid (which is not in the shape of a sharp crest). It is impossible to make direct comparison with *Microceratops* from the Upper Cretaceous of China (Bohlin, 1953: fig. 14) and Mongolia (Maryanska and

Osmolska, 1975); however, bones of representatives of this genus known to us are not characterized by pronounced roughness and inflated structure.

Notes. Because the teeth of ceratopsians older than *Kulceratops* - the Aptian - Albian (possibly only late Aptian) psittacosaurs (Osborn, 1923, 1924a; Weishampel et al., 1990a) (Pl. XII, fig. 1) and the ceratopsians that replaced *Kulceratops* in the Cenomanian - the protoceratopsid *Asiaceratops* (Nessov et al., 1988) (Pl. V, figs. 15-19; Pl. VI, figs. 19-37) - are similar in many respects in the character of the serrations and crest shape on the crowns, one can assume that the morphology of teeth for *Kulceratops* gen. n. is also similar to that known for psittacosaurs (Pl. XII, fig. 5) and *Asiaceratops* (Pl. V, figs. 2, 5, 6, 15-19; Pl. VI, figs. 19-37). The new genus differs from known psittacosaurids in the shorter length and lesser height of the maxilla and the considerable roughness of the structure ("inflated state") of its protruding parts. It can be noted that the structure of teeth of the early Cenomanian *Asiaceratops* is reminiscent of that in Dryosauridae among the early ornithopods (Cooper, 1985: fig. 3) and in Psittacosauridae (Rozhdestvensky, 1978: 68), but this similarity is probably symplesiomorphic in nature.

The genus *Kulceratops* gen. n. of the late Albian (end of the Early Cretaceous) is characterized by inflation of features of the maxilla and the shortness of the latter, and was apparently more derived in its known characters than the genus *Asiaceratops* from the early Cenomanian (beginning of the Late Cretaceous). Both genera belong to different evolutionary branches at the rank of at least subfamilies.

Kulceratops kulensis, sp. n.

Pl. IV, fig. 12

The name is derived from the name of Lake Khodzhakul that disappeared in the year when the jaw was discovered.

[53/54]

Holotype. - CCMGE No. 495/12457, left maxilla, with broken anterior process; Karakalpakistan, ravines northeast of the Khodzhakul settlement, Lower Cretaceous, upper Albian, lower or middle part of the Khodzhakul Formation, site SH-21.

Material. Maxilla.

Description. The jaw contains eight groups of alveoli for teeth. Most of these have two openings; in some alveoli, the near-root parts of teeth are still visible. Comparison with the maxilla of *Asiaceratops salsopaludalis*, at maximum size (Nessov et al., 1989: pl. I, fig. 5) (Pl. V, fig. 1), shows that the number of tooth series of *Kulceratops* could hardly have exceeded 10, but probably was eight or nine.

Notes. The roughness of the structure of the jaw indicates an advanced ontogenetic age of the animal. At the same time, the number of tooth series in the holotype of *K. kulensis* sp. n. is low compared with that known for much larger and considerably more recent, mostly Campanian protoceratopsids (Kurzanov, 1990, 1992) that lived 18 to 20 million years after *K. kulensis* sp. n., and also for *Asiaceratops salsopaludalis*. In general, the early protoceratopsids were small; the maxilla (Nessov et al., 1989: pl. I, fig. 5) (Pl. V, fig. 1) and centrum (Pl. VI, fig. 5) belonged to the largest specimens of *Asiaceratops*. The noted maxilla has only nine tooth series; six or seven tooth series are observed in the mandible in the available material. Judging from the size of the jaws in *Bagaceratops*, one can assume that in *Asiaceratops* the distance from the anterior end of the snout up to the posterior margin of the frill was approximately 16-20 cm; the same measurement in *Kulceratops kulensis* was 18.5 cm. Contrary to the doubts expressed by S. M. Kurzanov (1992: 83), we must accept the view that protoceratopsids living at the boundary between the Early and Late Cretaceous had a smaller number of vertical tooth series than the Campanian forms and were smaller than the latter.

The new species is apparently the first protoceratopsid from the Early Cretaceous, except for the discovery of bones of problematic identity from the Lower Cretaceous of Idaho (Weishampel et al., 1990b), and the postcranial skeleton of *Stenopelix* from the Berriasian of Germany (Weishampel et al., 1990a; references therein), which has been referred to ceratopsians, pachycephalosaurs, and ornithischians of obscure taxonomic position.

Distribution. Coast of basin with normal salinity (sea gulf) with forests of Platanaceae and Araucariaceae (Pl. XI, fig. 21) of the late Albian of Karakalpakistan.

Family CERATOPSIDAE Marsh, 1890

Subfamily CENTROSAURINAE Lambe, 1915

Note. It is not necessary to change the name of the subfamily due to the preoccupied nature of the generic name *Centrosaurus* and substitution by the name *Eucentrosaurus* (Chure and McIntosh, 1989: 89), as the original generic name (which had already been used for a lizard) was not the type for the family group.

[54/55]

Genus *Turanoceratops* Nessov et L. Kaznyshkina, 1989

Note. This species differs from *Eucentrosaurus* in having a narrower medial part of the frill and from *Monoclonius* in that the base of its nasal horn is not compressed laterally (Dodson, 1990: 239); it differs from *Brachyceratops* in the absence of suture between the right and the left halves of the nasal horn and its greater length.

Turanoceratops tardabilis Nessov et L. Kaznyshkina, 1989

Pl. VII, figs. 1-8, 15-21, 9?-14?, 22?

Holotype. - CCMGE No. 251/12457, left maxilla with teeth, but with broken anterior, posterodorsal, and posterior processes; Uzbekistan, Dzharakuduk; Upper Cretaceous, upper Turonian, lower (basal) part of the Bissekty Formation, site CBI-27.

Material. Teeth, maxilla and predentary, medial part of the parietal, squamosal, nasal and supraorbital horns, braincase, vertebrae, distal parts of humeri(?)

Description. Teeth (Pl. VII, figs. 1-8, 9?) usually with bifurcated root, except apparently for the teeth at the beginning and the end of the tooth row (Pl. VII, fig. 6). The median enamel crest is very pronounced. Judging from the shape of the wear facets, plant food was mostly cut off (Ostrom, 1966) rather than ground. One of the teeth has a wear facet similar to one noted for the lower teeth of *Leptoceratops* (Ostrom, 1966), which could represent a brief phase of crushing the food after completing the phase of cutting.

The maxilla (Pl. VII, fig. 21) (Nessov et al., 1989: pl. I, 19) was found only one meter above the base of the Bissekty Formation (i.e., one meter above the marine layer usually dated as early Turonian and 25 m below the level dated as late Turonian by sharks). The bone contains only two teeth in the vertical series (one functional and one replacing), which, in its level of primitiveness, correlates with the condition typical of protoceratopsids rather than for the Campanian - Maastrichtian ceratopsids with three or four teeth in each series. The distinguishing feature of ceratopsids is the double-rooted structure of the teeth; this feature is present in *T. tardabilis* (Pl. VII, figs. 1-5), although the most anterior and posterior teeth in the tooth rows possibly have not yet attained double-rooted structure (Pl. VII, fig. 6). The external surface of the maxilla has a larger number of openings for vessels and nerves than in the Chasmosaurinae. The maxilla in *T. tardabilis* had a relatively abruptly elevated ventral edge in front of the tooth row, which has been noted in many North American ceratopsids.

The predentary (Pl. VII, fig. 19b) has no sharp edges inside and outside the alveolar surfaces. Such sharpened areas are known in chasmosaurines (Lehman, 1989: fig. 12G-J).

The medial bridge of the frill (parietal) (specimen No. 723) has a slightly visible medial crest. It was apparently narrower than in *Eucentrosaurus* (Lull, 1907: pl. XXIV, fig. 1; Dodson, 1990), but wider than in *Monoclonius belli* (Lull, 1907: pl. XXI, figs. 1-2) or *Monoclonius crassus* (Hatcher, 1907: fig. 75).

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The squamosal (Nos. 717-718) has a relatively strongly concave lateral side. The sloping notch occupying apparently a large portion of this side is longitudinally extended backwards and possibly slightly upwards. On its lateral side, the bone has several relatively large openings, situated far from one another, which probably served to provide blood supply and innervation of the corium underlying the relatively thick keratinous cover. The remaining part of the posterolateral edge of this bone is sharp and straight and has no traces of adjoining supraoccipital spines. On the medial side in front and below, there is a strong eminence with a rather wide but relatively short area for connection with the paroccipital process of the braincase. The groove-like hollow that served as a place of support for the quadrate is deep and short. In front and below, this hollow is delimited by a sigmoidal, weakly curved crest with a sharp edge, which bends around the hollow on the lateral side and connects to the protruding area for contact with the paroccipital process. In medial view, the crest and the area form an S-shaped structure in a horizontal position. Comparison with the corresponding area in cf. *Monoclonius*, *Torosaurus*, and *Chasmosaurus* (Lehman, 1989: figs. 8-9; Dodson and Currie, 1988: fig. 2) shows for *Turanoceratops* a lesser width and length in the area of contact between the squamosal and paroccipital process, but also a considerably greater width and depth of the groove for contact with the quadrate. In the structure of the squamosal, *T. tardabilis* is most similar to cf. *Monoclonius* from the Campanian of Canada.

The braincase (No. 628) with a broken occipital condyle (Fig. 5) has a shape quite typical for Ceratopsia; it is short and slightly raised forwards and upwards. The distance from the ventral edge of the foramen magnum to the medial notch between the basioccipital projections is close to 50 mm; the height and width of this foramen are 29 and 25 mm, respectively. (The opening is rather large, the distance between its upper edge of the latter and the upper paroccipital process could have been approximately 43 mm; the apex of this process is broken off.) Compared to that of *Eucentrosaurus* among centrosaurines (Weishampel et al., 1990a: fig. 29.5), the braincase of *Turanoceratops* has (in posterior view) narrower basioccipital processes, and the basipterygoid processes have moved slightly further backwards, and a higher position of the ventral edge of the largely destroyed paroccipital processes. The long axes of the latter were apparently oriented not toward the sides, but slightly upwards. The foramen magnum is relatively round. The medial crest above the foramen magnum is wider than in *Eucentrosaurus*, but not as strongly raised. The crest situated between the latter and the paroccipital process is narrow and weak; its beginning is separated from the foramen magnum by a depression. The dorsal (medial) supraoccipital process was apparently not as high as in *Eucentrosaurus*; anterior to it, the surface of the braincase descends abruptly at a short distance. Anterior to the basioccipital processes, there is wide, tall pneumatic cavity inside the bones; the region above the posterodorsal area of the brain cavity is also pneumatized.

The differences from the braincase of *Chasmosaurus* among the Chasmosaurinae (Lehman, 1989: fig. 6) are much more significant. They primarily concern a much less pronounced relief pattern in *Turanoceratops,* the area above the foramen magnum, the presence (on the midline) of a median knob that is oriented backwards and slightly **[56/57]** upwards, rather than a narrow crest separating two pockets, which are even deeper than in *Eucentrosaurus*.

In *Turanoceratops*, compared to *Chasmosaurus*, the basioccipital processes (when viewed from behind) also appear to be separated by a short distance. In comparison with *Chasmosaurus*, the braincase as a whole and its details in *Turanoceratops* appear, in lateral view, even more compressed anteroposteriorly than in *Eucentrosaurus*. This particularly concerns the position of the basipterygoid processes in *Turanoceratops*, which are situated not in front of, but almost below the anteroposteriorly short basioccipital processes, and the position of the foramen ovale closer to the base of the occipital condyle on a more abruptly upwards extending external crest of the laterosphenoid, in a higher position of the paroccipital processes in *Turanoceratops*.

Distribution. Late Turonian and probably Coniacian, coastal plains of the Kyzylkum region.

[57/58]

3. SOME FEATURES OF THE HABITAT AND DISPERSAL ROUTES OF DINOSAURS

The majority of localities with dinosaurian remains and tracks in northern Eurasia metioned in Parts 4.1, 4.3, and 4.4 is associated with the margins of coastal plains bordering brackish-water basins with complex and variable outlines. This is particularly established by the fact that in many Jurassic and Cretaceous localities the deposits with dinosaurian remains are notably variable in distribution, bearing features typical of basin rather than river conditions. Another proof is that bones and teeth of dinosaurs occur together with remains of vertebrate groups of marine and liman lagoon origin.

Thus, in the Jurassic of the Fergana Depression, dinosaurian remains occur most frequently in areas with fossil assemblages containing teeth of the sharks *Polyacrodus* and *Palaeobates* (which are typical of basins with fluctuating but mostly low salinity) and in areas containing remains of carnivorous, brackish-water bony fishes of the group Ichthyodectiformes. The abundance of the latter could have also been determined by high productivity at the base of the trophic pyramid in brackish waters. In the Cretaceous of Uzbekistan, Kazakhstan, and Tadzhikistan, the greatest diversity of dinosaurian remains was found in localities with common occurrence of remains of the skates and sharks *Polyacrodus*, *Hybodus*, *Myledaphus*, *Parapaleobates*, *Baibishia,* and others (Pl. XI, fig. 20; Pl. XII, figs. 4-6, 16-17, 30), which preferred brackish waters. Occurring in the same area were remains of mostly brackish-water fishes, less frequently remains of marine groups of Osteichthyes and Teleostei including *Lepidotes*, *Belonostomus*, Pycnodontiformes, some Elopidae, Albulidae, Ichthyodectiformes, and relict Pholidophoriformes (Pl. V, fig. 21; Pl. VIII, fig. 11; Pl. IX, figs. 25-26; Pl. XI, figs. 12-16; Pl. XII, figs. 10, 15, 19-27), turtles, which were semi-marine in ecology and presumably liman inhabitants, and rather large crocodylians (e.g., Pl. III, fig. 8; Pl. IV, fig. 18; Pl. XII, figs. 28-29).

In the upper Turonian-Coniacian of Dzharakuduk (Uzbekistan), remains of dinosaurs are frequently associated by large (10-12 cm or even longer), fusiform structures with spiral crests stretching from pole to pole. These are egg capsules of cartilaginous fishes, possibly belonging to the family Heterodontidae or, more likely, to representatives of Archaeoselachii, specifically the genera *Polyacrodus* and *Hybodus*. These capsules are identified here as *Palaeoxyris* n. sp. (see also Khabakov [1927]).

Commonly occurring in such localities are wood damaged by brackish-water, wood-boring mollusks (Pl. XII, fig. 11) and phosphatized coprolites of carnivorous vertebrates, mostly cartilaginous and bony fishes (Pl. XII, fig. 12).

In some localities (Parts 4.1.3.39, 4.1.3.70, 4.1.3,89?, 4.1.3.96, and others), dinosaurian bones were buried in clays and sands that became compressed over time and then were subject to boring by brackish-water or marine mollusks of the family Pholadidae or groups close to them. **[58/59]**

Localities with remains of diverse Jurassic and Cretaceous dinosaurs quite commonly show evidence of high biological productivity of the coastal ecosystems, which was based on the effects of estuary upwelling, wind tides that provided for inflow of nutrients into the aquatic-wetland-forest ecosystems.

Not infrequently only large bones and teeth of dinosaurs were discovered in the Jurassic and Cretaceous deposits during initial exploration. However, remains of very small, mostly young dinosaurs and bones of small vertebrates can be recovered at the same localities through washing and sieving of the matrix. Probably such organisms were used to some extent by the young of carnivorous dinosaurs for food. A particularly high diversity of the dinosaurs and other vertebrates in the Jurassic and Cretaceous is noted for those parts of the coastal plains that had relatively deep interbasin channels. In the Jurassic, at the boundary between the Bathonian and Callovian, small theropods were common near such channels. The presence of not only diverse small theropods but also of ceratopsids (Pl. VII, figs. 1-9, 11, 12, 15-21), along with the oldest forms of mammals close to ungulates (Pl. XI, fig. 6), was noted near the coastal regions of such channels of the late Turonian - Coniacian (the first half of the Late Cretaceous) in the Kyzylkum (as well as in similar biota from the latter half of the Late Cretaceous [Campanian - Maastrichtian] in North America).

The banks of such channels were usually covered by forests during both the Jurassic and Cretaceous. Horizontally lying trunks of conifer trees in the Middle and Upper Jurassic of Kirghizia and numerous leaves of *Phoenicopsis* in the adjacent layers are known. In the upper Albian, Cenomanian, and Coniacian of Uzbekistan (Pl. XIII), buried forests, sometimes associated with leaves of sycamores and other angiosperms as well as with cones of conifers, are known (Pl. XI, figs. 21- 22). In the Santonian - lower Campanian of the North-Eastern Aral region, remains of relatively xerophytic, small-leafed angiosperms occur with vertebrate remains (Shilin, 1986). As a whole, the nature of vegetation and humidity of soils near the aforementioned channels in Asia varied considerably during the Jurassic - Cretaceous.

Wind-tide phenomena in the region of the channels resulted in fluctuations of water levels in the basins, inundations of plains covered by forest, and strong currents of alternating direction in the interbasin channels (Ro_ek and Nessov, 1993: 7-10 and fig. 2). The bidirectional character of the currents determined by winds to some extent blocked the meandering of channels and determined salinity fluctuations in the waters flowing through them. During seasons with low wind, in the channels and other deeper parts of the basins, vertical stratification arose in waters with abundant organic detritus and low oxygen concentrations near the bottom, slightly increased salinity, and peculiar chemistry and lower temperature of near-bottom waters. Strong winds mixing such waters with surface waters or their penetration into shallow areas could have caused the death of some of the aquatic, mostly gill-breathing animals such as sturgeons, Polyodontidae, many groups of Teleostei (Pl. IX, fig. 23; Pl. X, fig. 19; Pl. XI, figs. 18-19; Pl. XII, figs. 2-3, 7-8, 31-32). In such basins with an unstable gas regime, aquatic vertebrates that were able to breathe atmospheric air to some extent were dominant.

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These included amioid fishes (Pl. XII, figs. 13-14, 32), known from the Jurassic to the present day, Jurassic relict labyrinthodont amphibians, and some of the last Asian lungfishes. Abundant during the late Turonian - Coniacian in biota of this kind were Lepistosteidae (Pl. VII, fig. 23; Pl. XI, fig. 17), which were able to breathe air and are represented in the record from the Early Cretaceous up to the present day, as well as aquatic Amphibia - Proteoidea (Family Batrachosauroididae) (Pl. XI, fig. 11), water-birds, and turtles.

After strong rains on land, freshening of waters in the shallow limans and in the aforementioned channels could have had an unfavorable impact on organisms adapted to relatively high salinity including normal marine salinity. Freshwater as well as terrestrial organisms that were not resistant to increase in water salinity (Ro_ek and Nessov, 1993: 7-10 and fig. 2) and to inundation could have been subjected to harsh conditions during wind tide from the sea to the lower regions of the land and shallow liman areas. It was the availability of dead fishes, aquatic amphibians, as well as land lizards and mammals that could have attracted diverse carnivorous dinosaurs, including their small species and young, to the banks of interbasin channels and adjoining banks of limans.

Consumption of dead aquatic vertebrates washed ashore and thrown onto the coast could have been significant for some insect groups, including carnivorous Hymenoptera, which were noted above in the discussion concerning the ecology of segnosaurs (Part 1.1). Higher abundance of insects of different groups (including scavengers and coprophages) in such areas could have attracted small birds (Pl. XI, fig. 9), insectivorous mammals (Pl. II, fig. 22; Pl. XI, fig. 7), lizards (Pl. I, figs. 25-27; Pl. III, figs. 23-25; Pl. XII, figs. 9, 34), and terrestrial amphibians (Pl. XI, fig. 10). The diversity of anuran amphibians in this environment was quite significant (Ro_ek and Nessov, 1993), possibly because of mosaic nature and ecotone type of the biota. The number of species was moderate, but the abundance of individuals, particularly of caudate amphibians, was very high

(Nessov, 1981, 1988a). All this could have been very important for the concentration of small theropods searching for food.

Repeated episodes of estuarine upwelling (particularly with an increase of fresh-water flow from the land) provided (Schopf, 1982) for the inflow of phosphates and other essential nutrients in the brackish-water basins and interbasin channels. The existence of estuary fronts and their shift during wind-tides promoted activation of biological processes on the bottom and phytoplankton concentration, favoring maintenance of high productivity among different consumers (Largier, 1993). Nutrients were delivered to semi-closed, shallow-water liman basins not only by estuary upwellings but also by water flow from the land. These nutrient elements were accumulated by aquatic biota of semi-closed basins, specifically by phytoplankton and plants. Common among the latter are remains preliminarily identified as parts of stems and leaf-stalks of the family Potamogetonaceae. The presence of aquatic plants in such shallow-water areas with weak currents is indicated by the discovery of the phosphatized aquatic beetles of the family Hydrophilidae (Nessov, 1986: fig. 1, 13). **[60/61]** This is nowadays a typical insect group associated with algal growth in still waters.

Nutrients in the water of limans were assimilated not only by aquatic organisms, but also by plants that grew on periodically inundated land. Sycamores, laurels, and possibly magnolias are among such plants known from leaf remains from the Coniacian deposits at Dzharakuduk. Nutrients brought to the shores of limans could have moved through food-chains including insects and vertebrates to areas more remote from the basins. The phosphatized, three-dimensionally preserved prothorax of a weevil of the family Circulionidae has been found in the Coniacian deposits of Dzharakuduk. Based on the identification by B. A. Korotyaev (Nessov, 1986: fig. 1, 12), this beetle belongs to the Errhininae, a group now feeding mainly on herbaceous near-water vegetation. Several large phosphatized cockroach oothecae (groups of eggs) were found in a hole of a fossilized branch (about 8 cm diameter) in the Coniacian of the Kyzylkum. Modern representatives of these insects are quite common in forest litter. Having the mostly poorly specialized mouthparts, they feed mainly on partially decomposed plant remains and mycelia growing on them. It is highly probable that the branch with the groups of eggs laid in it was initially in humid soil in litter of the coastal forest. Then it was washed from the coast with the tide and sank in an interbasin channel where, due to the chemical composition of the water (Ro_ek and Nessov, 1993) primarily as a result of excessive saturation with phosphates and as a result of high acidity, phosphatization of the rather delicate organic structures, even at the tissue and cellular level, readily occurred (e.g., Martinson et al., 1986). The aforementioned cockroaches and the weevil could have been eaten by birds (Pl. XI, fig. 9), young theropods, lizards, and mammals, all of which were capable of carrying nutrients further away from the water bodies onto the land.

Spores and pollen were recorded in the spore-pollen assemblages of the Callovian (near the boundary between the Middle and Late Jurassic) of the Northern Fergana in the layer of gray clays with remains of dinosaurs and in the adjacent layers (Aliev et al., 1983). These belonged in particular to alga-like forms, clubmosses (*Selaginella* and others), ferns (*Osmunda*, *Eboracia*, etc.), and gymnosperms (*Gingko*, Cheirolepidiaceae, pine trees, and others). Charophytes of the genus *Jurella* are known from the Callovian in the vicinity of Tashkumyr in Kirghizia (Kyansep-Romashkina, 1974). Remains of wood of the gymnosperms *Xenoxylon*, *Phyllocladoxylon*, and *Podocarpoxylon* were found at somewhat higher levels (Krymgolts et al., 1969). Common here are also small aquatic gastropods, specifically detritophages of the genus *Valvata* (identified by G. G. Martinson), already cited remains of fishes, labyrinthodont amphibians, turtles of the genus *Xinijangchelys* (dominant in the community and possibly in the diet of theropods), rare lizards, small pterosaurs, and crocodylians. In North-Eastern Fergana, strata correlating with those containing remains of the theropods of the end of the Bathonian - Callovian were found to contain beetles, the shark *Polyacrodus*, Osteichthyes of the order Pholidophoriformes, caudate and anuran amphibians, the lizard *Changetisaurus*, crocodylians, and supposedly mammals. Among plants, ferns and gymnosperms have been recorded for this interval.

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Silicified conifer trunks are known from the late Barremian - middle Aptian of Mogoito (Buryatia), and pollen of angiosperms was already present in the pollen assemblage; in 1990, a small, fusiform seed with a series of crests extending from pole to pole was found.

In the late Albian of Khodzhakul (Karakalpakistan), we found remains of small-leaf sycamores and silicified conifer wood and cones (Pl. XI, fig. 21). In the Albian of the Central Kyzylkum (Khudaiberdy'yev and Tashmukhamedova, 1981), the ferns *Laccopteris*, *Weichselia*, *Gleichenia*, *Adiantites*, *Aspleium*, *Cladophlebis*, and others are known from leaf remains, whereas *Piceoxylon* and *Podocarpoxylon* are known from remains of wood.

Remains of leaves of sycamores, cones of Cupressaceae (Pl. XI, fig. 22), spores of *Selaginella* and the ferns *Ophioglossum*, *Osmunda*, *Aneimia*, *Lygodium*, and *Schizaea*, and pollen of the conifers *Podozamites*, Cheirolepidiaceae (sometimes up to 35 %), Pinaceae, and cypresses or Taxodiaceae, and also angiosperms (Shvetsova, 1969) are known from the Cenomanian of Karakalpakistan.

In the Cenomanian of the Central Kyzylkum, wood of *Phyllocladoxylon* and *Podocarpoxylon* has been found (Khudaiberdy'yev and Tashmukhamedova, 1981).

Known from spore-pollen assemblages from the Turonian (Nadyrshin and Shvetsova, 1967) in the Kyzylkum Region are mosses (sphagnum), diverse and probably abundant *Selaginella*, ferns (species of the genus *Schizaea* are dominant, *Lygodium*, *Ophioglossum*, and *Alsophila*, which could have been tree-forming), gymnosperms (including Pinaceae, also Taxodiaceae and Cupressaceae not distinguishable by pollen, and *Podozamites*, dominant Cheirolepidiaceae, Podocarpaceae or *Gingko*, plants of *Ephedra* and *Gnetum* types), and angiosperms. The presence of *Gingko* and *Taxodioxylon* has been established by remains of silicified wood in assemblages with vertebrate remains from the Turonian - Senonian of the Kyzylkum; annual rings indicate seasonal climatic changes (Khudaiberdy'yev and Tashmukhamedova, 1981; Khudaiberdy'yev, 1991). Based on observations in the upper Turonian - Coniacian of Dzharakuduk, remains of silicified conifer wood occur in the former marshes with the presence of sodium ions, which entered with the tide of brackish waters; silicon in the form of ortho- or metasilicate ions, had a silicifying effect on horizontally lying wood (data by the author and L. B. Golovneva). Underground flow of waters rich in Fe^{2+} ions led to formation of sideritic concretions around the trunks of wood buried on the bottom of the basins. Thick growths of sycamores on slightly elevated areas were present near the coasts of limans. Laurel trees and gymnosperms constituted only a small percentage of the community. Thick stands of sycamore forests buried in place were preserved (Nessov, 1980: fig. 1; Nessov, 1988b: figs. 1, 7, 8) (Pl. XIII); represented among these as an admixture were trees with leaf morphotypes corresponding to *Viburnum*, *Celatrum*, and *Laurophyllum*; Platanaceae proper had small leaves, which was possibly related to soil salinity.

During aridization in the Santonian - early Campanian of the Central Asian part of the CIS, floras became more xerophytic and small-leaved, and sycamores stopped being dominant near watercourses and water bodies. Compared to the Turonian - Coniacian, the proportion of remains of angiosperms **[62/63]** and conifers that were subject to damage by wood-boring insects increased abruptly (Nessov, 1988: fig. 1, 9-13).

High productivity of the coastal vegetation provided by the natural input of nutrients and by a sufficiently constant water supply and drainage attracted various herbivorous dinosaurs. This, in turn, led to a relatively pronounced concentration of large theropods that had the role of predators and scavengers. The causes of concentration of small theropods in this habitat have already been discussed. This led to a particularly tense biotic situation for terrestrial (but not aquatic) vertebrates in the vicinity of interbasin channels. This situation was determined by the high abundance and high diversity of semiterrestrial and terrestrial organisms, which were not infrequently bound by competitive relations. The evolution of some vertebrate groups, including mammals, lizards, and small theropods, could have occurred much more rapidly in such habitats rather than in regions with a rigid abiotic habitat and low diversity of inhabitants, but with simpler and less stressful biotic conditions including less competition.

Apparently for aquatic, specifically gill-breathing vertebrates, the abiotic environment near interbasin channels was, on the contrary, rigorous and demanding, in particular because of the strong, abrupt fluctuations in salinity and oxygen content of the water, variations in acidity, and the degree of saturation with nutrients and metabolites. This could have favored the existence of only a few well-adapted forms of gill-breathing vertebrates capable of a broad range of response. Of the aforementioned aquatic organisms those with few or no competitors in such habitats could have been evolving slowly. At the same time, organisms that fortuitously during the course of their evolution became adapted to such conditions had a chance to become abundant and survive for a long time without undergoing significant evolutionary changes because of sufficient adaptations that permitted their existence in such environments as phylogenetic relicts. In the Jurassic faunal assemblages of Kirghizia including dinosaurs along with evolutionarily advanced crocodylians and tortoises, the following forms that have obviously "survived their time" are observed: Palaeoniscidae, Ptycholepididae, lungfishes and sharks, mostly of the Triassic appearance, and labyrinthodont amphibians (the majority of which became extinct in the Triassic). During the Albian - Cenomanian, obvious relicts were bony fishes of the genus *Lepidotes* and the shark *Acrodus*, which has been known since the Triassic. In the Turonian - Coniacian assemblages, relict forms included Pholidophoridae among Osteichthyes (mostly known from the Jurassic) and sharks of the genera *Polyacrodus* and *Hybodus* (which achieved the acme of their development during the Triassic).

Eventually a large portion of brackish-water organisms in the Jurassic and Cretaceous assemblages containing dinosaurs could have been related to the fact that such groups of fishes and other vertebrates capable of a wide range of response were able to live in habitats with strong fluctuations in the abiotic parameters, but with high biological productivity due to abundance of nutrients entering the ecosystems. The large amount of phosphates moving through the food chains provided for a sufficiently large amount for the ecosystem. A certain amount of phosphates left biotic **[63/64]** turnover with the burial of vertebrate skeletons. The retention of the former nature of the biota suggests input of new amounts of nutrients from other sources. In the functioning ecosystem, coprogenic material was deposited in the richest foraging areas. Phosphate ions from this coprogenic material could have been accumulated in muddy waters (particularly after the residual organics were utilized by microorganisms). The high concentration of phosphate ions in muddy water combined with low oxygen content (or lack of oxygen) protected even the finest phosphatic remains from chemical dissolution even under acidic conditions. The same circumstances, in combination with an increase in water temperature (and corresponding decrease of calcium phosphate solubility), provided for phosphatization of the soft tissues of invertebrates (Martinson et al., 1986) and vertebrates. In a number of foreign localities, this type of phosphatization is known for skin and muscles in fishes and wing membrane in pterosaurs; probably the same applies for the fossilization of the "beak" in Ornithischia, of the keratinous cover of the skull, skin of the body, limbs, tongue, tail in hadrosaurids, sauropods, ceratopsids, and other dinosaurs (Brown, 1916b, 1917; Chure and McIntosh, 1989: 192). Therefore, the environment in the vicinity of interbasin channels (near the margins of the coastal plains in general) at the boundaries between water and land, forests and open spaces, was attractive for many dinosaurs and, at the same time, favorable for the fossilization of their remains. The phosphate in the skeleton and teeth of the terrestrial dinosaurs on the coastal plains could have to a large extent originated in aquatic ecosystems.

It should be noted that the fauna of dinosaurs and other terrestrial vertebrates inhabiting areas immediately adjacent to the interbasin channels was characterized by highly specific features. Thus it was in a similar environment in both Asia and the western part of North America where ceratopsids were fairly numerous; caenagnathids occurred as well. For the first time in both regions under such conditions, but at somewhat different times (earlier in Asia), the dominance of placental mammals is established (Nessov, 1985b); the diversity and abundance of multituberculates, a group of archaic herbivorous mammals (Pl. XI, fig. 5), declines or remains low. The first herbivorous forms among placental mammals, the oldest preungulates (e.g., Pl. XI, fig. 6), appear in such habitats near channels. The latter, along with other factors, could have had a negative impact on the well-being of the herbivorous dinosaurs, particularly on their young. However, it should be remembered that preungulates, similar to representatives of the families of mioclaenids and periptychids, co-existed with ornithischian dinosaurs in Asia for approximately 15 million years before the latter became extinct, but did not appear immediately before extinction of the dinosaurs or immediately after this event, unlike the situation in western North America (Archibald, 1989). Comparison of Maastrichtian climates, floras, and faunas of western and northeastern Asia (Nessov and Golovneva, 1990) and western North America shows that the last known remains of dinosaurs in Canada and USA may date from the end of the middle Maastrichtian or early part of the late Maastrichtian.

The occurrence of bones and teeth of Jurassic and Cretaceous dinosaurs in marine fossil assemblages with normal salinity is accidental; they are few and mostly belong to forms that inhabited the coasts of basins with normal marine salinity. These **[64/65]** fossil assemblages are characterized by a low diversity of dinosaurs. Usually, only remains of sauropods and theropods, less commonly ornithopods, and particularly rarely armatosaurs are observed here. Such groups (primarily theropods, which possibly "made their living by using their legs") are most frequently documented by individual tracks and by trackways left on the bottom of salty shallow-water areas. Theropods could have moved along the coasts in shallow waters in search of dead marine vertebrates.

The diversity and abundance of dinosaurs that lived in regions of inland sediment accumulation were apparently low. Preservation of their remains in such regions probably was hampered particularly in humid climates, with an abundance of plant detritus that was buried in the sediments (e.g., in the Lower and Upper Cretaceous in the east of the Vilyui-Lena basin). Pronounced acidity of the ancient surface, soil, ground and mud waters and a low content of dissolved phosphates under conditions of sediment accumulation had a negative impact on the preservation of phosphatic remains.

At high latitudes in both hemispheres (Browers et al., 1987; Davis, 1987; Parrish et al., 1987; Paul, 1987, 1988; Monastersky, 1988; Nelms, 1989a,b; Rich and Rich, 1989; Nessov and Golovneva, 1990; Molnar, 1991; Benton, 1992; Milner and Hooker, 1992; Hecht, 1993), remains of dinosaurs have been found in deposits formed during periods of relative warming (Nessov and Golovneva, 1990; Benton, 1991). Thus, in the middle Maastrichtian of the Kakanaut River in the Koryak Highlands, their remains occur together with apparently thermophilic Cycadales of the genus *Encephalartopsis* (Krassilov et al., 1990), deciduous Cycadales of the genus *Nilssonia*, a diverse flora of angiosperms (including forms with smooth-margined leaves), some *Gingko*, and conifers. According to V. A. Krassilov (1981), plant communities with abundant cycadophytes could have played an important role in the diet of herbivorous dinosaurs. It should be assumed that food dependency on cycadophytes was the highest in ceratopsids with their scissor-like, cutting dentition (Weishampel and Norman, 1987) and in troodontids of the genus *Troodon* that probably gnawed seeds out of cycadophyte cones. Such dependency could have been lower in hadrosaurids and especially sauropods.

In the Maastrichtian of Kakanaut and in the Campanian - Maastrichtian of Alaska (Nelms, 1989a), young individuals of hadrosaurids constituted a large portion of the dinosaurian populations. This shows that long annual migration of these dinosaurs to low latitudes was hardly probable (Nessov, 1992). Climates of that time at high latitudes in the Northern Hemisphere, judging based on the nature of the floras (Nessov and Golovneva, 1990), permitted the dinosaurs to exist in the high-latitude regions year round, probably with winter migrations westwards towards the Okhotsk-Chukot volcanogenic zone (Fig. 7) and surviving the winter on the warm ground of the calderas or in the water of the warm springs (Nessov, 1991, 1992). Possibly in similar areas in localities with endogenic warming of soils, nests were built by such high-latitude dinosaurs, comparable to present-day tropical primitive forms of megapods (Megapodidae). Under the humid climate conditions of Beringia with frequent clouds and rains and with "shielding" against the heat of the sun, it was apparently not the heat from the sun, but endogenic heat from the ground near

[65/66] volcanic regions that permitted reproduction by hadrosaurids, troodontids, and possibly other theropods at high latitudes of northeastern Asia, and of dinosaurs of the same groups and the ceratopsid *Pachyrhinosaurus* (Nelms, 1989b) in northwestern North America. Apart from the aforementioned groups (theropods - troodontids, hadrosaurids - subfamilies of hadrosaurines and also lambeosaurines or saurolophines), small representatives of the hypsilophodontid family settled in the Northern and Southern Hemispheres (discoveries in southern Australia and Antarctica; Weishampel et al., 1990a; Milner and Hooker, 1992). The tooth of an ornithischian dinosaur was identified by us in the private collection of P. Zederstrom from the lower Campanian Asen locality in southern Sweden. Nearest to the pole are the tracks of iguanodontids and theropods in western Spitsbergen and remains of hadrosaurids on Bailot Island in the Canadian Arctic (D. A. Russell, oral communication).

Warming periods at high latitudes during the Jurassic and Cretaceous were, to a large extent, connected to changes in the nature of vertical circulation of the oceans and changes in the amount of heat transmitted by the atmosphere and particularly hydrosphere to the high latitudes (Nessov and Golovneva, 1990; Nessov, 1992a,b). Based on paleobotanical and

[FIGURE 7 HERE]

Fig. 7. Location of occurrences of dinosaurian remains in the basin of Kakanaut River (2) in relation to the Okhotsk-Chukot volcanogenic zone (1); the position of the latter is given based on E. L. Lebedev (1987).

[66/67]

paleozoological discoveries at high latitudes and associated climatic changes in the mid-latitudes, the warmest periods beyond the Arctic Circle, including those on the Bering Land Bridge (which connected Asia and North America), were in the late Albian, early Turonian, late Santonian - early

Campanian, and middle Maastrichtian. It was during these intervals that migrations of different dinosaurian groups across Beringia could have taken place. The most protracted warm period occurred there at the end of the Santonian to the beginning of the Campanian (German, 1988). In western Asia, judging from the changes of regional dinosaurian faunas during climatic changes, the richest assemblages of these animals inhabited warm, semihumid coastal plains during the Coniacian.

For the Early to Middle Jurassic, considering the paleogeographic relations of land masses during that time (Sinitsin, 1966), one can expect a certain similarity between dinosaurian faunas in Europe and Asia and also within the boundaries of Asia. However, during the Late Jurassic and during most of the Early Cretaceous, a certain endemicity of Asian dinosaur faunas must have been formed as a result of the isolation of Asia from Europe and North America by seas. These suppositions, however, must be tested through future discoveries of vertebrate remains. In China as well as in the Central Asian Region of the CIS during this time interval, thick-toothed forms dominated among sauropods (Dong, 1992). One would expect a notable similarity between the Bathonian-Callovian faunas of sauropods and theropods in China and Kirghizia, at least at the generic level.

Hadrosaurids already appeared in both Asia and North America (Utah) in the late Albian (R. Cifelli, oral communication; see also Russell [1984: 23] and Haubold [1990: table 7]). However, no evidence is known for the presence of the Asian psittacosaurids, recently dated as Aptian - Albian, in North America (Russell, 1984; Weishampel et al., 1990a; Lucas, 1993). One of the possible explanations is that psittacosaurids could have become extinct before the beginning of the late Albian, when the dispersal of hadrosaurids took place. It cannot be excluded, however, that for psittacosaurids and a number of other dinosaurs the relatively cold humid land covered by forest in the contact area between northeastern Asia and northwestern America at that time and later could have played the role of a bridge selectively; psittacosaurids (known to range northward up to the southern part of the Kemerovo Region) simply did not reach the Bering Land Bridge.

Unfortunately, dinosaurian faunas from the first half of the Late Cretaceous (Cenomanian, Turonian, Coniacian, and Santonian) of North America are very poorly known (Russell, 1984; Parrish and Eaton, 1991), and therefore it is difficult to trace and date the course of migration of a number of dinosaurian groups from Asia to North America. Considering the existence of one of the important thermal maxima at the beginning of the early Turonian, one can expect immigration of some theropod groups, such as troodontids, to or from North America at that time. Ceratopsids most probably already existed in Asia at the beginning of the Turonian, and they could have invaded North America at that time (during a short warming phase) or during the more pronounced and protracted late Santonian - early Campanian thermal maximum. The evidence in favor of the latter assumption is that ceratopsids have not been discovered in Canada until the early Campanian in the Milk River Formation (Fox, 1972), in the USA (Utah) until the upper Campanian levels (Kaiparovits Formation), and have not yet been discovered in the Albian, **[67/68]** Cenomanian, and Turonian (see Parrish and Eaton [1991]). If this is true, the diversity of Campanian ceratopsids of North America probably does not reflect their radiation in the place of invasion, but shows that a relatively large number of lineages of Asian ceratopsids migrated from Asia into the western half of North America. In this case, one can expect notable diversity in future discoveries of East Asian pre-Maastrichtian ceratopsids. The late Santonian - early Campanian thermal maximum could have been used for crossing the Bering Land Bridge not only by ceratopsids but also by saurolophine hadrosaurids, large tyrannosaurids, and precondylarth mammals of the *Zhelestes* and *Gallolestes* types that possessed evolutionary tendencies typical of condylarths proper. Separately, most thermophilic groups of lizards and some small theropods (Oviraptorosauria and others) could have invaded North America at that time. Some condylarths could have invaded North America during the middle Maastrichtian, when the small theropod *Troodon* sp. cf*.* *T. formosus* Cope could have moved from North America to Asia. At least than two migrations across Beringia were assumed for ornithomimids (Yacobucci, 1990).

The similarity of Campanian-Maastrichtian dinosaurian faunas from Asia and from the western part of North America has been known fairly well for a long time (Brett-Surman, 1979; Chure and McIntosh, 1989; Weishampel et al., 1990a; and references in these works). The western part of North America was at that time separated from its eastern part (Williams and Stelck, 1975; Russell, 1989) by a longitudinal seaway. Within this time interval, the eastern part of North America had various connections with the European land mass. The connection between Asia and the western part of North America across the Bering Land Bridge (which was relatively wide at that time) created an ancient continent known as Asiamerica in the Northern Hemisphere during the Late Cretaceous (Fig. 2). The midcontinental seaway of North America and the Turgai Strait (separating Asia from Europe) were evidently similar in hydrology. Both had strong, cool surface currents that were directed southward and then westward and warm deep-water currents of more dense waters toward the north (Nessov, 1992a,b). The major part of the deep warm waters could have penetrated the Arctic Ocean through the deep areas of the Atlantic that became open. The Turgai Strait and the North American midcontinental seaway had similar roles as barriers to dinosaurian dispersal.

In the southwest, Asiamerica was separated from Africa by the Tethys Ocean with its powerful, westwardly directed trade currents. In the southeast, this continent was separated from South America by the Panama Strait. The latter had a current continuing the Tethys trade current. These trade currents precluded faunal exchange between the Northern and Southern Hemispheres. These currents carried waters of the surface currents of the aforementioned straits westward and eventually into the Pacific Ocean where also silt-brush-wood "rafts" promoting migrations of terrestrial tetrapods must have been carried. All of the above factors determined the particular importance of the land connections through Beringia in the history of dinosaurian faunas in Asia and the western part of North America. Further search for new localities containing **[68/69]** terrestrial tetrapod assemblages of the Late Cretaceous in the region of the Bering Land Bridge is needed.

The largest gap in the history of the dinosaurs and other tetrapods of the coastal plains of Asia, as, for instance, at mid-latitudes in the Northern Hemisphere, encompasses the Callovian-Barremian interval, with relatively scanty data available for the Tithonian-Berriasian (e.g., Lucas, 1993). The least amount of data falls on the first half of the Early Cretaceous as a whole and particularly on the Hauterivian stage. Within the aforementioned intervals as well as for the Aalenian and beginning of the Middle Jurassic - a time of strong cooling - well-dated remains of dinosaurs are nearly or completely lacking. Erosion of friable sediments with dinosaurian remains on the coastal plains situated above the oceanic erosional basis could have take place (Lisitsyn, 1988) during oceanic regressions (decrease in sea level) occurring due to centrifugal forces in the course of changes in the planet's rotation rate (Katz, 1988). The following processes took place: transfer of remains by water currents, weathering and transfer of destroyed fossils to lower levels up to the edge of the continental slope and sea floor, and redeposition in localities now inaccessible for prospecting. Remains that were transferred to the sea floor have been or will be destroyed in subduction zones. It is not an overstatement to say that our knowledge of the dinosaurs of some time intervals is thousands or millions of times less than, for instance, our knowledge of the dinosaurs during the Campanian or Maastrichtian (see also Haubold [1990]).

The gaps in the dinosaurian record for the interval between the Callovian and late Barremian or even late Albian can be filled to some extent through an analysis of the taxonomic identity of the dinosaurs that left trackways in the Upper Jurassic and Lower Cretaceous coastal marine deposits. It is to be hoped that it will be possible in the future to verify to some extent the nature of changes in dinosaurian faunas from the Late Jurassic through the first half of the Early Cretaceous. By analogy with the historical changes in the composition of dinosaurian faunas during the Albian - Campanian along the western edge of Asia, it can be assumed that during the interval from the Late Jurassic to first half of the Early Cretaceous dinosaurian faunas were subject not to gradual changes, but rather to abrupt changes associated with strong regressions of the seas and liman lagoon basins. Such short critical intervals must have been followed by periods of relative stasis in the composition of the communities.

The rapid replacements of terrestrial vertebrate assemblages of the coastal plains during regional and global regressions of the world's oceans were associated with the appearance of many important new land connections between continents separated by shelf seas, with the joining of territories where, prior to these regressions, isolated faunal complexes had developed for a long time. This probably could have been followed by dispersal of the most competitive species in each ecological niche. The intensity of competition during such short periods could have been increased abruptly due to the drying of deltaic areas and decrease in the number and area of locations suitable for life. Such drying resulted from a drop in ground-water level controlled by **[69/70]** sea level. The abrupt environmental change resulted from the replacement of the existing vegetation by an essentially more xerophytic vegetation. Water flows cutting into the soft sediments of deltas and coastal plains led to development of a relatively dissected relief, different from the previous one.

All the aforementioned factors would have inevitably led to fragmentation of environments favorable for dinosaurs. In each of such fragments retaining habitats relatively favorable for life, the processes of final elimination of less competitive forms should have been faster because of the scarcity of resources (Nessov and Golovneva, 1990: 202; Archibald, 1993: 93) than in the more extensive areas. In the latter, less competitive species could have potentially been able to find an area with specific conditions where they would be ecologically more successful than their new competitors. Therefore, it can be assumed that at the end of the Jurassic a moderate rearrangement of the dinosaurian communities could have taken place during the course of a moderately strong regression, whereas one of the strongest changes in the composition of the dinosaurian faunas could have taken place in the Hauterivian and then moderate changes could follow after the termination of the transgressions during the late Barremian - late Aptian and late Albian.

The dinosaurian fauna of the late Barremian - middle Aptian in Buryatia (regarding its age see Nessov and Starkov [1992]) probably included segnosaurs or representatives of the baryonychid-spinosaurid lineage and also a small theropod, and mainly sauropods as dominant forms among or the only herbivorous dinosaurs known there. In this respect, the given fauna is similar to a number of faunas of Gondwana and Euramerica during this or later periods and also to dinosaurian assemblages from the Jurassic of the Northern and Southern Hemispheres. Faunas with a dominance of the sauropods are unknown in Asiamerica after this interval. It is curious that in the fauna of the late Barremian - middle Aptian psittacosaurids, which are known in the Early Cretaceous of Asia south and west-north-west of Buryatia, have not been discovered. Either psittacosaurids were not among the dominant forms in this fauna or, more probably, were dominant in a slightly younger fauna and existed at the same time as the bony fish *Lycoptera*, in particular *L. fragilis* (Cockerell, 1924; Rozhdestvensky, 1955a: 778). At that time, during the peak of marine transgression and brackish-water ingression, shallow-water coastal deposits with remains of psittacosaurs could have accumulated over the very extensive Asian territory. If the ages for the assemblages with sauropods in Buryatia, psittacosaurids in the Kemerovo Region, and advanced iguanodontids in Mongolia and China are correct, the change in the composition of dominant groups of herbivorous dinosaurs from sauropods to small primitive ceratopsians and ornithopods occurred from the late Barremian - middle Aptian to late Aptian - Albian, during a wide interval of the Early Cretaceous (Wing and Tiffney, 1987).

The (late) Albian assemblage of dinosaurs in Karakalpakistan demonstrates the typical features of Late Cretaceous Asiamerican associations: presence of hadrosaurids along with ceratopsians and a "shift" for sauropods from dominance to a subordinate position among herbivores. It is curious that the change from the Barremian - middle Aptian assemblages of dinosaurs to the Albian assemblages occurred during the time of **[70/71]** the explosive diversification of the angiosperms (Vakhrameyev, 1988) and possibly, to a large extent, was associated with the latter.

It was not until the beginning of the Cenomanian that troodontids appeared in the fossil record of western Asia (Uzbekistan). However, they were present in the late Aptian of Mongolia (Khovboor) and in the late Albian of western North America (Parrish and Eaton, 1991).

The replacement of dinosaurian groups on the coastal plains at the Cenomanian - Turonian boundary was among the most abrupt ones throughout the entire Late Cretaceous. At that time, the protoceratopsids, which were dominant among herbivorous dinosaurs in Uzbekistan during the early Cenomanian, nearly disappeared from that region. As replacement of species, if not genera, occurred, the hadrosaurids become dominant at this boundary. The Ceratopsidae could have appeared in Uzbekistan at the same time, although they are not known in the record until the late Turonian. At the Cenomanian - Turonian boundary, replacement among small theropods took place: temporary disappearance of troodontids with large tooth serrations and appearance of new groups, as well as replacement among ankylosaurs. It is important to note that there were also notable changes in other vertebrate groups at the boundary between the Cenomanian and Turonian: turtles, mammals, cartilaginous fishes, Actinopterygii, etc. This usually coincided with the disappearance of some families and subfamilies and appearance of totally different ones; a great many genera were replaced. Only very few genera succeeded in crossing the Cenomanian - Turonian boundary (e.g., the actinopterygian *Belonostomus*, the sharks *Hybodus* and *Polyacrodus*, the turtle *Anatolemys*, and the dinosaurs *Troodon* and *Chilantaisaurus*). Such replacement, as was already mentioned, was observed not only for the continental - liman complexes in Uzbekistan, but also for seas on the Russian Platform: disappearance of ichthyosaurs, spread of mosasaurs, very important replacements among sea turtles, bony fishes, and sharks. The Cenomanian - Turonian replacement of faunal assemblages is noted also in sections of the continental liman Bainshirein Formation of Mongolia, where a fauna with turtles of the genus *Kizylkumemys* is replaced by a fauna with *Lindholmemys*. Apparently, the appearance of sharks of the genus *Hybodus* in eastern Mongolia with a slight increase in salinity in the basins and strengthening of their connections with waters of higher salinity dates to the beginning of the dispersal of a fauna including *Lindholmemys*, most probably at the beginning of the early Turonian. The previous invasion of brackish-water sharks (genus *Asiadontus*) in the region apparently took place during the late Aptian. At least the basin of sediment accumulation of the Iren Dabasu Formation was brackish. The time of its existence correlates with the second fauna of the Bainshirein time (including *Lindholmemys*). It is not surprising that a study of turtles known from Iren Dabasu (Gilmore, 1933; Currie and Eberth, 1993) identified representatives of *Lindholmemys* rather than *Kizylkumemys* that are known from the Cenomanian of Uzbekistan and Mongolia. In the context of all the aforementioned, one may anticipate the discovery of new evidence in support of an important replacement from the Cenomanian to the Turonian, in as yet unexplored continental liman faunas (including dinosaurs) and in North America.

The assemblages of dinosaurian eggshell of North Fergana belong to the lower part of the Turonian-Santonian interval. (The lower part of the Yalovach Formation differs drastically from the Aptian ones [Khodzhaosmanian Formation].) Obviously no species were shared between these two intervals.

The fauna of dinosaurs and other vertebrates of the late Turonian - Coniacian of the Kyzylkum and North-Eastern Aral region, or at least a part of it, **[71/72]** developed in pre-Turonian times, but, in view of the data presented in the previous paragraph, this apparently did not occur until the end of the Aptian. Development of this fauna took place in some other region. In the Kyzylkum-Aral region, the fauna was most diverse and abundant during the humid climate phase. One can therefore assume that the region where the faunas merged was characterized by a sufficiently humid climate. In this fauna, many evolutionarily advanced groups appeared very early: for example, the genus *Eoscapherpeton* among caudate amphibians, *Shachemys* and adocid turtles, lizards of the family Priscagamidae, small advanced eusuchian crocodylians, early nyctitheriid and preungulate mammals, etc. Apparently, the habitat of formation of this rich, warmth-loving fauna including approximately 65 to 70 families of aquatic and terrestrial vertebrates was characterized by climatic conditions favorable for the existence of different vertebrates. However, for the same reason, this habitat was characterized by high biotic complexity. The latter could have determined high rates of evolutionary selection, there being abundance of competing forms, which became extinct or shared and redistributed ecological niches, or because of basically new adaptations (or new combinations of adaptations) literally "discovered" new ecological "spaces" with a multitude of vacant niches. All this suggests that the fauna of terrestrial vertebrates of the late Turonian - Coniacian of Dzharakuduk and Tyulkeli evolved in warmer and relatively humid conditions, possibly south of those areas where it was discovered. It is quite possible that this fauna and also a similar vertebrate assemblage from Iren Dabasu in China developed in southern and southeastern Asia (Fig. 2) where the fauna of the late Turonian - Coniacian of Dzharakuduk, in turn, is very similar in the composition of brackish-water sharks, skates, Chondrostei (Acipenseridae and Polydontidae), Amiidae, Lepisosteidae, relict Pholidophoroidea (Nessov, 1986: fig. 2, 10-11), Aspidorhynchidae, Elopidae and other bony fishes, three families of caudate amphibians, some anuran amphibians, a number of important groups of turtles, lizards, pterosaurs, dinosaurs, birds, and mammals including precondylarths to the later faunas of the Campanian - Maastrichtian in the western regions of the USA and Canada (e.g., Estes, 1964). Because, within the earlier Turonian - Coniacian fauna, a series of groups (caudate amphibians - scapherpetontids, placental mammals, Lepisosteidae, various turtles, lizards, etc.) in Uzbekistan demonstrate an evolutionarily more derived state of important morphological features than the currently known related forms from the Campanian - Maastrichtian of North America, it is quite probable that the Turonian - Coniacian fauna of the Kyzylkum and Aral region was not ancestral to the North American one. Apparently both faunas, including the diverse dinosaurs, had their origin in an initial fauna of the Northern Hemisphere spread, as was already indicated, most probably through the south of Asia (Fig. 2). Unfortunately, access in that region to deposits containing remains of such an "ancestral" community may be extremely difficult because of the tectonic consequences of the northward shift of the Indian plate. However, one can hope for the discovery of such remains in southeastern Asia because contact between the Indochina "microcontinent" and Asia was established early, no later than the end of the Triassic (Buffetaut, 1984); the **[72/73]** history of climates in this region (Sinitsyn, 1966) suggests the existence of this "ancestral" community of warmth-loving forms. Evidently not all vertebrates groups represented in such a hypothetical "ancestral" community of southern Asia could have invaded North America. Thus the sauropods of the late Turonian - Coniacian of Asia and the Maastrichtian of North America, judging based on the relief of tooth enamel (Kues et al., 1980) (Pl. III, fig. 9), definitely were not closely related although they may belong to the same family. Apparently sauropods, being relatively thermophilic (they are not known in the rich assemblages from the Cretaceous of Canada, and have not been observed north of England and apparently north of Blagoveshchensk on the Amur River [Nessov and Golovneva, 1990]) in Eurasia could not use the cold Bering Land Bridge for migration from one part of Asiamerica to another. The co-occurrence of ceratopsids and sauropods in a single assemblage is known in North America only in the middle southern part of the USA (Lozinsky et al., 1984; Weishampel et al., 1990a). Apparently the fauna of the Turonian - Coniacian of Dzharakuduk also correlates with a similar latitudinal climatic zone or at least a similar annual temperature regime.

It is curious that the Santonian vertebrate fauna from the southwestern edge of the Asian land mass, which replaced the aforementioned Turonian-Coniacian fauna in many groups (particularly fishes), already strongly differs from the Campanian-Maastrichtian assemblages of North America: Lepisosteidae and the skate *Myledaphus* are absent; there seem to be no Pholidophoroidea; and Precondylartha etc. have not yet been discovered. It should be noted that the faunas of the early Cenomanian of Karakalpakistan, which precede the (Turonian - Coniacian) Bissekty fauna, and those from the beginning of the early Turonian of Dzharakuduk (Uzbekistan) also resemble none of the known faunas in North America. However, as has already been stated, without adequate knowledge of the Cenomanian and Turonian-Santonian faunas of North America we cannot make such comparisons with certainty.

One can assume that the dispersal of the dinosaurs, particularly of amphibiotic forms, could have proceeded most readily in coastal regions (Fig. 2) rather than through the interior of the continent. This assumption is based on the rapid change in the nature of sediments from the coastal regions of the Turonian - Coniacian in Uzbekistan toward the interior: the proportion of red-colored deposits and their carbonate content increased and silicification of wood took place without formation of encrusting sideritic concretions. There evidently was a notable difference in humidity between the coastal areas and the interior. The relative humidity of the coastal areas (along the edges of relatively arid land) could have been determined the moistening action of morning breezes carried by ascending air currents above the relatively strongly heated land and relatively regular mid-day rains.

The greatest similarity between the dinosaurian faunas of the coastal plains of southwestern Asia and Central Asia (Inner Mongolia [China] and Mongolia proper) occurred during the late Turonian - Coniacian and in part during the Cenomanian.

Undoubtedly a change took place (although it was not as significant as the change between the Cenomanian and Turonian) in the dinosaurian faunas of southwestern Asia (Uzbekistan, **[73/74]** Tadzhikistan, and Kazakhstan) near the Coniacian - Santonian boundary. It was apparently determined mostly by the increase in aridity and associated changes in the vegetation (Shilin, 1986). The following events took place at that time: a shift of dominant forms among hadrosaurids from *Gilmoreosaurus* to *Aralosaurus* and apparently also the replacement of primitive ceratopsids with two teeth in each vertical series by more advanced ones, and dispersal of larger theropods with a complete or partial replacement of the dominant *Alectrosaurus* by the larger, thick-toothed *Tarbosaurus*. Judging from the discoveries of bones and teeth in North-Eastern Aral region, the dominance of hadrosaurids increased.

Based on eggshell assemblages, changes in the composition and general simplification of dinosaur complexes are noted from the Santonian through the early Campanian of Northern Fergana, as well as an increase in size of relatively long eggs with crestlike and knobbed relief and angusto-canaliculate perforation. Very scanty data are available regarding skeletal remains of dinosaurs in the west of ancient Asia during the period of increase in temperature and aridity in the late Santonian - early Campanian. However, the scant data available suggest the existence of peculiar dinosaurian faunas at that time.

In the middle Campanian of southern Kazakhstan (Kyrkkuduk II), there is again an increase in the number of groups similar to those known from the Campanian - Maastrichtian of North America. These are, in particular, the crocodylian *Brachychampsa* and the relatively large *Troodon*, which is much larger than the early Cenomanian one from Sheikhdzheili II and similar in the size of teeth and the nature of their serration to the North American type species of the genus. Because crocodylians - the durophagous *Brachychampsa* - are known in North America from the Albian to the Eocene, whereas they did not appear in western Asia until the middle Campanian, it is quite probable that the relatively long and strong late Santonian - early Campanian thermal maximum at high latitudes (German, 1988; Nessov and Golovneva, 1990) permitted two-way faunal exchange between Asia and western North America; usually only the consequences of migration in one direction - from Asia to North America - are observed.

No evidence regarding the dinosaurian faunas of the late Campanian - Maastrichtian in Uzbekistan, Kirghizia, and Tadzhikistan is available. At that time, relatively thin (mostly marine) strata were deposited, and their taphonomy is unfavorable for conservation of dinosaurian remains. However, in the future, one could hope for the discovery of important late Campanian - Maastrichtian dinosaurian material in eastern Kazakhstan where transgressions of brackish waters scarcely penetrated, whereas areas of land situated to the southwest were covered by marine transgressions. At the same time, in the Far East and North-East, it is the Campanian-Maastrichtian stage of dinosaurian faunal development that may be represented most completely on the entire CIS territory. The dinosaurian assemblage already mentioned for the middle Maastrichtian of Kakanaut including *Troodon* (very similar to *T. formosus*) is obviously of North American origin. Thus, at least for the Campanian-Maastrichtian, one can expect to obtain new evidence of immigration by some dinosaurian groups from North America into Asia and dispersal there. At the same time, it should be assumed that migration from Asia across Beringia was still more common. Future study of late Albian - Santonian faunas of western North America (Utah **[74/75]** etc.) can be expected to reveal new evidence of mutual exchange of dinosaurian groups between the two parts of Asiamerica. Not dwelling in detail on the extinction of the dinosaurs at the end of the Cretaceous (Ginsburg, 1990; Haubold, 1990; Weishampel et al., 1990a; Archibald, 1992, 1993; Charig, 1993; and references in these works), we should note that a drop in as well as a considerable rise of sea level could have led to fragmentation of habitats on the coastal plains covered with forests and on wetland plains occupied by dinosaurs. Small refugia where earlier conditions were retained sometimes could not provide stable living conditions for small populations. A process of progressive biotic impoverishment among large organisms could have commenced. Such a process is known for insular faunas. The above refugia were in essence fragments of the former habitat, islands in spaces that were unsuitable or insufficiently suitable for life (Nessov and Golovneva, 1990: 202; Archibald. 1993: 93). In insular faunas, not only individual forms, but also groups of related species can disappear. For instance, the extinction of the ankylosaurs (if they strongly depended on ovophagy, i.e., eating eggs of other dinosaurs) most probably was inevitable after disappearance or notable decline in the numbers of herbivorous dinosaurs. Considering the drying of coastal plains and changes in their vegetation during marine regressions (because of the lowering of groundwater levels in deltaic areas) it can be assumed that habitats suitable for the dinosaurs on coastal plains could have almost disappeared at the boundary between the Maastrichtian and Danian. The change occurring in the system of planetary oceanic and atmospheric circulation, with profound changes in the transfer of heat and humidity across the planet and in climatic patterns (Nessov, 1992a,b), could have completed the process of extinction of the dinosaurs in the last refugia. Extinction of small populations of dinosaurs during the cooling during the late Maastrichtian (if that stage is divided into three parts) could have occurred because of the possible relationship between the future sex of developing embryos and incubation temperature (Paladino et al., 1989). The relationship between sex ratios of the young and slight temperature changes of the clutch has been established for modern crocodylians, a number of turtles, and some lizards. Abrupt shifts in the sex ratio of the small endangered populations of dinosaurs could have had an important role in the extinction of such widely distributed forms as the herbivorous, semiaquatic hadrosaurids.

In general, pronounced heterochronies can be noted by comparison of the Asian faunas containing dinosaurs with each other and with faunas from North America, Europe, and Gondwana. Thus, in Asia, sauropods (as dominant consumers of vegetation in the assemblages, but not as a dominant taxonomic group) are not known later than the late Barremian - middle Aptian. However, in Gondwana and Europe, sauropods apparently played an important role in the faunal assemblages almost to the very end of the Cretaceous. Eosuchians of the order Choristodera are not known in Asia later than the Aptian - Albian, except for the short-term invasion of the large choristoderan *Simoedosaurus* into Asia from Europe in the late Paleocene. In North America, Choristodera survived into the Eocene, whereas in Europe they also existed in the Oligocene. The low rigidity of biotic habitat on the respective land masses could have been the cause of survival of such relicts. **[75/76]** Protoceratopsids were only dominant on the coastal plains of western Asia during the early Cenomanian, whereas in inland regions of Asia (Mongolia and northern China) where the climate was probably more arid (Jerzykiewicz and Sweet, 1987) they "persisted" as dominants and subdominants into the Campanian and possibly even longer in North America. Dominance of hadrosaurids in southwestern Asia was established since the late (possibly early) Turonian. In Mongolia, this process was not as fast and clearcut; it was not completed until the end of the Campanian to beginning of the Maastrichtian. Whereas the Lepisosteidae disappeared in western Asia approximately at the boundary between the Coniacian and Santonian, they existed in North America throughout the remaining part of the Senonian and Cenozoic, surviving there along with the Amiidae to the present day. The history of the western North American family of caudate amphibians Dicamptodontidae that survived to the present day is similar. However, they probably originated in Asia during the Early Cretaceous. Turtles of the family Nanhsiungchelyidae did not appear in the record of western Asia until the end of the Albian and the beginning of the

Cenomanian, but they survived as dominants into the Campanian in Mongolia and even into the Maastrichtian in North America. Preungulate mammals (similar to the families Mioclaenidae and Periptychidae) appeared in the Central Asian region of the CIS (Dzharakuduk II) during the Coniacian. In Canada and the USA, related forms are known from the boundary between the Cretaceous and Paleogene. All this demonstrates that, zoogeographically speaking, the western part of North America was the edge of Asiamerica. Being isolated by the Bering thermal filter from Asia, which was more extensive and had a more diverse fauna, North America long retained relict groups of former Asian invaders. The Bering filter protected North American faunas from invasion by new, evolutionarily advanced vertebrate groups from Asia for a relatively long time. Whereas biotic conditions could have played a sufficiently important role in the extinction of the dinosaurs (interactions with competitors such as herbivorous mammals) it cannot be ruled out that dinosaurs disappeared at least in some regions of Asia earlier than in western North America.

The Asiamerican kingdom, as opposed to the Euramerican - Gondwanan one, can be distinguished based on the zoogeography of the dinosaurs and other tetrapods during the Albian - Late Cretaceous. The former is divided into the West American Region (with differences in dinosaurian faunas between the southern and northern parts) and the Asian region. The boundary between the regions extended in all likelihood along the edge of the western, most humid part of Beringia, possibly west of the Okhotsk-Chukot volcanogenic zone (Fig. 7). Within the limits of the Asian region, the Turanian and Mongolian subregions can be distinguished. Probably at least one more area of the same rank can be distinguished in southern Asia.

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[77/78]

4. APPENDIX. LOCALITIES OF REMAINS OF BONES, TEETH, EGGSHELL, AND TRACKS OF DINOSAURS IN NORTHERN EURASIA

In 1983, a map of world's dinosaur discoveries was presented at the Zoological Institute of the Academy of Sciences during an exhibition dedicated to dinosaurs from the Havre Natural History Museum (France). On that map, only 10 localities were shown for the USSR, although the actual number of localities known for the USSR at that time was approaching 200. Publications on the dinosaurs discovered in the CIS, particularly the early works, have been very incompletely covered in the most recent worldwide bibliographic review of the group (Chure and McIntosh, 1989). Another large summary review on the dinosaurs of the world with a chapter listing localities (Weishampel et al., 1990a) listed only 21 localities for the CIS (one belonging to the Jurassic, 7 to the Lower Cretaceous, and 13 to the Upper Cretaceous), two of these contain tracks and two eggshell. This list is incomplete and covers only a very small portion (approximately 1/10) of the localities actually known and already reported in the literature. Furthermore, the list contains numerous inaccuracies and errors, regarding both placement of localities in the republics, formations, and age intervals (a discovery attributed to the Jurassic probably dates to the Devonian) and the composition of dinosaurian assemblages. At least one locality on this list (for the Cretaceous of the Jewish Autonomous Region) probably does not actually exist. A new review of data on the dinosaurs of the world is now being prepared, but it may again be incomplete. Therefore, the author considers it necessary to inform all interested researchers concerning the data accumulated in recent years.

In establishing names of localities from the author's own work or from literature data, the author encountered certain difficulties. It is sometimes not easy to make a decision, whether different levels with remains exposed at a considerably large distance from each other should be listed as different localities or as one and the same location. Difficulties of this kind are related to the fact that sometimes, for example, in the North-Eastern Aral Region, ravines and chains of exposures stretch for tens of kilometers, but toponyms and landmarks are rare. In other cases, for instance, near the Sultan-Uvais ridge in Karakalpakistan, the density of different landmarks and toponyms is very high; localities with distinct faunal assemblages of different ages are situated not far from each other; and the question arises which of the toponyms among the closest ones is to be regarded as the name of locality or how far two localities should be separated on ravines of an interrupted chink [chink = cliff of a plateau in Middle Asia] to be regarded as different

[78/79]

[FIGURE 8 HERE]

Fig. 8. Localities with remains and tracks of dinosaurs on the territory of the CIS without taking into account discoveries in Middle Asia and Transbaikalia. Numbers in the rectangles are sites with tracks of dinosaurs, numbers in ovals are localities with dinosaurian eggshell, triangles in the places of discoveries are remains redeposited into Paleogene-Neogene strata, other numbers refer to locations of discoveries of non-redeposited bones and teeth of dinosaurs.

[79/80]

localities. It is difficult to name fossil localities in a narrow, long, and canyon-like valley with sloping layers open to erosion on the sides and ranging in age from the Jurassic to the Paleogene and where the settlement along the river and the river have the same name. In all such instances, it is difficult to avoid subjectivity and provide a uniform approach to the creation of names for new localities.

Marked with an asterisk (*) below are localities and levels personally investigated by the author. Discoveries made by the author's assistants or by the author himself and identified by the author are marked with two asterisks (**), whereas discoveries by other researchers and identified by the author are marked with a single asterisk (*).

The numbers of localities with dinosaurian remains correspond in the text to the numbers on attached schematic maps (Figs. 8-11).

4.1. Bones and teeth of dinosaurs in Mesozoic deposits

Discoveries of Triassic dinosaurian remains are still unknown on the territory under consideration; previous records have not been confirmed (Yuryev 1954a: fig. 1; Zaichenko, 1983) (see also Parts 4.1.1.1 and 4.5.1.197).

4.1.1. Jurassic

1. Kadzhisai*, Southern Issyk-Kul area, Kirghizia, middle part of the Koktui Formation (the latter was earlier included in the Upper Triassic and now in the Lower Jurassic) and also the base of the Aktash Formation and exposure of the later Lower Jurassic. Based on data by E. L. Zaichenko (1983), dinosaurian bones presumably occur in this area. After two field surveys by P. V. Fedorov (oral communication) it appeared that the remains were parts of tree trunks, partially silicified and partially penetrated by calcite crystals. In strata of the Lower Jurassic at the same site, in the Dzhil Formation, P. V. Fedorov discovered a fragment of a large bone, which, judging by the microstructure, most probably comes from a dinosaur*.

2. Sarybulak*, stream near the town of Kokyangak, Kirghizia. Red sandstone at the base of the Balabansai Formation. Middle Jurassic, upper Bathonian. Bone cf. Ornithopoda* (Nessov and Fedorov, 1989).

3. Nichke*, stream of the lower Kyzylsu River in the basin of the Kyokart River, Kirghizia. Grey clays at the base of the Balabansai Formation. Middle Jurassic, upper Bathonian. Tooth of a small theropod "Coelurosauria"**.

4. Sarykamyshsai I*, right bank of the stream near city of Tashkumyr, Kirghizia. Channel between basins; the channel partially filled with turbidites and landslide sediments, gray clays, clays of the Balabansai Formation, 43 m from its base (site FTA-30). Upper part of the Middle Jurassic, Callovian. Short, thick tooth of Sauropoda (cf. Camarasauridae)**, teeth and bones of theropods -- small cf. Coeluridae** and average-sized Megalosauridae** (Nessov, 1988a) or Ceratosauria**. Teeth of theropods (Verzilin et al., 1970).

In the same locality* on the eastern slope of the noted dry valley and 66 m from the base of the formation. Sandstone with gravel (site FTA-1l). Upper

[80/81]

[FIGURE 9 HERE]

Fig. 9. Localities of skeletal remains, eggshell, and tracks of dinosaurs in the Middle Asian Region outside the Fergana Depression. (Symbols as in Fig. 8.)

[81/82]

part of the Middle Jurassic, Callovian. A relatively large tooth of Megalosauridae** or Ceratosauria**, large bones of theropods with strong pneumatization. A short tooth of a sauropod of the same type as in Camarasauridae** or Cetiosauridae** (dominance of sauropods with thick relatively short teeth at the end of the Middle Jurassic and beginning of the Late Jurassic is noted also for China [Dong, 1992]).

In the same locality*, but in the valley situated further east 2 m up the section, in red sandstones. Upper part of the Middle Jurassic, Callovian. Proximal and distal parts of a femur of Sauropoda* (now in the museum of the Institute of Mines), fragments of dinosaurian vertebrae.

5. Kamyshbashi, locality in the southern part of the Fergana Depression, Uzbekistan. Balabansai Formation (lower part?). Upper part of the Middle Jurassic, Callovian (Kaznyshkin, 1988). Sauropoda (Stratigraphic Dictionary, 1979: 480), based on the type of teeth most probably belonging to Camarasauridae*, but not to Diplodocidae (Kaznyshkin, 1988: pl. X, 22). Caudal vertebrae and fragments of a scapula of sauropods, a tooth of a theropod (Burakova et al., 1980). M. N. Kaznyshkin (1988) noted the erroneous reference by N. N. Verzilin et al. (1972) to the discovery of sauropod bones in the Shurab Formation (Middle Jurassic, Callovian) in the northern area of Shurab, Tadzhikistan.

6. Changet I* (left side of the river valley) in the village of Changet, Kirghizia. Red clays of the Balabansai Formation. Upper part of the Middle Jurassic, Callovian. Long caudal vertebra of a small theropod ("Coelurosauria"?)*, long tooth of (?)Sauropoda*. Higher (3 m) in section, part of the sacral vertebra of a small theropod (Nessov and Fedorov, 1989).

7. Uurusai*, right side of the lower dry river bed near Tashkumyr, Kirghizia. Red clays of the Balabansai Formation, 32 m below conglomerates of the Lower Cretaceous (site FBH-6). Upper part of the Middle Jurassic, Callovian. Incomplete girdle bone (coracoid?) of a dinosaur*. Area near the mountain pass between the upper Uurusai and upper Kichiachisai*, i.e. further west of the locality in Uurusai (site FBH-7). Further west and 3 m up the section (site FBH-7a). Upper part of the Middle Jurassic, Callovian. Teeth of Megalosauridae** or Ceratosauria**, large metapodial of a dinosaur".

8. Balabansai I* (right side), 5 km north-north-west of Tashkumyr, Kirghizia. Middle upper part of the Balabansai Formation. Upper part of the Middle Jurassic, Callovian. Pelvic bones, sacrum, part of femur, several trunk, sacral, and caudal vertebrae of Sauropoda. Discovery by N. N. Verzilin, 1967.

9. In the same area*, but on the left side, not in Eastern Fergana (Rozhdestvensky, 1972), but in the northern part of the depression, upper part of the same formation, very close to its uppermost part (approximately 6 m; Rozhdestvensky, 1969: photo on p. 255). Middle - ?Upper Jurassic, Callovian - ?Oxfordian. A large representative of sauropods (skull and a large part of tail not preserved), attributed to Cetiosauridae (Rozhdestvensky, 1968b). This is a discovery by N. N. Verzilin of 1966. The reidentification of this skeleton as *Apatosaurus* (Diplodocidae) (Rozhdestvensky, 1977: 108) is doubtful.

9. Dzhiddasai I*, upper part of a dry river bed, 6-7 km north-north-west of Tashkumyr, Kirghizia. Upper part of the Balabansai Formation (interval 6-9 m from its top). Site FBH-23. Middle -?Upper Jurassic, Callovian - ?Oxfordian. Teeth of small theropods**.

10. Khodzha-Karshavar, upper Tashmush River, southern slope of the Hissar mountain range, Surkhandarya Region, Tadzhikistan. Limestones of the Tupolang Formation, Upper Jurassic. Tooth of dinosaur (Novoselskii and Novoselskaya, 1993), now probably lost.

[82/83]

11. Teete, left side of the stream 2-5 km from the mouth, a right tributary of the Bootomoiu River (south-west of the village of Nyurba), basin of the Vilyui River. Sakha Republic (Yakutia). Remains of the dinosaurs are being studied by S. M. Kurzanov who visited this area in 1988. According to an oral communication from A. I. Guryev (Yakutsk), these remains, in the form of isolated teeth of dark color and few small fragments of bone, occur relatively low above the low water level at the boundary between loose sands and a more dense sand lens. The remains belong to the dinosaurs of Jurassic appearance (S. M. Kurzanov, oral communication).

In 1993-1994, the author visited the region in which the locality is situated. The results of study of the Upper Jurassic, Lower Cretaceous, and Upper Cretaceous rocks along the Vilyui River from the settlement of Nyurba to the city of Vilyuisk and near the settlement of Promyshlennyi, and also in the lower parts of the rivers Tyung, Lepiske (Lyampushka), and Linde, and along the Lena River (near the Sangar settlement and near the Chirimyi-Khaya mountains), show that at the end of the

Jurassic and throughout the Cretaceous the preservation of phosphatic remains of vertebrates here was unlikely because of high acidity of the environment for sediment accumulation, sometimes in combination with the absence of buffering of waters by phosphate ions. The environment that favored conservation of vertebrate remains in the course of sediment accumulation and diagenesis most probably

[FIGURE 10 HERE]

Fig. 10. Localities of dinosaurian remains and eggshell in the Fergana Depression. (Designations as in Fig. 8.)

existed in the region during Baiocian (Baiocian-Bathonian) ingression of marine and brackish waters, under conditions of estuary upwellings near river mouths. In the west of the Vilyui syneclise, differentiation of geological formations belonging to the Upper Jurassic and Lower Cretaceous in small sites is difficult. Therefore, it is possible that dinosaurian remains in the region of Kempendyai (Part 4.1.2.16) in fact do not belong to the Cretaceous ankylosaurs but rather to the Jurassic stegosaurs.

[83/84]

I. P. Tolmachev determined presence of dorsal spine of *Stegosaurus* sp. in collections of the zoologist O. Herz (Tolmachow, 1904). The weathered bone was found on the bank of the Vilyui River (80 km up the Akhtaranda River). It supposedly comes from coal-bearing deposits of the Jurassic (such rocks in this region may belong also to the Lower Cretaceous). The cited identification was later declared erroneous by its author (Tolmachoff, 1924; Tolmachoff, 1926). If we take into account the later discovery of the Upper Jurassic and/or Lower Cretaceous deposits with remains of dinosaurs (armatosaurs including the stegosaurs and the ankylosaurs in the basin of the Vilyui River (stream Teete and/or region near Kempendyai settlement) (Rozhdestvensky, 1973; see also Part 4.1.2.16) it is thus probable that the aforementioned bone found by O. Herz could have belonged to a dinosaur. It should be noted at the same time that fragmentary remains of mammoths, woolly rhinoceroses, primitive bison, and horses are frequently found in this region. They fall out and are washed out of Quaternary deposits in the upper parts of ravines and occur on paths along the valley slope; subsequently, after being frozen into the bank during the winter, they may be subject to repeated strong erosion in the spring by moving ice forming "ice polyhedrons" pebble. The elucidation of this issue will require study of the bone found by O. Herz, which, it is to be hoped, could have been preserved in a museum.

12. Lenger, vicinity of Tashkent, Uzbekistan. Upper Jurassic. Large bones (dinosaurs?). (B. V. Prizemlin, oral communication). This information requires corroboration.

13. Taseeva (left bank of the river with the same name in the lower part of the Angara River), Siberia, Russia. Kanarai Formation. Upper Jurassic - Lower Cretaceous. Dinosaur (phalanx of a theropod?) (Ilyukhiuna and Fuks, 1961; Stratigraphic Dictionary, 1979). The locality is situated approximately 430 km north-east of the locality with remains of the Early Cretaceous (probably Aptian) psittacosaur (see part 4.1.2.24).

On the locality indicated for the Jurassic of the Volyno-Podolia (Zborzewskj, 1834) see Part 2.5.204.

On discoveries that were treated as bone and scales of Jurassic dinosaurs at the locality Aulie, Kazakhstan, see Part 4.5.198.

4.1.2. Lower Cretaceous

14. Koi-Kara, elevation in the lower basin of the Emba River, Kazakhstan. Sands of the lower half of the Lower Cretaceous. Two vertebrae of *Embasaurus minax* Riab. (Riabinin, 1931b, 1949), Megalosauridae(?). They were reidentified as belonging to primitive Theropoda indet., but not to carnosaurs, because the vertebral centra are platycoelous (Weishampel et al., 1990a: 311).

P. S. Lyubimova (1967) noted bones of vertebrates in the middle current of the Emba River (Barremian). B. P. V'yushkov shared with L. I. Khozatsky (oral communication) unpublished data on bones of large vertebrates (apparently dinosaurs from the Lower Cretaceous, Hauterivian-Barremian, of the middle current of the Emba River near Karalikol Moolo).

15. Changet II*, left [edge] of the valley, Fergana Depression, Kirghizia. Sandstones of the upper part of the Khodzhiabad Formation, 22 m below the top of the layer of eolian origin. The lower half of the Lower Cretaceous? or more probably upper Barremian - middle Aptian. Accumulation of bones and teeth **[84/85]** presumably forming a pellet left by a small theropod*. It included in particular ossified ligaments of young ornithopods*, a fragment of a rib of a dinosaur*, bones from the foot of a turtle, etc. (Fedorov and Nessov, 1990).

At the same locality, Tyulek Formation (lower Changet subformation, which approximately corresponds to the middle and upper parts of the Khodzhiabad Formation). Lower Cretaceous, upper Barremian - middle Aptian. Vertebra of a dinosaur (Stratigraphic Dictionary, 1979).

16. Kempendyai, basin of one of the rivers among Bootomoiu, Tonguo, and Namano in the Vilyui system, Saha Republic (Yakutia, Russia). Sangar series, second of four beds from below (Korchagin, 1972), which belongs, based on remains of pelecypods, to the Lower Cretaceous, Valanginian, bluish-gray sands. The discoveries were reported as found in chalks (Rozhdestvensky, 1973). The age was given as Berriasian - Valanginian (Weishampel et al, 1990a); however, it may appear to be younger, as young as late Aptian, or even older - Late Jurassic. Humerus, ribs, and vertebrae of Ankylosauria (Korchagin, 1972; Rozhdestvensky, 1973). It remains unclear whether stegosaurs or ankylosaurs were present in the region of Kempendyai (see also Part 4.1.1.11) or whether both groups were present, and whether there is only one level or two levels with dinosaurian remains in the region (one Jurassic, the other Early Cretaceous).

[FIGURE 11 HERE]

Fig. 11. Localities of dinosaurian remains in Transbaikalia. (Symbols as in Fig. 8.)

In 1993, the author investigated deposits of the Sangarian series in the region of the Verkhoyansk depression (right bank of the Lena River) - Batylykh, Eksenyakh, Khatyryk formations (Lower Cretaceous) and rocks of the Vilyui series (left bank of the Lena River) - Agrafen, Chirimyi, and Linden formations (Upper Cretaceous). No remains of Mesozoic vertebrates were found. However, **[85/86]** the middle part of the Batylykh Formation and the Agrafen Formation were identified as most promising for the discovery of vertebrates. Special attention should be paid to analogues of these formations situated further north in those areas where the former presence of brackish waters was noted.

17. Mogoito* (series of ravines in the locality) (Dmitiriyev and Rozhdestvensky, 1968; Nessov and Starkov, 1992), southwest of Gusinoye Lake, Buryatia, Russia. Sandstones of the Murtoi Formation. Lower Cretaceous, upper Barremian - middle Aptian. Very small theropod (phalanx found by G. A. Dmitriyev), relatively small Ornithomimidae* or Oviraptorosauria? (discovery of femur by A. I. Starkov), large, strongly curved ungual phalanx of a theropod (Dmitriyev, 1960; Rozhdestvensky, 1970: fig. 2; Rozhdestvensky, 1976); one should not exclude, however, that this phalanx may be from a segnosaur (*Chilantaisaurus*? sp.) or spinosaurid. The phalanx does not belong to *Therizinosaurus* sp. (Rozhdestvensky, 1971: 23; Weishampel et al., 1990a) or therizinosaurids (Rozhdestvensky, 1976: fig. 2a); a second, similar discovery was made by A. I. Starkov (oral communication). Sauropoda with short, thick teeth and procoelous, robust caudal vertebrae are also represented here (cf. *Chiayusaurus* sp.*) (Pl. III, fig. 13; Pl. IV, fig. 1). Osteoderms from the locality attributed to armatosaurs** (Nessov and Starkov, 1992) may belong to the sauropods, some of which have dermal ossifications along the back and dorsal surface of the tail (Norman, 1985; Sanz and Buscalioni, 1987). A part of a phalanx or metapodial figured and referred to a theropod (Riabinin, 1937a), judging from the relief of the articular surface, may also belong to a sauropod. Deep depressions on the sides of the distal part of this bone show that it does not belong to a segnosaur. The identification of one of the bones (distal part of a tibia) as an ornithopod (Dmitriev, 1960, 1962) was not confirmed by subsequent investigation.

18. Atsai*, 1 km southeast of the settlement and springs, west of the Gusinoozerskaya Depression, Buryatia, Russia. Murtoi Formation, loose sandstones in hollows for poles of power lines. Lower Cretaceous, upper Barremian - middle Aptian. Bones of sauropods** (Nessov and Starkov, 1992).

19. Northwest of the Gusinoozerskaya Depression, east of Burul* Mountain, Buryatia, Russia. Murtoi Formation?, Lower Cretaceous. Bones of dinosaurs (Dmitriyev and Rozhdestvensky, 1962).

Discovery of one bone of *Allosaurus sibiricus* Riab. (Ivanov, 1940) was indicated at the base of sand layer (500 m) in the region of the Gusinoye Lake (probably Murtoi Formation). The identification was probably made by A. N. Riabinin.

20. Krasnyi Yar*, ravine and locality on the right bank of the Khilok River; 1-2 km lower than the place of inflow of a number of channels of the Shibertui River into it. Sandstones of Murtoi Formation. Lower Cretaceous, upper Barremian - middle Aptian. Dense accumulation (35 x 15 cm) of eight to ten fragments of bones of sauropods** (mostly ribs) with coarse damage presumably by teeth of carnivorous dinosaurs**. This accumulation is interpreted as pellet (undigested remains of food bolus, consisting originally of flesh and bones subjected to gastric juice in the stomach and ejected through the gullet [Nessov and Starikov, 1992]).

21. Tarbagatai, old mines in the region of the Tarbagatai railway station, valley of the Khilkok River, Chita Region, Russia (should not be confused with the Tarbagatai Station in Buryatia). Apparently this locality was erroneously cited as Udinsk (Charig, 1973). Top of the second [carbon layer] (Tolmachev, 1926) called "Tigin" layer (Ivanov, 1940). Based **[86/87]** on more recent data, the discovery was made in the Zugmar Formation (Stratigraphic Dictionary 1979), in the Tignin Formation (ibid. 1979) or in the Turgin Formation (A. K. Rozhdestvensky, oral communication). Metatarsal of a theropod *Allosaurus*(?) *sibiricus* Riab. (Riabinin, 1914) or *Antrodemus sibiricus* (Riab.) (Rozhdestvensky, 1977) or ?*Chilantaisaurus sibiricus* (Riab.) (Weishampel et al., 1990a). Similarity (Weishampel et al., 1990a: 200) to loosely articulated metatarsals attributed to the type

species of the genus *Chilantaisaurus* (Hu, 1964) from the Aptian-Albian of China and belonging, in our opinion, to Segnosauria, suggests that the bone may belong to *Chilantaisaurus*.

22. Arbagar anticline (Arbagar-Kholdon coal-field), eastern Transbaikalia, Russia. Lower Cretaceous. Sand-gravel layer below the lower coal-bearing horizon (thickness of the latter - 50 m). Distal part of the metapodial of a small carnivorous reptile (preliminary identification by A. N. Riabinin) (Ivanov, 1940). Apparently this discovery as a presumably dinosaurian bone was noted later (Dmitriyev, 1962).

23. Mouth of Zaza River, Zaza-Vitim Depression, Transbaikalia. Sands and sandstones. Lower Cretaceous (?). Bones of dinosaurs (Sarkisyan, 1958: 220). Probably the same locality with bones of dinosaurs of the Lower Cretaceous was cited as Zazin Hollow, Transbaikalia (Dmitriyev, 1962).

24. Shestakovo (=Shestakovsky Yar), River Kiya in the basin of the Chulym River, Kemerovo Region, Russia, but not Gorno-Altai Autonomous Region as claimed by Weishampel et al. (1990a: 104). Red clays at the base of the Shestakovo (=Ilek) Formation (Lebedev, 1958; Rozhdestvensky and Khozatsky, 1967). Lower Cretaceous, upper Barremian - Aptian, most probably upper Aptian; earlier date was Neocomian (Rozhdestvensky, 1955a,b, 1973), Hauterivian - Barremian (Golbert et al., 1968), or Aptian-Albian (Rozhdestvensky, 1973). Skull and separate postcranial skeleton of *Psittacosaurus* sp. (Rozhdestvensky, 1971) or *Psittacosaurus mongoliensis* (Rozhdestvensky, 1955a,b, 1960, 1973, 1977). For all known species of this genus, an Aptian - Albian age is often accepted (Weishampel et al., 1990a), but at least for several species it may be restricted to Aptian or early - middle Albian.

25. Teleumbet, one of the easternmost elevations of the left bank of the Middle Emba River, Kazakhstan. Sandstone (Lower Cretaceous, Aptian) with oysters occurring at the base. Dinosaurian bones (Vakhrameyev, 1952: 31).

26. Shubar-Zhilan, area situated between rivers Emba, Sagiz, and Uil, Western Kazakhstan. Small pebble conglomerates, gravel, and sandstone. Lower Cretaceous, Aptian. Weathered bones of vertebrates (Vakhrameyev, 1952), possibly from dinosaurs.

27. Area situated between rivers Karaungur and Karakuldzha, Eastern Fergana. Lower part of the Khodzhaosmanian Formation. Lower Cretaceous, Aptian. Dinosaurian vertebra (discovery by A. E. Dovzhikov) (Simakov et al., 1957: 55).

In the region of the village of Kampyr-Ravat (see also Part 4.1.3.60), a fragment of dinosaurian bone is known in the same formation on the Karadarya River (Simakov et al., 1957: 52).

28. Karakul* (north-north-eastern shore of the lake), Karakalpakistan. Sultanbobin Formation. Lower Cretaceous, upper Aptian (Clanseyan). Thin, long tooth of Sauropoda (the only one found among several thousands of bones and teeth not belonging to dinosaurs).

29. Khodzhakul I* (ravines north of the basin of the former lake [Plate XIVb] situated not farther north than Sultan- **[87/88]** Uvais (=Sultan-Uiz-Dag) mountain range (Yuryev, 1954; Rozhdestvensky and Khozatsky, 1967), but north of the sublongitudinal range of Sheikh-Dzheili, west-north-west of the Sultan Uvais range proper, Karakalpakistan. Lower part of the Khodzhakul Formation. Lower Cretaceous, lower middle Albian. Strongly curved, large, and considerably laterally flattened ungual phalanx of a relatively large segnosaur, Segnosauria indet.* (discovered by Sh. Zhuraev in 1978).

At the same locality*, lower or middle part of the Khodzhakul Formation (however, stratigraphically higher than the previous discovery), sites SH-20 and SH-21. Lower Cretaceous, upper Albian [Vraconian] (Nessov, 1977, 1988a). Occurrence of dinosaurian remains in locality CX-20 is 0.38% in the sample of 9,092 bones and teeth of vertebrates (data of L. B. Golovneva, L. A. Nalbandyan, and the author). Small theropods cf. Coeluridae**, relatively small carnosaur with relatively strongly flattened teeth "*Laelaps*" sp. cf. "*L.*" *explanatus* Cope (Lambe, 1902: pl. MX, figs. 11-12; Osborn 1924b: fig. 7). Possibly this is a peculiar species of *Alectrosaurus*. The locality yields long, slender teeth of Sauropoda** (Diplodocidae or Titanosauridae), small plates of pelvic armor, polygonal and irregular in shape, and teeth of Shamosauridae**. From this locality, vertebrae of hadrosaurids are also known; two specimens were found by A. D. Arkhangelsky (1931), and they were mentioned and described by A. N. Riabinin (1921, 1931a). Also found at locality CX-20 were teeth of primitive small hadrosaurids, *Gilmoreosaurus* (?) *atavus* sp. n.** (Pl. IX, fig. 1) and teeth strongly flattened along the sides, cf. Hypsilophodontidae** (Nessov, 1985a), similar with those noted for the upper Turonian - Coniacian of the Kyzylkum (Pl. X, figs. 20-23); however, it is possible that these teeth belong to young hadrosaurids. The archaic protoceratopsid *Kulceratops kulensis* g. n., sp. n.** (Pl. IV, fig. 12) was cited from the discovery of the upper jaw (Nessov, 1988a). A portion of a large jaw was found in the area of ravines facing south, near the northern slope of the highway from the plateau, 20-25 m below the edge of the chink and apparently at the Albian level. The edge of the jaw (opposite to the alveolar one, probably in the area of the posterior antorbital opening) has vertically oriented inflations, which apparently contain the deepest parts of teeth roots. The alveoli are moderately compressed on the sides. Inflations analogous to those noted are present in the lower part of the dentary in *Ceratosaurus* (Gilmore, 1920 - see photo, not the drawing). Based on the identification by A. K. Rozhdestvensky, to whom the bone was given, it belonged to a previously unknown theropod. Data on the discovery have not been published.

30. Chanak, vicinity of railway station of Tashkent Chul', Southern Kazakhstan. Gray limestone of the upper part of the Lower Chanak subformation. Lower Cretaceous, Albian (Belenky and Mirkamalova, 1965). Fragments of petrified bones (Mirkamalov [1941] - cited by Belenky [1961]), possibly dinosaurian remains.

31. Sheikhdzheili I*, northern foot of the Sheikhdzheili range, Karakalpakistan. Middle part of the Khodzhakul Formation. Lower Cretaceous, upper Albian (?). Bones of dinosaurs**.

32. Remains of dinosaurs and tetrapods that cannot be identified were reported by N. N. Verzilin (1975: fig. 5) from the Alamyshik Formation (Lower Cretaceous, Albian) in the area between the cities of Osh and Iski-Naukat (=Eski-Nookat) in the southeast of the Fergana Depression, Kirghizia.

33. Remains of vertebrates, most probably of dinosaurs, from an unnamed locality of Southern Fergana, Kirghizia (Verzilin, 1975: fig. 3 II), were reported for the Alamyshik Formation (Lower Cretaceous, Albian).

[88/89]

34. Abshir, river in the Alai range, south of Fergana Depression, Kirghizia. Red sandstones and clays of the Tokubai Formation (Lower - Upper Cretaceous, Albian - Cenomanian). Bones of dinosaurs (Martinson, 1989: 82).

Possibly the same area was cited as an unnamed locality in southeastern or eastern Fergana, Tokubai Formation (lower part) (Martinson, 1969: 19). Lower - Upper Cretaceous, upper Albian - Cenomanian. Dinosaurian bones (Sochava, 1968: 64, 85).

35. There are unconfirmed reports of discoveries of some dinosaurian remains in Mangyshlak (Riabinin, 1931b; Yuryev, 1954a).

A reference to Ornithopoda in the Lower Cretaceous (lower Hauterivian) of Georgia (Weishampel et al., 1990a) probably refers to tracks of ornithopods in the upper of the two horizons at the Sataplia locality (see Part 4.4.2.193).

4.1.3. Upper Cretaceous

36. Kurshab, area near river mouth, Fergana Depression, Kirghizia. Red sandstones of the Kurshab Formation (Sharikhan and Karaalmin formations). Lower Cretaceous, upper Albian -- lower Turonian, Hadrosauridae ("*Trachodon*") (Stratigraphic Dictionary, 1979).

37. Itemir I*, Central Kyzylkum, Uzbekistan. Itemir wells are situated not north-east (Izmailov and Dominik, 1938), but west-north-west of the Bissekty well. Kulbikin bed*. Lower? - Upper Cretaceous, upper Albian? Cenomanian. Bones of dinosaurs**, including "two vertebrae of complex articulation" (Izmailov and Dominik, 1938: 89).

Itemir well*. Upper Cretaceous, Cenomanian. Bones of dinosaurs** (Martinson, 1968: 93).

Borteskent well*. Upper Cretaceous, Cenomanian. Vertebrae of Ornithischia (Martinson, 1968). Apparently the same discoveries were cited as the bones of an ornithischian dinosaur (Martinson, 1969: 26).

Argabai well*. Upper Cretaceous, Cenomanian. Bones of dinosaurs**.

Dzharakuduk well*. Upper Cretaceous, Cenomanian. Moderately large theropods with teeth strongly compressed on the sides; these are possibly referable to *Alectrosaurus* sp. ** For the area from Borteskent to the Dzharakuduk well, dinosaurian bones were reported earlier (Sochava, 1968: 65).

38. "Krasnaya Gora" [Red Mountain], Central Kyzylkum, Uzbekistan. Upper Cretaceous, base of the Cenomanian (material of I. M. Abduazimova, collected in 1989). Sauropods* (metapodial and fragment of distal articular end of femur and shoulder bone).

39. Sheikhdzheili II*, Southwestern Kyzylkum, Karakalpakistan. Upper part of the Khodzhakul Formation (site SSHD - 8 and S SH D - 8a). Upper Cretaceous, lower Cenomanian (Nessov, 1988a). Contents of dinosaur remains - 0.48-0.69% in samples including 12,214, 3,522 and 2,590 bones and teeth (data of L. B. Golovneva and the author). Teeth of Deinonychosauria (identification by A. K. Rozhdestvensky from collections made by the author). Small *Troodon asiamaricanus* sp. n.** among troodontids (Nessov, 1985b: pl. III, fig. 1) (Pl. I, fig. 23), earlier attributed by the author to the genus *Pectinodon* (Nessov, 1985a; Nessov, et al., 1987) before a revision of the latter. Teeth of relatively small carnosaurs "*Laelaps*" sp. cf. "*L.*" *explanatus* Cope and *Alectrosaurus* sp. **, teeth considerably flattened along the sides as in Torvosauridae. Ungual **[89/90]** phalanx of a segnosaur Segnosauria indet. ** (Pl. II, fig. 6), most probably belonging to a different smaller species than the one noted for the lower -- middle Albian in Part 4.1.2.29. A small sauropod with long, slender teeth (Diplodocidae or Titanosauridae)** (Pl. III, fig. 10), teeth and osteoderms of the pelvic armor of ankylosaurids Shamosauridae**. Supraoccipital of typical shape, vertebrae (Nessov, 1977, 1981), teeth, phalanges of digits of a very small hadrosaurid cf. *Gilmoreosaurus* sp. **. Dominant in the dinosaurian assemblage of protoceratopsids is *Asiaceratops salsopaludalis* Ness. et L. Kazn.** (Nessov, et al., 1989), earlier erroneously attributed to Psittacosauridae (Nessov, 1981; Chure and McIntosh, 1989) (Pl. IV, figs. 13-17; Pl. V, figs. 1, 3, 6-7, 10-13, 15-19; Pl. VI, figs. 1, 7, 27-28, 32, 36).

40. Khodzhakulsai*, Southwestern Kyzylkum, Karakalpakistan. Upper part of the Khodzhakul Formation. Upper Cretaceous, lower Cenomanian. A relatively large theropod *Laelaps* sp. cf. "*L.*"

explanatus Cope or *Alectrosaurus* sp.** with considerably flattened teeth as in torvosaurids. Teeth of ?Deinonychosauria** (Nessov, 1977), a sauropod with slender, long teeth**. A protoceratopsid *Asiaceratops salsopaludalis* Ness. et L. Kazn. ** (Pl. V, figs. 2, 4-5, 8, 14). Teeth and vertebrae of hadrosaurids are indicated as "Gadrosaurus sp." by S. S. Shults (1972: fig. 31). A vertebra from a conglomerate of the vicinity of Khodzhakul found by A. D. Arkhangelsky (1931) (Riabinin, 1931a: fig. 5) possibly comes from this place, but most probably from the upper Albian at locality 4.1.2.29.

41. Chelpyk (=Cholpuk)*, residual mountain (Plate XIVa) north of the west extremity of the Sultan Uvais range, Karakalpakistan. Upper part of the Khodzhakul Formation (site SCH - 1. Upper Cretaceous, Cenomanian. Theropods "*Laelaps* sp. cf. "*L.*"*explanatus* Cope or *Alectrosaurus* sp. ** with teeth considerably flattened laterally, sauropods with slender and long teeth** (Pl. III, fig. 11), ankylosaurids** (Nessov, 1985b: pl. I, fig. 9) (Pl. IV, fig. 10), and also *Asiaceratops* sp. ** among protoceratopsids (Pl. VI, fig. 24), hadrosaurids** (Nessov, 1977).

42. Karatepa* (small elevation near the Chelpyk mountains), Karakalpakistan. Upper part of the Khodzhakul Formation. Upper Cretaceous, Cenomanian. Hadrosauridae**, bones of dinosaurs**.

43. Chain of small elevations north-east of the outskirts of the settlement Kipchak*, Karakalpakistan. Khodzhakul Formation. Lower?-Upper Cretaceous, Albian? - Cenomanian. Bones of dinosaurs**. Similar remains were found by U. Yunusov (oral communication) near the road from Nukus to Turtkul.

44. Chumyshkul*, ravine on the northeastern edge of the lake, near Chelpyk Mountains, Karakalpakistan. Khodzhakul Formation. Lower - Upper Cretaceous, Albian-Cenomanian. Bones of dinosaurs**.

45. Karachadalysai*. Ravine on the eastern edge of the Sultan-Uvais Range, Karakalpakistan. Upper(?) part of the Khodzhakul Formation. Upper Cretaceous, Cenomanian. Hadrosaurids (cited as "*Gadrosaurus* sp." by Shultz [1972: fig. 31]).

46. Kyrkkyz*, hills with fortress on the top, east of Sultan-Uvais Range, Karakalpakistan. Upper part of the Khodzhakul Formation. Upper Cretaceous, Cenomanian. Bones of medium-sized theropods**, hadrosaurids** (Nessov, 1980).

47. Kulkala*, hills between the eastern extremity of the Sultan-Uvais Range and the Ayazkala elevation, Karakalpakistan. Upper part of the Khodzhakul Formation. Upper Cretaceous, Cenomanian. Hadrosaurids** (Nessov, 1980).

[90/91]

48. Aravan I, river bank south of the Fergana Depression, Kirghizia(?). Red-colored, friable clays, sandstone, gravels, and conglomerates. Upper Cretaceous, Cenomanian. Dinosaurian bones (Martinson, 1989: 79).

49. Kylodzhun (=Klaudzin)*, in the vicinity of the settlement, left bank of the Sarykungoi stream, Southeastern Fergana, Kirghizia. Lower part of the Sharikhan Formation. Upper Cretaceous, Cenomanian. Bones of hadrosaurids (Verzilin et al., 1970; Verzilin and Nessov, 1978).

50. Gulcha, south of the Fergana Depression, Kirghizia. lower part of the Sharikhan Formation. Upper Cretaceous, Cenomanian. Large bone fragment of Sauropoda? (Rozhdestvensky, 1973; Rozhdestvensky and Khozatsky, 1967), dinosaurian bones, vertebrae (Verzilin, 1967; Martinson, 1968: 64).

51. Sufikurgan* (vicinity of the village), left bank of the Gulcha River, Kirghizia. Sharikahn Formation. Upper Cretaceous, Cenomanian. Large femur of a carnosaur*, discovery by P. V. Fedorov. Bones of dinosaurs**.

52. Changet III*, Northeastern Fergana, Kirghizia. Sharikhan Formation. Upper Cretaceous, Cenomanian. Large theropod*, hadrosaurid* (collections by P. V. Fedorov).

53. Kara-Alma*, Northeastern Fergana, Kirghizia. Upper Changet series (presently Sharikhan Formation). Upper Cretaceous, Cenomanian. Weathered bones of hadrosaurids, discoveries by A. M. Obut (Simakov et al., 1957: 54, 55, 93). For the same part of the Changet series, bone fragments

of dinosaurs have also been reported from the Kochkor-Ata Range, apparently on the left bank of the Kurshab River in Eastern Fergana.

54. There are 10 localities, without specifying the names, containing bones of dinosaurs (mostly hadrosaurids) in the Sharikhan Formation (Upper Cretaceous, Cenomanian) in the Northeastern and Southeastern Fergana (Verzilin, 1976: fig. 1); two of these (54a, 54b) are localities situated near the settlement Lyagan* and on the Karakuldzha River (Verzilin and Nessov, 1978: 57). Two unnamed localities with dinosaurian remains were plotted on the map by N. N. Verzilin (1975: fig. 3, III) in the Karaalmin Formation (Upper Cretaceous, middle-upper Cenomanian) Northeastern and Southwestern Fergana, Kirghizia, and Tadzhikistan.

55. Karakuldzha, approximately 15 km up the river from the village of Karakuldzha, Fergana Depression, Kirghizia. Karaalmin Formation. Upper Cretaceous, Cenomanian. Bone (dinosaurian), 1 m in length (Verzilin, 1967). In red-colored deposits in a river cliff (Upper Cretaceous, Cenomanian?), part of the tibia of a large hadrosaurid was found (Martinson, 1968: 59).

56. Suzak, eastern part of the Fergana Depression, Kirghizia. Level below the layers with oysters (Rozhdestvensky and Khozatsky, 1967). Upper Cretaceous, Cenomanian. Part of sauropod skeleton (pelvis, sacrum, femur) (Rozhdestvensky and Khozatsky, 1967; Rozhdestvensky, 1973).

57. Tuskar* (=Tuskari), right bank of the river near the Meshkovo settlement, Kursk Region, Russia. Phosphate-bearing sands and sandstone of the Sekmenevsk Formation. Lower-Upper Cretaceous, Albian - Cenomanian rather than Cenomanian - Santonian (Weishampel et al., 1990a). Among the series of remains, there are bones of Neogene - Quaternary ungulate mammals (e.g., Kiprijanow, 1883: pl. VI, fig. 6) and bones of presumably Albian - Cenomanian age. One of the bones was interpreted as a humerus (Kiprijanow, 1883: pl. V, fig. 4) and was referred to a new species, *Poekilopleuron schmidti* Kipr. Later (Rozhdestvensky, 1973) it was reidentified as the tibia of theropod *Megalosaurus* sp. Recently, the discovery was cited as Theropoda indet. (Weishampel et al., 1990a). There is some doubt, however, **[91/92]** about attributing this bone to a theropod, because it has (Kiprijanow, 1883: pl. IV, fig. 4B) a slitlike pit, which is not typical of

theropods, separating the region of contact with other bones from the side of the diaphysis. Fragments of ribs (ibid.: pl. IV, figs. 1-3) do not provide significant evidence for their dinosaurian identity and probably belonged to marine reptiles.

This appears to be the second (in terms of date of publication) record of a discovery of dinosaur remains (other than their tracks; see Romanovsky [1882]) on the territory of the CIS. The name *Poekilopleuron* is sometimes used as a junior synonym of *Megalosaurus* (Rozhdestvensky and Tatarinov, 1964).

Marsh (1897), who had visited museums of St. Petersburg and Moscow and had spoken with various paleontologists, did not find and did not learn anything that would point to discoveries of dinosaurs in what was then Russia. Perhaps sincerely trying to encourage Russians to search for dinosaurian remains and presenting them for museum exhibitions he wrote: "... the dinosaurs of Russia, like snakes in Ireland, are only known by being absent" (cited [in Russian] by Riabinin 1915: 134). However, prior to his visit, a figure and descriptions of dinosaurian tracks had already been published. Initially, they were attributed to the Upper Triassic (now they are dated as Middle Jurassic); they are now called *Gabirutosaurichnus tianschanicum* (Rom.) (Romanovsky, 1882,1884, 1890) (see Part 4.4.1.184). An article with a description of the aforementioned remains from the Tuskar River (Kiprijanow, 1883) was published well before the visit of Marsh. The description and illustration of the fossil *Macrodontophion* from Ukraine, regarded as a tooth and attributed by the author of the original description to a dinosaur (among other possibilities) (Zborewski, 1834) (see Parts 4.1.1.13 and 4.5.205), was also available long before Marsh's visit. Our study of the Tuskar River in 1984 revealed (on a river bank and river bottom) numerous teeth of sharks (*Hybodus* and others) of Cretaceous age, fragments of bones of pre-Turonian ichthyosaurs (the group became extinct at the boundary between the Cenomanian and Turonian), fragments of fossilized bones and teeth of proboscideans and rodents (probably of Neogene - Quaternary age) and flint tools of various types. Apparently, part of the material studied by V. Kipriyanov did not come from bedrock of Cretaceous age. It would be worthwhile to reinvestigate and revise this material.

58. Dzharakuduk I*, a relatively flat area with shallow ravines north-north-east of the Dzharakuduk settlement, Central Kyzylkum, Uzbekistan. A layer of red-colored rocks (Upper Cretaceous, lower part of the lower Turonian) below the bed of sea-bluish clays, but above the reliably dated Cenomanian deposits. The horizon is situated within the Uchkuduk Formation. Bones of hadrosaurids**, tooth of a small theropod**, bones of dinosaurs**. In the upper part of the layer, there are gastroliths* presumably from dinosaurs** (Stokes, 1982; Gillette, 1990). Represented in this very peculiar assemblage are organisms typical of the Cenomanian or Eocene of mid-latitudes of Asia (turtles of the family Carettochelyidae) and those typical for the late Turonian - Coniacian (thick-shelled turtle *Lindholmemys* and skate *Myledaphus*). It is difficult to establish conclusively whether these data refer to a mixed death assemblage of organisms of different ages or to a faunal complex with an unusual community of organisms that co-existed at the same time. However, the existence of carettochelyids of the genus *Anosteira* that differed sharply from the Cenomanian *Kizylkumemys* is known for the Turonian (possibly lower Turonian) of the eastern Kyzylkum (collections of A. I. Shevnin in the mines) and probably from the **[93/94]** Dzhaman-Kokcha Ridge in Karakalpakistan and from the vicinity of the settlement Kulkuduk in Central Kyzylkum, Uzbekistan. As the early Turonian complex mentioned is truly different from the Cenomanian and late Turonian - Coniacian one, it may contain as yet unknown dinosaurs.

One of the branches of the caravan routes passed along the ravines of Dzharakuduk across areas of the Skeleton Desert from Bukhara to Khorezm along areas with countless springs of the Mynbulak depression. Currently, as it happened in the past, dinosaurian bones and bone fragments (particularly frequently vertebrae) are carried by mud-streams from the ravines to the plain and here they are quite common among fine detritus and permanently growing, sloping talus cones. These remains are conspicuous and therefore known to the local people. It is quite probable that these remains were encountered by people moving with caravans of goods from China. It is probable that "fish teeth" that were exported by Khorezm into countries further to the south (see Masson, 1934) not only included mammoth tusks from the north, but also teeth that belonged to ancient fishes and reptiles widely known in the East as medicinal remedies. The stories about bones of giants within the boundaries of the present-day Central Asian part of the CIS without doubt were made up not on the basis of the relatively rare remains of extinct proboscideans, but, more likely, based on discoveries of dinosaurian remains (which are quite common in several regions of Uzbekistan, Kirghizia, and Tadzhikistan). These possibly served as a basis of popular beliefs about the dragons “Adzhdarkho" among the Khivin Uzbeks and "Aidakhar" among the Kazakhs who now inhabit a large part of Central Kyzylkum.

59. Kichik-Karakol (brook), left tributary of the Gulcha River, 17 km southwest of the village of Sufikurgan, Southern Kirghizia. Lower part of the oyster layer. Upper Cretaceous, lower Turonian. Tooth of a very young (newborn?) individual of a hadrosaurid* from a sample of clays washed through a sieve (discovery by V. N. Filichev).

60. Kampyr-Ravat (see part 4.1.2.27), settlement along the Kara Darya River, eastern part of the Fergana Depression, Kirghizia. Bone-bearing breccia at the base of *Exogyra* beds (Upper Cretaceous, lower Turonian) consisting of fragments of dinosaurian bones (Simakov et al., 1957: 57, 58; Yuryev, 1954 a). Earlier level with bones belong to the Cenomanian (Bezobrazova, 1929). Discoveries by P. D. Trusov, 1928.

61. Uchkuduk, Central Kyzylkum, Uzbekistan. Gray clays of the Uchkuduk Formation. Upper Cretaceous, lower Turonian. Large bones (possibly from dinosaurs or plesiosaurs) (material of V. B. Sapozhnikov and N. P. Kovaleva).

62. Tyulkeli* hill, 80 km north of the Dzhusaly settlement, North-Eastern Aral Region, Kazakhstan. Grayish-yellow and gray clays at the base of the lower third of the Zhirkindek Formation. Upper Cretaceous, lower Turonian. Relatively large theropods with laterally flattened teeth (*Alectrosaurus*?)**, sauropods?**, hadrosaurids**.

At the same locality*, but at the base of middle sandy third of the Zhirkindek Formation. Upper Cretaceous, lower Turonian. Dinosaurian assemblage as for previous locality, except, along with theropods** and Sauropoda?**, there is also *Gilmoreosaurus* sp. cf. *G. arkhangelskyi***.

At the same locality*, middle part of the Zhirkindek Formation. Upper Cretaceous, upper Turonian -- Coniacian. Laterally strongly flattened teeth of carnosaurs**, bones of theropods**, hadrosaurids**.

63. Bukantau ridge in Central Kyzylkum, Uzbekistan. Gray clays of Dzheirantui Formation. Upper Cretaceous, lower Turonian. Bones **[94/95]** of tetrapods (Muzafarova, 1963), which may also include dinosaurian bones. The bones were found at the base of the formation (Stratigraphic Dictionary, 1979); their taxonomic identity is not provided.

64. Kulkuduk*, 1-1.5 km south or southeast of the settlement, south of the Bukantau Mountains, Central Kyzylkum, Uzbekistan. Upper Cretaceous, lower Turonian. Ankylosaurids?*, hadrosaurids** (materials of I. M. Abduazimova and the author). Unusual turtles of the family Carettochelyidae have been observed in this assemblage (as for Parts 4.1.3.58 and 4.1.3.65).

At the same locality, upper Turonian? - Conciacian? Large theropods with teeth that are considerably flattened along the sides, ankylosaurids*, hadrosaurids* (material of I. M. Abduazimova).

At the same locality, base of the Bissekty Formation. Upper Cretaceous, upper Turonian - Coniacian. Lambeosaurine hadrosaurids*, sauropods*, ankylosaurids* that cannot be identified more precisely (collections of I. M. Abduazimova).

65. Dzhaman-Kokcha I*, ridge east of the Sultan-Uvais Ridge and the Kyrkkyz and Ayazkala mounds, Karakalpakistan. Supposedly lower part of the Beshtyubin Formation. Upper Cretaceous, lower Turonian. Vertebrae of dinosaurs** (Nessov, 1977).

66. Mansurata I, slope of elevation in Tashkent Chul', Southern Kazakhstan. Middle or upper parts of upper Chanak subformation. Upper Cretaceous, lower Turonian (Belenky and Mirkamalova, 1965). Brown clays, orange sands, and conglomerates. Bones of reptiles (apparently remains of dinosaurs) (Belenky, 1961: 47, 49).

In the same locality, probably in the Syuk-Syuk Formation (Belenky, 1961: 53), dinosaurian bones were found in purplish-pink sandstones.

67. Aigyrbulak, well in the Kuldzhuktau Ridge, Central Kyzylkum, Uzbekistan. Sandstones of the Upper Cretaceous, Turonian (Vinokurova and Zhukova, 1962). Ungual phalanx of a dinosaur (theropod or ornithopod), vertebrae of dinosaurs (identified by A. N. Krishtofovich).

68. Aznek, vicinity of the well in the Karakatin Depression, Central Kyzylkum, Uzbekistan. Upper Cretaceous, Turonian. Bones of dinosaurs* (determination of the age and collections by N. V. Shabanina and L. N. Shavlis).

69. Taikarshi, mound approximately 60 km south of Kulkuduk and from the Bukantau Ridge, Central Kyzylkum, Uzbekistan. Basal part of the Bissekty Formation. Upper Cretaceous, upper Turonian. Bones of large theropods* ankylosaurids*, hadrosaurids* (material of I. M. Abduazimova).

70. Dzharakuduk II* (=Bissekty, =Kulbeke, =Dzharakuduk), bluffs northeast and east of the Dzharakuduk settlement and the abandoned Dzharakuduk well (Arkhangelsky, 1916; Sosedko, 1937, 1938; Rozhdestvensky, 1964), Central Kyzylkum, Uzbekistan. Base of the Bissekty Formation (the given formal name replaced the former informal designation Taikarshi bed; Nessov, 1990). Upper Cretaceous, upper Turonian. The Beleutin Formation (Weishampel et al., 1990a: 128, locality 354) is not exposed there. A. D. Arkhangelsky (1916) noted that he had found bones of reptiles at approximately the same level in the lower part of a sandy layer. The material was described was the distal part of a humerus of Ceratopsidae and different bones of Hadrosauridae attributed to *Cionodon*? *kysylkumense* Riab. One of the vertebra of this series is here regarded as the lectotype for the species (Riabinin, 1931a: pl. II, fig. 1) (see also Part 3). This species is also represented by new material from the type locality, but from higher levels (Pl. IX, figs. 11?, 13, 14?, 16; Pl. XI, fig. 4, etc.), and is placed in the lambeosaurines**. Dominant at the lower level are remains of a much **[94/95]** more primitive hadrosaurid, *Gilmoreosaurus arkhangelskyi* sp. n.**, which belonged to the subfamily of hadrosaurines or even to a lower evolutionary stage (plesion) within the family. At the same level, possible gastroliths of dinosaurs** have been found. The holotype of the ceratopsid *Turanoceratops tardabilis*** (Nessov, et al., 1989: pl. VII, 21) and remains

of a relatively small carnosaur *Alectrosaurus* sp.** with relatively strongly flattened teeth, and vertebrae and jaws of hadrosaurids** were found 1 m above the base of the formation.

Level 26 m from the base of the formation* (site CDZH-17a, CDZH-17...). Upper Cretaceous, upper Turonian. Contents of dinosaur remains here is 0.37 - 1.60% in samples of 5,923, 6,957 and 4,023 bones and teeth of vertebrates (data of L. B. Golovneva, E. I. Bychkova, and the author). Teeth of Coeluroidea** (Nessov, 1981a,b: fig. X, 12) (Pl. II, fig. 10), Deinonychosauria**, cf. *Aublysodon* sp.** (Lehman and Carpenter, 1990; Weishampel et al., 1990a: fig. 6.26), lower jaws of *Caenagnathasia martinsoni* Currie, Godfrey et Ness.** (Caenagnathidae, Oviraptorosauria) (Pl. II, fig. 16) (Currie et al., 1994), and sacrum of an oviraptorosaur or ornithomimid (Pl. III, fig. 1). In the same locality, relatively large theropods *Alectrosaurus* sp.** are represented (Pl. I, figs. 1, 3, 5-6, 7?, 8, 10?, 11?; Pl. II, figs. 13?, 14?; Pl. X, figs. 9?, 10?), characterized by considerably flattened teeth, but with a larger number of teeth in the upper jaw than in the larger carnosaurs of the second half of the Late Cretaceous; ornithomimids**(Pl. II, fig. 19, etc.), segnosaurs Segnosauria indet.** (Pl. I, fig. 13; Pl. II, figs. 1-2, 4), sauropods with slender, long, "pencil-shaped" teeth (Nessov, 1981a), ankylosaurs** (Pl. IV, fig. 6), small ornithopods** similar in the structure of tooth crowns to hypsilophodontids (Nessov, 1981b: fig. X, 13) (Pl. X, figs. 19-23). The hadrosaurine *Gilmoreosaurus arkhangelskyi* sp. n.** is also recognized here (Pl. VIII, figs. 2, 3?, 6-7, 9?; Pl. IX, figs. 2, 4, 7-10, 14?; Pl. X, figs. 3?, 4?, 5, 11?-14?; Pl. XI, figs. 1-2). The following material has been found: teeth (Nessov, 1985b: pl. II, fig. 4) and vertebrae of Lambeosaurinae**, remains of *Turanoceratops tardabilis* Ness. et L. Kazn.** (Pl. VII, figs. 2-4, 15-18), belonging to Centrosaurinae (Chure and McIntosh, 1989; Lehman, 1991); but earlier, before the revision of composition of ceratopsid subfamilies, placed in Monocloniidae (Nessov, 1981a); the braincase of a relatively small ceratopsid was discovered (see Chapter 3). Possible gastroliths of dinosaurs** have been found here.

Level approximately 52 m above the base of the formation* (site CBI-4). Upper Cretaceous, Coniacian. Earlier, the entire formation was dated as late Turonian (e.g., Pyatkov et al., 1967) or as undivided late Turonian - Santonian (Sochava, 1968). The dinosaurs are largely the same as for the level 26 m above the base of the unit. Furthermore, the femur of *Archaeornithomimus*(?) *bissektensis* sp. n.** (Pl. II, fig. 7) and the braincase of a relatively small dromaeosaurid** (Pl. II, fig. 17) have been found; remains of ankylosaurs ** (Pl. IV, figs. 4, 5, 11) are relatively common here. Remains of ceratopsids** (Pl. VII, fig. 19) and hadrosaurids** are very rare. The assemblage of mammals from this area is very peculiar.

Level approximately 57 m above the base of the formation* (site CBI-14, lower part of the site CBI-17). Upper Cretaceous, Coniacian (Nessov, 1988a). The composition of this assemblage or two assemblages already mentioned for the Bissekty Formation at Dzharakuduk is partially similar to that known from the Iren Dabasu Formation of northern China (Rozhdestvensky, 1966, Weishampel and Horner, 1986; Mader and Bradley, 1989; Smith and Galton, 1990; Currie and Eberth, 1993) and from the upper part of the Bainshiren Formation of Mongolia.

[95/96]

Coeluroidea**, dromaeosaurids (Ostrom, 1969) of small size have been noted at this level. Judging from the relatively wide and short maxillary bone (supposedly of a young individual), the latter had a wider and possibly somewhat shorter rostral part of the skull than *Deinonychus antirrhopus* (Ostrom, 1969) (discovered by the author and identified by S. M. Kurzanov). Teeth of deinonychosaurs (Pl. II, fig. 11) from this locality possibly belong to the same species as the braincase (Pl. II, fig. 17). There is a report of the discovery of mandibles of ornithomimids (Rozhdestvensky, 1964). However, it would now be desirable to check the identity of these discoveries not only against ornithomimids, but also archaic Oviraptorosauria of the family Caenagnathidae. Discovered here was the ungual phalanx, possibly from digit I of the manus, of an oviraptorosaur (Pl. II, fig. 8). Laterally strongly flattened, thecodont teeth of a problematic theropod (or bony fish of the family Saurodontidae), named *Asiamericana asiatica* sp. n. (Pl. II, fig. 9) were found. Observed at the same locality, in the assemblage, are moderately large theropods with strongly laterally flattened teeth as in torvosaurids (compare with Britt [1991]); we attribute them to *Alectrosaurus* sp.**(Pl. I, figs. 19?, 20), as remains of young theropods**. Within the assemblage of this level there are also teeth of theropods - cf. *Aublysodon* sp.** (Lehman and Carpenter, 1990; Weishampel et al., 1990a: fig. 6.26; and data in Currie and Eberth [1993] on referral of *Alectrosaurus* to Aublysodontinae), *Euronychodon asiaticus* sp. n.** (Nessov, 1985b: pl. II, 16; Nessov, 1986: fig. 3.3), and cf. *Richardoestesia* sp.** (Currie et al., 1990; Rowe et al., 1992). Caudal vertebrae are represented here cf. *Dryptosaurus* sp. or cf. *Hypsibema*? sp.** (Pl. III, fig. 6) (see Gallagher [1990: fig. 11]); possibly these belong to segnosaurs or a group related to them. Present here are ungual phalanges and preungual phalanges (Pl. II, fig. 3), vertebrae, strongly expanded distal parts of humeri, vertebrae, and teeth of segnosaurs Segnosauria indet.**. Possibly a strongly pneumatized basisphenoid and a frontal also belong to the latter group (Pl. II, fig. 12). The segnosaurian species noted here differs in the considerably smaller size of ungual phalanges from that in the early middle Albian of Karakalpakistan (Khodzhakul), but is possibly the same as in the Turonian - Coniacian of Iren Dabasu in China (Mader and Bradley, 1989). Represented here are also vertebrae, ungual phalanges, and teeth of sauropods (cf. Diplodocidae or cf. Titanosauridae**) (Nessov, 1985b: pl. II, fig. 7) (Pl. III, fig. 2), remains of both very young specimens (diameter of teeth approximately 2 mm) and large adult specimens (with centrum length of approximately 38-40 cm). There are ankylosaurids**, hadrosaurine (or an even more primitive representative of Hadrosauridae) *Gilmoreosaurus arkhangelskyi* sp. n.** (Nessov, 1986: fig. 2, 5) (Pl. VIII, figs. 1, 8?, 19?; Pl. IX, figs. 3, 5-6, 12?, 17) and also rare teeth and vertebrae of relatively large Lambeosaurinae**. Quite rare are teeth of small cf. Protoceratopsidae**; there is a ceratopsid *Turanoceratops tardabilis* Ness et L. Kazn.** (Nessov, 1986: fig. 2, 4). One tooth is quite similar to one reported from the upper part of the Lower Cretaceous of Texas (Winkler et al., 1990b: fig. 9.1). There are possible gastroliths of dinosaurs.**

The presence of the family Ceratopsidae was first recorded for this locality by A. N. Riabinin (1931a) and A. K. Rozhdestvensky (1964) with various degrees of doubt. The latter author was inclined to assume the ankylosaurian nature of the horn-like bony remains from the Upper

Cretaceous of the Central Asian region of the CIS. This level as well as the level 26 m above the base of the Bissekty Formation (called Taikarshi bed in the past, as was already noted, but not Beleutin Formation [Weishampel et al., 1990a: 128, 308, 313]) is most **[96/97]** notable for the discovery of the braincase of *Itemirus medullaris* Kurz. (Kurzanov, 1976; Kurzanov, 1987: fig. 37). This discovery should be dated as late Turonian - Coniacian. It is possible that this theropod does not belong to the carnosaurs (Weishampel et al., 1990a: 313) or may be a tyrannosaurid (Chure and Madsen, 1993), but its generic name is probably not a junior synonym of *Alectrosaurus*. In general, the diversity of dinosaurs in this and many other assemblages from the Upper Cretaceous of the Turanian Plate and the Fergana Depression is rather low in comparison with other vertebrates known from remains in this time interval; along with dinosaurs, there may be 50 to 60 or more families. In the mass of phosphates accumulating at any given moment in the form of skeletons of different vertebrates, dinosaurs also were far from being dominant. On this level and also on the above layer (see below), there are quite a few cases of former boring of dinosaurian bones by the bivalve mollusks of the family Pholadidae or closely related forms. Evidently boring of bones took place after their first burial in the fine-grained, relatively dense rock (before redeposition into sandy sediments). Cases of boring of bones by deep passages, which are rounded in cross-section, in the Upper Cretaceous of North America (Rogers, 1992) also could have been related with the activity of brackish-water pholadids or pelecypods closely related to them, rather than scavenger beetles.

Level 8-12 m above site CBI-14 (site CBI-5a)*. Upper Cretaceous, Coniacian. The composition of dinosaurian assemblage is the same as on the previous level (e.g., Pl. I, figs. 2, 5; Pl. II, fig. 15; Nessov, 1986: figs. 1, 7). In loose yellow sands lying in the upper part of the 4 m thick interval referred to CBI-5a, bones of the distal part of a hindlimb of a specimen of a large hadrosaurid** were discovered; they were articulated with each other and also immediately adjacent to each other. They are spread by a shifting layer of sand in one level over a distance of approximately 3.5 m from northeast to southwest. This is so far the only discovery of dinosaurian remains of Dzharakuduk (not those belonging to skull, atlas-axis, limb girdles, and sacrum) preserved in natural articulation.

Level near the top of the Bissekty Formation (site CBI-7a)*. Upper Cretaceous, Coniacian-? lower Santonian. Relatively large theropods *Alectrosaurus* sp** with laterally considerably flattened teeth, hadrosaurids**, bones of dinosaurs**.

Similarity has been noted between the composition of the Dzharakuduk fossil assemblages and of Campanian - Maastrichtian ones in North America (Nessov, 1979), which may be related to the distribution of some Asian vertebrates in the western part of North America during the thermal maximum at the end of the Santonian and during first half of the Campanian (German, 1988; Nessov and Golovneva, 1990)

At the same locality, Aitym Formation*. Upper Cretaceous, Santonian. Bones of hadrosaurids**.

At the same locality, Dzhetymtau bed, a few meters below the layer of yellowish calcareous shell accumulations. Upper Cretaceous, upper Senonian or Campanian? Bones of dinosaurs**.

71. Karamurun*, northeastern part of the Bukantau Ridge, Central Kyzylkum, Uzbekistan. Bissekty Formation. Upper Cretaceous, upper Turonian - Coniacian. Large teeth of theropods**, flattened as in torvosaurids, hadrosaurids**.

[97/98]

72. Eddum, locality in the south of the Aristantau Ridge, Central Kyzylkum, Uzbekistan. Upper Cretaceous, upper Turonian - Coniacian. Small theropods* (teeth), hadrosaurids* (collections of I. M. Abduazimova).

73. Tyulantash, sites near the middle of the way from the Kokpatas Mountains to the western edge of the Auminzatau Ridge. Bissekty Formation? Upper Cretaceous, Coniacian. Ankylosauridae*, Hadrosauridae* (material of Yu. N. Kornienko).

74. Pitnyak*, left bank of the Amu Darya, Turkmenistan. Upper Cretaceous, Coniacian. Bones of dinosaurs (material of A. P. Vadilo and the author).

75. Bzoubai*, elevations near the settlement in Southwestern Kyzylkum, Uzbekistan. Upper Cretaceous, Coniacian. Bones of dinosaurs**.

76. Tamdy-Truba, settlement and elevation 40 km south from the city of Uchkuduk, Central Kyzylkum, Uzbekistan. Bissekty Formation? Upper Cretaceous, upper Turonian - Coniacian - ?Santonian. Ankylosaurids*, hadrosaurids (lambeosaurines?)* (collections of I. M. Abduazimova).

At the same locality, base of the Aitym Formation. Upper Cretaceous, Santonian. Small theropods*, carnosaurs*, ankylosaurids* (dominant), hadrosaurids* (collections of I. M. Abduazimova).

77. Daugyztau I* a small isolated ravine 9 km south of the settlement Daugyztau, west of the road, Central Kyzylkum, Uzbekistan. Upper Cretaceous, upper Turonian -- Santonian. Large theropods with strongly flattened laterally teeth**, hadrosaurids**.

78. Koturbulak, settlement in the eastern part of Betpakdala, on the northeastern slope of the Malyi Karatau Ridge, Kazakhstan. Sandstone of the Buralkenyntuz Formation or Koturbulak Formation (Nikiforova, 1960). Upper Cretaceous, upper Turonian - Santonian or Coniacian? - Santonian. “Deinodontids”, ankylosaurids, sacrum of a hadrosaurid (Nikiforova, 1960).

From the sand-pit near this settlement, in sands of the Koturbulak Formation (Upper Cretaceous, upper Turonian - Santonian), bones of hadrosaurids are known (Tsirelson et al., 1986: 105).

79. Beshbulak, 2 km west-south-west of the settlement, northeastern part of Central Kyzylkum. Upper Cretaceous, upper Turonian - Santonian. Vertebra of a hadrosaurid* (collections of N. P. Kolomiitsev).

80. Dzhamanuru, 3-3.5 km west of the Dzhamanuru settlement, northern slope of the Bukantau Ridge, Uzbekistan. Upper Cretaceous, upper Turonian - Santonian. Dinosaurian bones (including hadrosaurid vertebrae)*. Collections of Ya. B. Aisanov.

81. Daugyztau II*, series of sites 3-4 km west of the Daugyztau settlement, Central Kyzylkum, Uzbekistan. Upper Cretaceous, upper Turonian - Santonian. Vertebrae of hadrosaurids**, bones of dinosaurs**.

82. Tassuyekkoba, sites on the plateau and west of it in the valley of the Chu River, Kazakhstan. Sandstones of the Buralkenyntuz Formation (Nikiforova, 1960: fig. 24). Upper Cretaceous, upper Turonian - Santonian. Bones of dinosaurs (Nikiforova, 1960: 57). In the same region, bones that cannot be identified were cited for Sor Karoi [sor = salt-covered ground that may be area temporarily filled with water] (Nikiforova, 1960: 56); the same name was used for the locality 4.1.3.144.

83. Malyi Karakol, 14 km west of the settlement, Betpakdala, Kazakhstan. Sandstones of the Buralkenyntuz(?) Formation. Upper Cretaceous, Santonian? Fragments of dinosaurian bones (Nikiforova, 1960: 59).

84. Koskuduk*, northwestern edge of the Karakata Depression, Central Kyzylkum, Uzbekistan. Upper Cretaceous, upper Turonian - Santonian. Bones of dinosaurs, including hadrosaurids**.

85. Geisu, river in Northern Armenia. Upper Cretaceous, Coniacian - Santonian based on discoveries of ammonites (data on the age and discovery by A. A. Atabekyan).

[98/99]

Tubular limb bone of a theropod*. This is the first discovery of dinosaurian remains in Armenia.

A. K. Rozhdestvensky (1973) indicated (without providing more detail) discoveries of terrestrial reptiles in marine deposits of the Caucasus.

86. Kainarbulak, 3-4 km west of the Kainarbulak settlement, left bank of the Dzhamankitai River, south-western slope of Karatau Ridge, Kazakhstan. Koturbulak Formation. Upper Cretaceous, Coniacian - Santonian or Senonian (Stratigraphic Dictionary, 1979). Bones of dinosaurs (oral communication from O. A. Fedorenko). Possibly this is the same locality as 4.1.3.78.

87. Dzhalpakshi, mountain on the southern slope of the Dzhetymtau Ridge, Central Kyzylkum, Uzbekistan. Kynyr Formation. Upper Cretaceous, Coniacian - Santonian. Ankylosaurids*, hadrosaurids* (collections of I. M. Abduazimova).

88. Zhaldyrbas-Takyr, region of the Beshkuduk well, Central Kyzylkum, Uzbekistan. Upper part of the Kynyr Formation. Upper Cretaceous, Coniacian - Santonian? Large theropods with considerably laterally flattened teeth*, average-sized theropods*, ankylosaurids*, hadrosaurids similar to *Gilmoreosaurus** (dominant) (collections of I. M. Abduazimova).

89. Kansai* (close to the Kyzylbulak spring or in the area between the settlements Aktash and Kyzylbulak; Rozhdestvensky, 1977). Northwestern Fergana, Tadzhikistan. Yalovach Formation, possibly only its upper part. The age is not Cenomanian - Turonian (Rozhdestvensky, 1964), but Upper Cretaceous, Santonian (Rozhdestvensky, 1977). The latter dating is supported by the identifications of brackish-water pelecypods of the group Trigonioidea by G. G. Martinson. We accept it for site FKA-7a (Nessov, 1988a) and a number of other localities corresponding to the "lower bone-bearing horizon" of A. K. Rozhdestvensky (1977). Content of dinosaurian remains here is 1.9% in a sample of 4,133 teeth and bones of vertebrates (data of M. V. Nazarkin, L. B. Golovneva, and the author). Dinosaurian remains are mostly associated with the "lower" and "upper bone-bearing horizons" (Rozhdestvensky, 1969). Three species of carnivorous dinosaurs (Rozhdestvensky and Khozatsky, 1967), dromaeosaurids (D. A. Russell, personal communication, 1988). The identity of mandibles of a primitive ornithomimid (Rozhdestvensky, 1969, 1977) should be checked not only against ornithomimids, but also primitive oviraptorosaurs of the family Caenagnathidae; cf. Oviraptoridae (D. A. Russell, personal communication, 1988). Large carnosaurs with an estimated body length of 10-11 m and skull length of approximately 1 m (Rozhdestvensky, 1977), theropods with considerably flattened teeth, cf. *Alectrosaurus* sp. **, and probably less frequently tyrannosaurids with relatively thick teeth**, teeth with anteroposteriorly wide and low crown from considerably smaller carnivores (Rozhdestvensky, 1977), sauropods with long, slender teeth possessing relatively smooth enamel, from diplodocids or titanosaurids**. Remains

of sauropods were indicated from this site earlier (Rozhdestvensky and Khozatskii, 1967), but this identification was questioned (Rozhdestvensky, 1977). Their presence was confirmed by our discoveries of 1981 and 1985. Teeth of ankylosaurids** (Nessov, 1988a; Nessov et al., 1989), lower jaw and other remains of small hadrosaurids (Lambeosaurinae), length 5-6 m (Rozhdestvensky, 1977). Teeth cf. Hypsilophodontidae** (Nessov, 1988a). Bones (Vyalov, 1945b; Vyalov et al., 1947; Verzilin and Nessov, 1978).

90. Kyzylpilyal* (=Isfara II, Nessov, 1980), right bank of the Isfara River, north of the settlement Kyzylpilyal, Southwestern Fergana, Tadzhikistan. Yalovach Formation. Upper Cretaceous, lower Santonian. Based **[99/100]** on identifications by I. A. Yefremov (Poyarkova, 1969: 136), Coeluridae, Ornithomimidae, Ankylosauridae, and Hadrosauridae are known from here. Teeth of deinonychosaurs** (Nessov et al., 1987), frontal of troodontid *Troodon isfarensis* sp. n. ** (Pl. III, fig. 12), sauropod with slender, pencil-shaped teeth** were found.

At the same locality, the lower part of the Palvantash Formation*. Upper Cretaceous, upper Santonian - lower Campanian. Hadrosaurids*. Dinosaurs (Vyalov, 1945a,b; Vyalov et al. 1947; Khozatskii, 1957). Bones of dinosaurs were also observed by us at one locality in the area between the Isfara and Shorsu rivers along the zone of outcrops extending eastwards from the locality Kyzylpilyal.

91. Zamuratsho* (=Isfara I, Nessov, 1980), left bank of the Isfara River south of the Zamuratsho settlement, Southwestern Fergana, Tadzhikistan. Yalovach Formation. Upper Cretaceous, lower Santonian. Bones of dinosaurs**. Apparently this place was meant (Simakov et al. 1957: 72) for dinosaurian bones reported from this level in Western Fergana, although, judging from the text, the site could have been also Kyzylpilyal (see Part 4.1.3.90), Selrokho, Aksarai, or Togap.

92. Naukat depression (south of Fergana Depression), probably near the city of Naukat (=Nookat), Kirghizia. Upper part of the Yalovach Formation. Upper Cretaceous, Santonian. Hadrosaurids (Poyarkova, 1969: 192). Fragments of dinosaurian bones in red sandstones and

conglomerates were noted near the city of Naukat by G. G. Martinson (1968: 56). Fragments of large dinosaurian bones were cited for the area between the Isfairam and Sokh rivers near the Kan settlement (Simakov et al. 1957: 68).

93. Aravan II, right bank of the river northeast of the city Iski-Naukat, south of the Fergana Depression, Kirghizia. Yalovach Formation. Upper Cretaceous, Senonian. Bones of dinosaurs* (discovery by D. V. Borkhvardt).

94. Changet IV*, near the mouth of the Bokai brook, Fergana Depression, Kirghizia. Yalovach Formation. Upper Cretaceous, lower Santonian. Teeth of tyrannosaurids with thick base (slightly flattened along the sides)*, sauropods*, hadrosaurids* (collections of P. V. Fedorov and the author) (Nessov et al., 1990).

L. I. Khozatsky (1957) pointed to remains of dinosaurs in the region of the Markai brook, but only Jurassic deposits are exposed there. (Possibly these data refer to the area situated somewhat downstream, near the Bokai brook.)

95. There are seven unnamed localities with remains of hadrosaurids and other dinosaurs in the Yalovach Formation (Upper Cretaceous, Santonian), in the northwestern and southwestern parts of the Fergana Depression (Simakov et al. 1957: 58) and in the southeastern part of the same depression. One of these is probably situated near the settlement of Adrasman (95a) where Z. N. Poyarkova (1965) found bones remains that cannot be identified. In one of the seven localities, dinosaurian remains are noted also for the lower Palvntash subformation. Upper Cretaceous, Santonian - lower Campanian (see also Part 4.1.3.122). Several additional localitites for the Yalovach, see N. N. Verzilin (1975: fig. 3, IV). G. G. Martinson (1969: 19) pointed to the presence of dinosaurian bones in the Yalovach Formation at an unnamed locality in Eastern Fergana.

96. Shatyrtyube I* (=Shatyrtau), ravine 3-3.5 km south of the isolated Shatyrtyube mound south of the Dzhetymtau II Ridge and southeast of the Bukantau Ridge, region of the Mullala well, Central Kyzylkum, Uzbekistan. Upper Cretaceous, Santonian. Theropods of average size (teeth and

vertebrae)**, sauropods with slender teeth**, hadrosaurids (hadrosaurines? and lambeosaurines)** (Nessov, 1989). The locality was discovered **[100/101]** by R. N. Dzhamaletdinov, and collections were made by the author. Here particularly in the Kynyr Formation, damage of bones by boring brackish-water pelecypods of the family Pholadidae is quite common. The type of occurrence of remains is "channel-lag." They are weathered and accumulated on the same level corresponding to the bottom of a wide strait or interbasin channel, oriented towards north-north-west.

97. Shatyrtyube II, 1 km east of the mound indicated. Upper Cretaceous, Santonian and lower Campanian. Hadrosaurids*, bones of dinosaurs* (collections of I. M. Abduazimova).

In the same area, relatively high part of the local layer, thickness of the Upper Cretaceous, Campanian - ?lower Maastrichtian. Ankylosaurids*, hadrosaurids (collections of I. M. Abduazimova).

98. Muinak, western slope of the former peninsula in the south of Aral Sea, Karakalpakistan. Sandstones with *Amphidonte asiatica*. Upper Cretaceous. Bones of sauropods* (collections of I. M. Abduazimova).

99. Syuk-Syuk (=Syok-Syok). in the vicinity of wells in the south of the Chimkent region, 10-12 km north of the Dzhilga (=Zhilga) station, Kazakhstan. Lower part of the Darbazin Formation (Rozhdestvensky, 1964a). Syuk-Syuk Formation (Stratigraphic Dictionary, 1979), rather than the Beleutin Formation (Rozhdestvensky, 1971: 30). Upper Cretaceous, Santonian. The age was earlier regarded as younger than that for *Jaxartosaurus* at Alymtau (Rozhdestvensky, 1971) and was dated as early Santonian (Rozhdestvensky 1977), but it is not late Turonian (Belenky and Mirkamalova, 1965) nor Cenomanian - Turonian (Rozhdestvensky, 1964b; Rozhdestvensky and Khozatsky, 1965). Tubular bone of a small theropod* and moderately thick tooth of a large theropod* (discoveries by A. O. Averianov), long, slender tooth of a sauropod*, lambeosaurine (Rozhdestvensky and Khozatsky, 1965) cited as hadrosaurid (Belenky and Mirkamalova, 1965; Belenky and Rozhdestvensky, 1963) or as *Procheneosaurus convincens* Rozh. (Rozhdestvensky,

1968a; Shilin and Suslov, 1982). The latter name is regarded as a junior synonym of *Jaxartosaurus aralensis* Riab., known from Alymtau (Weishampel et al., 1990a: 129) or as *Corythosaurus convincens* (Rozh.) (Maryanska and Osmolska, 1984). After the discovery of the skeleton of a young specimen of "*P*." *convincens* stratigraphically higher than the "dinosaur horizon" established by E. V. Ivanov in the 1920s (Stratigraphic Dictionary, 1979: 378; Rozhdestvensky et al., 1987), it became clear (Rozhdestvensky et al. 1987) that redeposition of dinosaurian remains from the Cretaceous to the Paleogene (Yefremov, 1944) was not as extensive as assumed previously (see Part 4.2). the facts do not support the concept of the unity of the "dinosaur horizon"; see Martinson (1968) who found bones of dinosaurs in gravels, sandstones, and clays and conglomerates occurring above these (both layers underlie the layer with skeleton of "*P*." *convincens* at Syuk-Syuk). The presence of hollows up to 15 mm in diameter in the bones of the skeleton of "*P*."*convincens* (Belenky and Rozhdestvensky, 1963), filled with a pink powdery mass, was possibly related to boring by pholadid pelecypods or primitive forms closely related to them in fine-grained substrate, which was later replaced by sand.

Unknown level within the limits of the Santonian - lower Campanian. Jaw with teeth that have serration of edges of the *Asiamericana* type (bony fishes of the family Saurodontidae or theropods).

100. Algabas, near Tashkent, at the boundary of Kazakhstan and Uzbekistan. Syuk-Syuk Formation. Upper Cretaceous, Santonian. Large bones (dinosaurs?) **[101/102]** (material of and identifications by N. N. Kostenko, V. B. Sapozhnikov, and N. P. Kovaleva).

101. Bogonale* (=Bogonaly), southwestern slope of the mountain in Tashkent Chul', Southern Kazakhstan. Gravels and conglomerates in the upper red sandstones. Upper Cretaceous, Santonian. Remains of dinosaurs (Martinson, 1968: 29).

102. Darbaza*, 2-3 km north-north-west from the Darbaza railway station, Southern Kazakhstan. Syuk-Syuk Formation or lower part of the Darbazin Formation(?). Upper Cretaceous, Santonian or lower Campanian? Remains of hadrosaurids from red sandstones (discoveries by V.

B. Sapozhnikov and N. P. Kovaleva). Bone of a hadrosaurid(?) from gray sandstones (discovery by B. V. Prizemlin).

103. Abdurassai and Syuren'atai, region of Chatkal Ridge, Uzbekistan? Syuk-Syuk Formation. Upper Cretaceous, Santonian. Bones of hadrosaurids*, bones of dinosaurs* (collections of I. M. Abduazimova).

104. Parlisai, ravine south of the valley of the Aksak-Ata River, Tashkent Depression, Uzbekistan. Coarse-grained sediments, occurring on Paleozoic, analogues of the Syuk-Syuk Formation? Upper Cretaceous, Santonian or lower Campanian? Bones of reptiles (Belenky and Mirkamalova, 1965), possibly dinosaurs.

105. Angren, Uzbekistan. Syuk-Syuk Formation?, coarse deposits on Paleozoic. Upper Cretaceous, Santonian. Bones of reptiles (Belenky and Mirkamalova, 1965: 37), possibly of dinosaurs.

106. Kazgurt* (=Fogelevo, = Fogelevka), pass across the Kazgurt Ridge on the new highway from Chimkent to Tashkent, Kazakhstan. Upper part of the Syuk-Syuk Formation (Suslov 1987). Upper Cretaceous, Santonian. Small theropods (Suslov, 1987), hadrosaurids (Shilin and Suslov, 1982) belonging to the same lambeosaurine genus as at Shakh-Shakh (Suslov, 1987).

On the road approximately 3 km north-north-east of the pass, there is an additional small outcrop of rocks of the Syuk-Syuk Formation with bones of dinosaurs.

107. Kyrkkuduk I*, area about 2 km in length along the northern foot of the Alymtau Ridge, 6-7 km south of the Kyrkkuduk well (Prinada, 1927), but, in our opinion, also 3-5 km southwest of the Kyrkkuduk well, Tashkent Chul', Southern Kazakhstan. This locality was erroneously placed in the Kyzylkum (Rozhdestvensky 1973; Rozhdestvensky 1977). The locality Kyrkkuduk was earlier frequently included in the locality Saryagach (Riabinin, 1938, etc.) even though they are separated by tens of kilometers without outcrops with dinosaurian remains. Syuk-Syuk Formation. Upper Cretaceous, Santonian. Bones of dinosaurs (the dinosaurian fauna of Kyrkkuduk and other places of the region is reported in greater detail in Part 4.1.3.121).

108. The locality Saryagach should now be called Chingeldy* (the name Saryagach, because of renaming the station or an error in the schematic map [Ivanov, 1926a; Riabinin, 1939: fig. 1] now belongs to a different railway station, much closer to Tashkent). Probably the name "Saryagach" used by Riabinin (1939: fig. 1) belonged not to a station but to a summer camp (Belenky, 1961: 49), where bones were first found by E. V. Ivanov.

G.G. Martinson (1968: 80) found bones of dinosaurs (Upper Cretaceous, Santonian) in the hollow immediately close to Chingeldy station.

[102/103]

109. Uzunkuduk (Yefremov, 1944; Riabinin, 1938), Tashkent Chul', Kazakhstan. Upper Cretaceous. Remains of dinosaurs.

110. Dzhilga Anticline * or area west of this anticline. Tashkent Chul', Kazakhstan. Upper Cretaceous. Remains of dinosaurs (Prinada, 1925).

111. Dovletsai. Tashkent Chul', Kazakhstan. Upper Cretaceous. Remains of theropods, ornithomimids, and ornithischians (Riabinin 1939).

112. Alymtau* Ridge, at the crossing of the ridge with the old road from Tashkent to Turkestan (Prinada 1927). Tashkent Chul', Kazakhstan. Upper Cretaceous. Bones of dinosaurs**.

113. Aigyr-Uch-Kan Ridge (=Aigyruchkan, Aigyryshkan mountains), where most probably fragments of skull bones (dinosaurs?) were noted in the Syuk-Syuk Formation (purple sandstones) (Riabinin 1939; Belenky, 1961). Upper Cretaceous.

114. Valley Tyulkesu (apparently not far from Chingeldy), Tashkent Chul', Kazakhstan. Bone fragments (dinosaurs?) have been discovered (Riabinin, 1939). Upper Cretaceous.

115. Dzhettytyube Elevation west of the Uzunkuduk well, Tashkent Chul', Kazakhstan. Upper Cretaceous. Ungual "articulation of a predator of allosaur type" was found (Prinada, 1925; Belenky, 1961: 53). This identification may refer to a tyrannosaur or segnosaur.

116. Road to Sharybkhana (=Sharapkhana) from Chingeldy to the Sary-Dzhilga valley, Tashkent Chul', Kazakhstan. Upper Cretaceous. Here remains of stegosaurs were reported (probably ankylosaurids) (Riabinin, 1939).

117. Sary-Dzhilga* Valley, Temirchi ridge or mountain in the region of the Suksunkuduk well, southeast of Chingeldy station (Riabinin, 1938: 39), Tashkent Chul', Kazakhstan. Upper Cretaceous. From this area, probably from the Cenomanian deposits, the sacrum of a hadrosaurine has been recovered (Riabinin, 1939: pl. XIV, fig. 1).

Some of the localities Nos. 107-117 may be synonymous, but relating them to each other cannot be done without additional examination of the localities.

118. Mansurata II, slope of the mountain in Tashkent Chul', Kazakhstan. Upper part of the Syuk-Syuk Formation (Upper Cretaceous, Santonian -- ? lower Campanian) (Belenky, 1961: 47, 49). Bones of dinosaurs.

119. Taskotan, upper part of the ravine in the Alymtau Ridge (=?Taskutan well; Belenky and Mirkamalova, 1965, p. 37), Tashkent Chul', Kazakhstan. Upper part of the local section, probably in the Syuk-Syuk Formation. Upper Cretaceous. Bones of terrestrial vertebrates, reptiles (dinosaurs?) (Belenky, 1961: 50).

120. Azatbash, mountain in Tashkent Chul', Kazakhstan. Lower part of the Darbazin Formation. Upper Cretaceous. Bones of terrestrial vertebrates (dinosaurs?) (Belenky, 1961: 53).

121. Dzhamsugum elevation, Tashkent region. Syuk-Syuk Formation, pink-purple sandstones. Upper Cretaceous, Santonian. Bones of terrestrial vertebrates (Belenky, 1961: 53).

The Beleutin Formation is not present in the Tashkent region (Rozhdestvensky, 1971: 30) and remains from the Syuk-Syuk Formation are not dated as Cenomanian (Riabinin, 1939: 5, 7). Formation along a coast was argued for the localities of dinosaurian remains in the Cretaceous of the Tashkent region (Eliseyev, 1958), but this (more exactly, the location in regions of former liman-lagoon sediment accumulation and on coastal **[103/104]** plains) is also typical for many other localities of the Jurassic and Cretaceous in the CIS. For the Tashkent region, mostly material from

Kyrkkuduk was described and depicted; only one bone from Suksun-Kuduk was shown on the photographic plate (Riabinin, 1939). Teeth of theropods were reported for a number of localities, but mainly for Kyrkkuduk. Initially, theropods from these localities were attributed to megalosaurids. Ungual phalanges of theropods are known (Prinada, 1925, 1927; Riabinin, 1938, 1939). Among "coelurosaurs", *Velociraptor*, *Coeluroides*?, *Ornithomimus*, *Oviraptor*? and *Alectrosaurus*? were identified. Possibly the last identification was made based on large, laterally flattened ungual phalanges of the same type as those noted by Gilmore (1933: fig. 9) and belonging (Mader and Bradley, 1989) to segnosaurs. Within the fossil assemblages of the Tashkent group of localities, the sauropod *Antarctosaurus*? (Riabinin, 1938) and a horn of Ceratopsia(?) (Riabinin, 1939: pl. XII, fig. 5) were noted; however, specific sites were not given. If the latter does belong to the ceratopsids, it is most similar to the nasal horn of centrosaurines of the *Eucentrosaurus* type. Apparently the ankylosaurs from here were identified (Riabinin, 1938) as stegosaurs of the family Nodosauridae; the latter family belongs to the ankylosaurs rather than stegosaurs, and it has so far not been reliably recorded for Asia. The hadrosaurid *Jaxartosaurus aralensis* Riab. of the lambeosaurines (Riabinin, 1937b, 1938, 1939; Rozhdestvensky, 1968a) dates to the Coniacian (Rozhdestvensky, 1971) and is represented in the region. *Bactrosaurus prindai* Riab., described by Riabinin from the same locality, was accepted as a junior synonym of this species (Rozhdestvensky and Khozatsky, 1967; Rozhdestvensky, 1971; Rozhdestvensky, 1977). However, the anterior parts of two types of dentaries depicted by Riabinin (1939: pl. III, figs. 1, 4 and pl. IV, fig. 1, 2?) and attributed to this species belong to at least two different species, if not different genera and even different subfamilies. In this connection, it cannot be excluded that dinosaurian assemblages in the region contained not only lambeosaurines (Riabinin 1939: pl. XIII, fig. 1a, sacrum), but also hadrosaurines (ibid.: pl. XIV, fig. 1, sacrum). Materials of hadrosaurids from that locality depicted in the literature (maxilla, dentary, surangular, sacra, etc.) are sufficiently representative for a revision in the light of new data on remains of the duck-billed dinosaurs.

Discoveries of *Cionodon kysylkumense* have been erroneously cited for this area (Weishampel et al., 1990a).

A. K. Rozhdestvensky and L. I . Khozatsky (1967) believed that the lambeosaurine *Jaxartosaurus aralensis* Riab. from Kyrkkuduk I was older than *Aralosaurus tuberiferus* Rozh. from Shakh-Shakh (see below). Yu. V. Suslov (1987) indicated that these two species from Shakh-Shakh and Kyrkkuduk may be conspecific. However, if *Jaxartosaurus* is attributed to lambeosaurines with certainty, hadrosaurine characters are apparent in *Aralosaurus* (Weishampel et al., 1990a); thus it was quite justified to attribute them not only to different species but also to different subfamilies.

Remains cited from Kyrkkuduk as Ceratopsidae? and cf. Ceratopsia, including a horn-like bone (Riabinin, 1939: pl. XII, fig. 5), were attributed to ankylosaurs (Rozhdestvensky, 1971), but these identifications should be checked. Gastroliths** and fragments of bones of dinosaurs** were found by the author in 1990 in shallow ravines immediately east of the Kyrkkuduk well.

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Remains of dinosaurs were noted in the Tashkent region by E. V. Ivanov (1926) (based on discoveries in 1923) and G. G. Martinson (1968: 79). I. A. Yefremov (1944) partly revised the identifications by A. N. Riabinin (1938, 1939) and cited for this locality Deinodontidae, Ornithomimidae, Sauropoda (?Titanosauridae), Stegosauria, Nodosauridae, Ceratopsia sensu lato, Hadrosauridae (Lambeosaurinae). The first name is probably a synonym of Tyrannosauridae, and the citations of stegosaurs and nodosaurids apparently refer to ankylosaurids.

122. An unnamed locality with bones of dinosaurs (Verzilin, 1975: fig. 5) exists in Western Fergana in the Palvantash Formation (lower subformation). Upper Cretaceous, Santonian - lower Campanian.

123. Kokkiya, left bank of the river close to the settlement of Uyuk, 45 km southwest of Kentau city, Southern Kazakhstan. Koturbulak Formation. Upper Cretaceous (Santonian - lower Campanian according to O. A. Fedorenko). Bones of hadrosaurids.

124. Baikhozha, 18 km north of the Baikhozha station, North-Eastern Aral region, Kazakhstan. Bostobin Formation. Upper Cretaceous, Santonian - lower Campanian. Bony spines were cited (Khozatskii, 1957: 18) as coming from a stegosaur, but may be remains of ankylosaurids (or ceratopsids?). Remains of dinosaurs were cited by K. V. Nikiforova (1960) for the lower Syr Darya without reference to an exact location.

125. Bozaby, northern edge of Moin-Kum (Rozhdestvensky 1964), southern edge of Betpakdala on the right bank of the lower Chu River, higher than the settlement of Malye Komkaly, near Lake Kokyi, located near the left bank of the river (90 km from the Pulyaevo settlement), Southern Kazakhstan. Eliseyev (1958), who worked at this locality, placed it on the right bank of the Chu River 90 km down the river from Gulyaevka. The same locality was noted as the southeastern edge of Betpakdala on the Lower Chu River (Yefremov, 1932, 1933). Conglomerates of the Upper Cretaceous, Senonian, based on the identification of sharks from this locality - Santonian (Eliseyev, 1958). The idea of redeposition of dinosaurian remains from the Cretaceous into Tertiary deposits (Yefremov, 1933, 1944) was subjected to reasoned criticism (Eliseyev, 1958). Carnosaurs, hadrosaurids ("trachodonts") (Yefremov, 1944). B. I. Eliseyev (1958 and references in this work) indicates formation of this and a number of other localities in a coastal region.

126. Shakh-Shakh*, 90 km north-east of the Dzhusaly station, North-Eastern Aral Region, Kazakhstan. Bostobin Formation, but not Beleutin Formation as cited by K. V. Nikiforova (1960), V. S. Bazhanov (1972), A. K. Rozhdestvensky (1971, 1976) and Weishampel et al. (1990a: 128). Upper Cretaceous, upper Turonian - lower Santonian (Rozhdestvensky, 1964b, 1971; Rozhdestvensky and Khozatsky, 1967), but more probably this is Santonian - lower Campanian rather than Cenomanian - Turonian (Rozhdestvensky, 1964b) or Turonian (Rozhdestvensky, 1976). V. I. Samodurov (1955), based on work by B. I. Eliseyev (1958), dated the deposits with remains of dinosaurs in this region as Santonian. P. V. Shilin (1968) dated remains of plants from the Bostobin Formation as Santonian - Campanian, ignoring the fact that, during the late Campanian, as a result of a transgression of the sea and liman-lagoon waters, the nature of sediment

accumulation must have changed, leading to the emergence of a geological unit different from the Bostobin Formation. Small theropods (Rozhdestvensky, 1964) and tyrannosaurids (Shilin and Romanova, 1978: pl. XXV, fig. 4); the latter are large and have relatively thick teeth. The following groups have been reported: cf. *Alectrosaurus* (Rozhdestvensky and Khozatsky, 1967 [identification was probably based on an ungual phalanx of a segnosaur]), ornithomimids (Rozhdestvensky and Khozatskii 1967: 87), troodontids (D. A. Russell, personal communication, 1988), deinonychosaurs (**[105/106]** Rozhdestvensky 1964, 1970: fig. 2b; Suslov, 1982: fig. 3); the last identification was probably based on large ungual phalanges of segnosaurs. However, the segnosaurs from this locality do not belong to ?Therizinosauridae (Rozhdestvensky, 1971: 235; Rozhdestvensky, 1976; Weishampel et al., 1990b: 128). Present at the locality are sauropods (Kozhamkulova and Orlovskaya, 1971) and ankylosaurids (Rozhdestvensky and Khozatsky,1967; Maryanska, 1977). The frontal of a hadrosaurid** (No. 720) found in the same region (not far) north of the Baibolat well, is identified as *Aralosaurus* and belongs to a hadrosaurid more primitive than *Tanius* (Buffetaut and Tong-Buffetaut, 1993). Other remains of hadrosaurids, previously cited as *Bactrosaurus* and *Jaxartosaurus* (Nikiforova, 1960: fig. 13; Rozhdestvensky, 1964), have also been found here. Hadrosaurines (Rozhdestvensky, 1968a) and an incomplete skull of *Aralosaurus tuberiferus* Rozh. were listed for this locality (Rozhdestvensky 1964, 1968a; Shilin and Suslov, 1982). Based on unpublished data of T. N. Nurumov (oral communication from staff of the Institute of Zoology, Academy of Sciences of Kazakhstan), sometimes articulated limb-bones of dinosaurs and groups of vertebrae (up to 23) are found in the lower part of the layer exposed near the Shakh-Shakh elevation.

127. Zhalmauz, edge of chink near the Zhalmauz well, region east of the Shakh-Shakh Mountains. Bostobin Formation. Upper Cretaceous, Santonian - lower Campanian. Dinosaurian bones (P. V. Shilin, oral communication).

128. Baibolat* (=Shakh-Shakh II) (Nurumov 1964; Nessov and Khisarova 1988), chink north of the Baibolat well, not infrequently considered together with Shakh-Shakh. Bostobin Formation.

Upper Cretaceous. Santonian - lower Campanian. Teeth of large theropods*, dromaeosaurids*, hadrosaurids*, lower jaw of Caenagnathidae were identified from washed materials from that locality (1962) (Nessov and Khisorova 1988: fig. 5; Currie et al., 1994).

M. E. Voskoboinikov (1953) apparently cited for this region (or somewhat further west?), 75-100 km north of the Syr Darya River, bones of hadrosaurids, ankylosaurs, and “deinodontids” dated as Coniacian by V. S. Bazhanov. Possibly some of these discoveries came from iron-rich sandstones (0.2-6 m) on Kokuyuk mountain.

129. Buroinak II*, southern part of the Buroinak Ridge in North-Eastern Aral region, Kazakhstan. Bostobin Formation. Upper Cretaceous, Santonian - lower Campanian. Weakly flattened teeth of large theropods (tyrannosaurids)**, sauropods?**, hadrosaurids**.

130. Buroinak I*, northern part of the same ridge, Formation and age are the same as for 4.1.3.129. Small theropods**, large and medium-sized theropods (Shilin, 1983), ankylosaurids or ceratopsids* (Pl. IV, fig. 8), hadrosaurids*.

131. Akkurgan* and mound Akkurgan-Boltyk*, North-Eastern Aral region, Kazakhstan. Bostobin Formation. Upper Cretaceous - Santonian - lower Campanian. Large theropods with teeth relatively thick at the base (tyrannosaurids)**, hadrosaurids (Shilin and Suslov, 1982). *Arstanosaurus akkurganensis* Susl. et Shil., placed in the Hadrosauridae in the original description (Shilin and Suslov, 1982), probably belongs to ceratopsids (D. A. Russell, personal communication, 1988; Nessov et al., 1989). The latter view is supported by the labiolingual division of tooth roots and the arrangement of replacing teeth in series one above the other and also the posterior orientation of the dorsal process of the maxilla. Nevertheless, *Arstanosaurus* was reconstructed in the appearance of a hadrosaur (Britt et al., 1990). The total length of the skull of *Arstanosaurus* could have reached 80-85 cm, and the animal **[106/107]** probably belonged to the centrosaurines and thus could have had a considerably developed nasal horn and small supraorbital horns.

132. Baibishe I*, approximately 130 km north-north-west of the Dzhusaly station, North-Eastern Aral Region, Kazakhstan. Middle or upper part of the Bostobin Formation (site BAI-3k). Upper Cretaceous, Santonian - lower Campanian (Nessov, 1988a). Small Coeluroidea**. large tyrannosaurids** (but smaller than those that lived in the end of the Campanian or beginning of the Maastrichtian of Mongolia [Nessov, 1988a]), sauropods**, hadrosaurids (relatively large with skull roof as in hadrosaurines) cf. *Lophorothon* sp.** (Nessov, 1985a; Rozhdestvensky et al., 1987), cf. Ceratopsidae** (fragment of mandible).

For an unnamed locality of the Bostobin Formation in the Aral Region, Stegosauridae were cited (Stratigraphic Dictionary 1979). Most probably this identification refers to ankylosaurids.

133. Egizkara*, edge of chink 2-3 km north-east of a solitary elevation, North-Eastern Aral Region, Kazakhstan. Upper part of the Bostobin Formation. Upper Cretaceous - Santonian? - lower Campanian. Vertebrae of hadrosaurids**. Remains of dinosaurs are also cited several kilometers northeast of this place, on the edge of the Bozoi plateau (Nessov, 1981a).

134. Khorkhut, North-Eastern Aral Region, Kazakhstan. Bostobin Formation? Upper Cretaceous, but not Lower Cretaceous (Yuryev 1954a). Remains of dinosaurs(?) (Yuryev 1954a; Rozhdestvensky and Khozatsky 1967).

135. Tyura-Tam, sandpit that was exploited for a short time near the Tyura-Tam station, North-Eastern Aral Region, Kazakhstan. Upper Cretaceous(?). Bone fragments, presumably from dinosaurs (P. V. Shilin, oral communication).

136. Zhuravlevsky*, settlement on the Ayat River (tributary of the Tobol), Kustanai Region, northern Kazakhastan. Yellow sandstones at the boundary of the Ayat and Zhuravlevskaya formations, immediately below the base of the latter. Upper Cretaceous, Coniacian - lower Campanian. Earlier discoveries of dinosaurian bones here were quite often dated as Maastrichtian. Vertebrae of hadrosaurids (Bazhanov, 1947; Khozatsky, 1949; Novokhatsky, 1954). This identification by V. S. Bazhanov was questioned by Rozhdestvensky (1973; 1977: 108). This was probably done without visiting the site and possibly without examining the material; the

remains were attributed to mosasaurs. Bones of the latter are quite common at this locality, but 0.5-2 m higher in the section, in the layer of clays and sands with phosphorites traditionally included in the base of the Zhuravlevskaya Formation. The latter, situated higher than the layer with phosphorites, has a late Maastrichtian date based on belemnites (Papulov et al., 1990).

Bones of dinosaurs from the upper part of the Ayat Formation of the Zhuravlevsky settlement have colors ranging from dark yellow to gray yellow whereas the remains of mosasaurs form the above layer are black or, less frequently, dark brown. Both bone-bearing levels are, for the most part, covered by grass and situated on a relatively inclined area of the shore slope, but are probably eroded by the combination of flooding and ice motion. A phalanx of the third digit of the hindlimb of a hadrosaurid** and the diaphysis of a femur of a theropod** of medium size in collections dating from 1992 confirm for this locality the presence of remains of dinosaurs that apparently inhabited the insular land west of the major branch of the Turgai Strait (Fig. 2).

137. Ulkenkalkan and Kshikalkan (=Bolshoi and Malyi Kalkan) elevations, situated 35 km north of the settlement Chilik **[107/108]** (Riabinin 1939: 6), south-western slope of Kshikalkan Mountains (Yefremov, 1944), western and eastern slopes (Shilin 1988); the site was noted as Kalkan on the right bank of the Ili River (Kirikov, 1928; Yefremov, 1944) or as a location near the settlement of Ayak-Kalkan (Rozhdestvensky, 1964), on the slope of the Dzhungarian Ala Tau Ridge, eastern Kazakhstan. Conglomerates. Upper Cretaceous, Santonian?- Campanian. Theropods, sauropods-titanosaurids, ankylosaurs? (noted as spines similar to spines of stegosaurs [Shilin, 1988]), hadrosaurids ("trachodonts"), which are dominant (Kirikov, 1928), and ceratopsids (Kirikov, 1928; Riabinin, 1931a; Shilin, 1988), among which there is "one fragment that may belong to a large triceratops" (Yefremov, 1957: 93; Yuryev, 1954a: 191).

138. Dzhurtan (based on A. P. Kirikov [1927]), ravine situated in the region of Chulak Ridge. Possibly a more correct name of this ravine, Dzhurtas, is given on the label of E. I. Belyaeva and M. G. Prokhorova for material from this locality; the name Dzhurmas cited by L. I. Khozatsky (1957) is probably erroneous. The ravine is situated southwest of the Kshikalkan Mountains, right part of the

Ili River basin, on the south-western slope of Dzungarian Ala Tau Ridge, Kazakhstan. Upper Cretaceous, Santonian? - lower Campanian. A. P. Kirikov (1927a,b), based on identifications by A. N. Riabinin, cites for this area hadrosaurids and ceratopsids and indicates that the latter family is "apparently represented by *Triceratops*". Dinosaurs (Khozatskii, 1957). Possibly the locality Kshikalkan (35 km north of the Chilik settlement) studied by E. I. Belyaeva and M. G. Prokhorov (Rozhdestvensky and Khozatsky, 1967) is a synonym of Dzhurtas (Dzhurtan) or is situated near it. Material from the Ili River (Gartman-Veinberg, 1928; Riabinin, 1938: 6) possibly comes from the same region where a horn, a number of epoccipitals, and fragments of limbs and pelvis of Ceratopsia, close to *Triceratops*, were noted (Gartman-Veinberg, 1928).

139. Karacheku (Eliseyev, 1958; Rozhdestvensky, 1964), Karachek according to A. N. Riabinin (1939), Karacheko according to L. I. Khozatsky (1957: 20), on the highway between Almaty and Taldykurgan (Rozhdestvensky, 1964), region of the Zhalaman station (the occurrence of dinosaurian bones near the Zhalaman railway station is sometimes considered separately from Karacheku). The locality was cited as being situated between the right bank of the Ili River and Malaisary Mountains and Arkharly mountain pass (Shilin 1988), west-north-west (60 km in a straight line) from the Bolshoi Kalkan and Malyi Kalkan Mountains (Kirikov 1927a,b), Kazakhstan. Conglomerates of the Upper Cretaceous, Santonian - lower Campanian, or of younger age within the Upper Cretaceous. Lower jaw of *Tarbosaurus* aff. *T. bataar* Malyeyev that belonged to *Tyrannosaurus* (Khozatsky, 1957; see also footnotes presumably made by V. S. Bazhanov for that article). For this locality or for Dzhurtas (Dzhurtan), the following groups were identified: “deinodontids”, ornithomimids, sauropods? (titanosaurids), stegosaurs?, ankylosaurs (acanthopholids) (Yefremov, 1944); records of the latter two groups may belong to ankylosaurs. Hadrosaurids (Yefremov, 1932) and large dinosaurs (Nurumov, 1964) were cited. A. P. Gartman-Veinberg identified Ceratopsidae (Yefremov, 1932, 1944), and A. N. Riabinin (1939: pl. XIV, fig. 2) cited a tibia of cf. Ceratopsia.

140. Sinegorsk (earlier known as Toyochara-gun), southern Sakhalin, Russia. Lower part of the Krasnoyarkovsk Formation. Upper Cretaceous, lower Campanian (D. A. Russell, personal communication, 1988) or Maastrichtian (Rozhdestvensky, 1977) or Campanian - middle Maastrichtian (Nessov and Golovneva, 1990). Level Mh7 or Mh6 of Mikho group, upper Coniacian - lower Santonian (Weishampel et al., **[108/109]** 1990a: 558) or late Santonian - early Campanian (ibid.: 129). Incomplete skeleton of *Nipponosaurus sachalinensis* (Nagao 1936, 1938) of lambeosaurines (subfamily of hadrosaurids) was found in a mine and is deposited in Japan.

141. Dzhetymtau II, ridge in the Central Kyzylkum, Uzbekistan. Conglomerates at the base of Dzhetymtau bed. Upper Cretaceous, lower Campanian? Carnosaurs, hadrosaurids (collections of E. M. Shmariovich).

142. Kyrkkuduk II*, northern foot of Alym Tau Ridge south of the Kyrkkuduk well, site "Gray Meza", southern Kazakhstan. Lower Darbazin subformation. Gray sandstones and sands. Upper Cretaceous, lower Campanian? - middle Campanian. Small theropods with densely serrated teeth and others with large serrations on teeth (cf. *Troodon* sp.)*, other theropods*, hadrosaurids* (mostly newborn and young, represented by teeth), and bones of dinosaurs* (discoveries by A. O. Averianov). American elements in the assemblage are represented by a dinosaur similar to *Troodon* and the crocodylian *Brachychampsa*. The presence of the latter genus is established in Asia for the first time; in North America, it is represented from the Albian through the Eocene.

143. Shurab*, Southern Fergana, Tadzhikistan. Upper Cretaceous, Senonian. Small dinosaurs (Khozatsky, 1957).

144. Karaoi (Karoi according to V. S. Bazhanov and B. I. Eliseyev [1958] and A. K. Rozhdestvensky [1973]), region of the Sarykuduk well near the settlement of Aksukuduk, left bank of the Ili River, northwest of Iliisk Station (Yefremov, 1944), Kazakhstan. Conglomerates of the Upper Cretaceous, Senonian. Ornithomimids, hadrosaurids (Yefremov, 1944). Chemical analysis of dinosaurian bones from here was made by B. S. Bazhanov (1947).

145. Kapchagai, region where the Kapchagai reservoir and Kapchagai city are now situated. Upper Cretaceous, Senonian. Bones of reptiles (Shilin, 1988), probably dinosaurs.

146. Tuzukul (southern edge of Moin-Kumy, Rozhdestvensky 1964) and Ashekol Lake situated near the eastern slope of the Karatau Ridge (Rozhdestvensky and Khozatsky, 1967; Rozhdestvensky, 1973), Kazakhstan. Green sandstones and conglomerates. Upper Cretaceous, Senonian. Hadrosaurids (Yefremov, 1944; Yuryev, 1954a; Rozhdestvensky and Khozatsky, 1967).

147. A series of localities or one locality between Chingeldy (this is not the location noted in Part 4.1.3.108) and Karachok (see Karacheku, Part 4.1.3.139), approximately 2 km from Karachok station along the old post road (Kirikov, 1927a), near Kopalroad (Kopa?) - Almaty, near northwestern slopes of the Chulak Mountains (Kirikov, 1927a) where remains of hadrosaurids and ankylosaurs were found (the latter are cited as Stegosauria [Riabinin 1939: 5, 6], but see Part 4.1.3.137 and 4.1.3.138 as possible synonyms), Kazakhstan. Conglomerates with petrified wood. Upper Cretaceous, Senonian. Remains of hadrosaurids and also bones that were attributed to stegosaurs but possibly belong to ankylosaurs.

148. Kushmurun* (sand-pit "Priozernyi"), Kustanai Region, Kazakhstan. Gray sandstones with gravel and phosphorites at the base of gray-colored layer, belonging to the Zhuravlevskaya(?) Formation. Upper Cretaceous, upper Santonian -- lower Campanian or upper Campanian - ?lower Maastrichtian. Remains of hadrosaurid, cited as *Hadrosaurus* sp., in marine assemblage (Prizemlin, 1993). These data need verification.

149. Baituma, Tastau mountains (2,200 m above sea level), Dzungarian Ala Tau Ridge, Kazakhstan. Sands and gravels of the Sasykkol Formation. **[109/110]** Upper Cretaceous, presumably upper Senonian or Campanian - lower Maastrichtian. Material from prospecting pit. Coelurosaurids (identification by B. V. Prizemlin, oral communication from E. G. Kordikova).

150. Several locations in the Volgograd Region including those near the farmstead Polunino, Russia. Upper Cretaceous, Campanian - Maastrichtian. Among the discoveries by A. A. Yarkov from this locality, there are fragments of bones that in tissue structure and shape resemble those of

theropods, sauropods, and armatosaurs. The remains, if they indeed belong to these groups, are relevant for the composition of the fauna of Fenno-Sarmatia from where large theropods are already known in southern Sweden (Persson, 1959), armatosaurs(?) from locality Ivo-Klak, and a small ornithischian (author's observations) form the locality Asen (upper part of the lower Campanian).

151. Kakanaut*, left bank of the river, basin of Pekulnei Lake, Chukot Autonomous Area, Russia. Upper part of the Kakanaut Formation. Upper Cretaceous, middle Maastrichtian (Nessov and Golovneva, 1990; Fedorov and Nessov, 1990). This is the northernmost and easternmost locality for dinosaurian remains in the country and in Asia (Nessov, 1990, 1992). Theropods *Troodon* sp. cf. *T. formosus* Cope** (Troodontidae) (North American element in the fauna), hadrosaurids (lambeosaurines?)**, traces of damage to hadrosaurid bones by teeth, presumably from large theropods**, a part of split bones may come from pellets of large theropods. On the right bank of the Kakanaut River, near the Perevalnyi stream, the fossilized spongy part of a large bone, possibly of a dinosaur*, has been found (Nessov and Golovneva, 1990).

152. Blagoveshchensk*, southern part of the city, Amur Region, Russia. Lower (or middle?) part of the Tsagayan Formation. Upper Cretaceous, middle Maastrichtian (Nessov and Golovneva, 1990), rather than Cenomanian - lower Senonian (Bolotsky and Moisyeyenko, 1988), because the complex includes turtles of the genus *Mongolemys*. This material, without doubt, dates to the Cretaceous, because sometimes bones of the postcranial skeleton are found in natural articulation with each other in this locality (Bolotsky and Moisyeyenko, 1988); remains here are not redeposited into Quaternary deposits (Rozhdestvensky 1957). Small theropods (Rozhdestvensky, 1957), troodontids, tyrannosaurids (Bolotsky and Moisyeyenko, 1988), the latter probably belong to *Tarbosaurus* sp.*, sauropods*? (one fragment of a narrow and long tooth)*. Large hadrosaurids (Rozhdestvensky, 1957; Bolotsky and Moisyeyenko, 1988) were preliminarily related to *Bactrosaurus* and *Aralosaurus* (Bolotsky, 1988). Identification is refined to a representative of Lambeosaurinae that had similarity with *Corythosaurus,* named *Amurosaurus riabinini* Bolotsky et

Kurzanov (nomen nudum?) (Bolotsky, 1990b), the second form is apparently referable to Saurolophinae (Bolotsky, 1990a). Fragments of dinosaurian bones are supposedly from pellets of large theropods. For data on the Sagibovskii Boguchan and Kordon elevations (Amur Region) see Part 4.5.202.

153. Taizhuzgen II (see also 4.3.180), left bank of the river, southern Zaisan Basin, Eastern Kazakhstan. North Zaisan Formation? Upper Cretaceous? Strongly weathered fragments of bones, possibly of dinosaurs. Fragments of bones and supposedly a splinter of a large tooth with thin enamel cover cited as "remains of dinosaur fauna" were found on the right bank of the western river head of the Taizhuzgen River slightly more **[110/111]** than 1 km southwest of deposits of bentonitic clays close to the place of contact between red-brown clay and quartz sand, on the sand slope (Bazhanov, 1973: 23).

154. Besh-Kosh, apex of the mountain, vicinity of Bakhchisarai, Crimea. Marine Deposits (glauconitic limestones). Upper Cretaceous, Maastrichtian rather than Danian, as was indicated in the original description of the remains (Riabinin 1945, 1946). Limb bones - part of femur, tibia 680 mm in length, metatarsals II and III, phalanx of a relatively small Hadrosauridae indet. (Weishampel et al., 1990a). The remains were described by A. N. Riabinin (1945, 1946), indicating a light skeletal built of the animal and small size unlike that of closely related hadrosaurids of the Late Cretaceous in Hungary and Netherlands. A. N. Riabinin proposed to name the dinosaur *Orthomerus weberi* Riab. in honor of G. F. Weber who had found these remains. This name should be emended to *O. weberae* Riab. In spite of the relatively low information value of hadrosaurid limbs for taxonomy, the materials still appear sufficient to determine the systematic position of the animal within the family on the basis of comparison of the bones rather than figures (Riabinin, 1945: fig. 1, pls. I-II; Riabinin, 1946: fig. 1).

155. Astashikha*, village on the right bank of the Bureya River in the area exposed beneath the former chapel at low water level in the river, Amur Region, Russia. Lower-middle part of the Tsagayan Formation or Arkharin Formation. Upper Cretaceous - lower Paleogene, Maastrichtian -

Danian. The material was apparently erroneously cited as redeposited into Neogene or Quaternary deposits (Rozhdestvensky, 1957). Large bone of dinosaur, possibly from pelvis (Rozhdestvensky, 1957; Krishtofovich and Baikovskaya, 1966; Bolotsky and Moisyeyenko, 1988; Nessov and Golovneva, 1990). Bony remains were first discovered at this site by A. Ya. Gurov.

156. Karaburinak, Central Kyzylkum, Uzbekistan. Upper Cretaceous. Bones of dinosaurs (collection of A. P. Vadilo).

157. Ktai (upper part of the river basin; Rozhdestvensky, 1964: 236), third dry ravine southwest of the Kokkiya River, southwestern slope of Karatau Ridge, Kazakhstan. Upper Cretaceous? Four articulated vertebrae of dinosaurs (oral communication from O. A. Fedorenko).

158. Maibulak, well 20-30 km west of the Bogdog meteorological station, Karatau Ridge, Kazakhstan. Upper Cretaceous? Dinosaurs (oral communication from S. T. Mursalimov).

159. Tebinbulak, Southwestern Kyzylkum, Karakalpakistan. Cretaceous. Large bones, possibly from dinosaurs (collections of I. M. Abduazimova).

160. Region of Guberlin mountains, specifically northwest of the Guberlya Mountains (Rozhdestvensky, 1973), northwest of the city of Orsk, right part of Ural River basin, Southern Ural region. Upper Cretaceous, Senonian. Tall, relatively short centrum (notably damaged) together with remains of mosasaurid lizards or in adjacent layers (Bogolyubov, 1912). The centrum was provisionally attributed to Acanthopholoidea and referred to the trunk region (Bogolyubov, 1912). With equal probability, it has been attributed to a marine reptile (Rozhdestvensky, 1973), but without indication of the systematic group. Referral to plesiosaurs seems to be excluded because of the great height of the centrum. It is not an ichthyosaur either because of the absence of the amphicoelous condition and because ichthyosaurs no longer existed in the Senonian. However, the short centrum and its notable height could have been characteristic of the caudal part of some but not all mosasaurids. **[111/112]** N. N. Bogolyubov (1912) did not note the procoelous state of the centrum and, at the same time, described similar uneven knobby anterior and posterior articular surfaces (in mosasaurids, in the absence of pathological changes, these surfaces are largely

smooth). This seems to indirectly contradict identification of the centrum as belonging to a mosasaur. Unlike in mosasaurids, the lateral surfaces of the vertebra, as noted by N. N. Bogolyubov (1912), are concave and have holes (with a diameter up to 5 mm: two on one side and one on the other) (cf. Weishampel et al., 1990a: fig. 22.7, I).

See also regarding bony remains from the Cretaceous in Part 4.3.183.

On the discovery identified as an imprint of dinosaurian skin, see Part 4.5.200.

4.2. Remains of Cretaceous dinosaurs, redeposited into Paleogene-Neogene deposits

161. Kok-Moinak* (Kokmuinak), eastern part of the Boam ravine (sometimes cited as its middle part), basin of the Chu River, Kirghizia. An isolated outcrop of conglomerates between rocks of the Paleozoic and Oligocene - Neogene red-colored deposits. I. A. Yefremov (1944) identified from there “deinodontids”, ornithomimids, and hadrosaurids. Possibly the material was redeposited into the Suluterek (Oligocene?) or Dzhetyoguz (Miocene) formations (Yefremov, 1944; Tarasov, 1968; Stratigraphic Dictionary, 1982: 328). Redeposition of dinosaurian remains from the Cretaceous into the Miocene has already been reported in the literature (Buffetaut et al., 1980). In 1981, the author did not succeed making new discoveries here. This site is shown on the map by a point approximately corresponding to Kok-Moinak (Weishampel et al., 1990a: locality 356a) does not belong to the Yalovach Formation and its age is not Late Cretaceous (Turonian - early Santonian). The composition of the assemblage cited for Kok-Moinak is identical with the number 355b, which is placed in the cited work on the territory of Tadzhikistan and apparently should called Kansai. However, the composition of the assemblage with this number does not correspond to Kansai, whereas locality 355a better fits the Kansai locality in terms of its composition, considering the reference to lambeosaurines (?=*Jaxartosaurus* sp.). The cited work contains a series of mistakes.

For data on the locality in the vicinity of settlement of Kochkorka (Kirghizia) see Part 4.5.201.

162. Aitym, 15 km from the Aitym settlement on the southern slope of the Altyntau Ridge, Central Kyzylkum, Uzbekistan. Collections are probably mixed (Khozatsky, 1957) and contain Upper Cretaceous and Paleogene fossils. The deposits were cited as upper Mesozoic (Rozhdestvensky and Khozatsky, 1967). Remains of dinosaurs.

163. Khodzhakul II*, surface of the high plateau east and north-east of the depression formerly occupied by Khodzhakul Lake, Southwestern Kyzylkum, Karakalpakistan. Sands with phosphorites, upper Paleocene. Mixture of remains of Paleogene and Late Cretaceous vertebrates. Noted among the latter are bones of *Asiaceratops* sp.*, different unknown protoceratopsids of similar age **[112/113]** (Pl. V, fig. 20) and turtles evidently redeposited from the Upper Cretaceous (Cenomanian) sediments.

164. Dzhaman-Kokcha II*, range east of the Sultan-Uvais (=Sultan-Uiz-Dag) Ridge and north of the fortress Kurgashinkala, Southeastern Kyzylkum, Karakalpakistan. Upper Paleocene. Bones of dinosaurs** redeposited from the Upper Cretaceous (Turonian-Santonian).

165. Baibishe II*, North-Eastern Aral region, Kazakhstan. Plateau 3 km north of the Baibishe well. Eroded bones of dinosaurs from the Late Cretaceous redeposited into upper Paleocene phosphate-bearing sands.

In the lower Syr Darya region, dinosaurian bones from the Cretaceous are known that were redeposited in the base of the Paleogene occurring on Turonian-Santonian (Nikiforova, 1960: 82).

166. Region of the Baibolat* well and Shakh-Shakh* Mountains, North-Eastern Aral Region, Kazakhstan. Reworked bones of dinosaurs in the lower part of marine Paleogene (data of T. N. Nurumov).

4.3. Eggs, clutches, and shell of dinosaurian eggs from the Cretaceous

167. Sarykamyshsai II*, creek near the city of Tashkumyr on the left bank of the Naryn River, 2.3. km up from the mouth of the brook, Kirghizia. Lower part of the Khodzhaosman Formation, 10-12 m from its base. Lower Cretaceous, Aptian or upper Aptian. Crest-patterned,

angusticanaliculate shell of small, slightly elongated eggs** (from psittacosaurids? or iguanodontids?) (Nessov and Kaznyshkin, 1986).

168. Balabansai II*, 4-5 km north-west from the city of Tashkumyr on the right bank of the Naryn River, Kirghizia. Red sediments in the lower part of the Khodzhaosman Formation, 4 m, 5 m, 13-16 m and 20 m above its foot. Lower Cretaceous, Aptian or upper Aptian. Same type of shell** of dinosaurian eggs as for Sarykamyshsai. A clutch of eggs of dinosaurs** has been found 5 m above the base of the formation; it is the only one known in the CIS with shell of the same type (Nessov, 1985a; Nessov and Kaznyshkin, 1986: fig. 2A; Nessov, 1988b: fig. 3, 2).

169. Beltau (Daugyztau III)*, ravine near sand-pits 7 km north-north-west of the settlement of Daugyztau, Central Kyzylkum, Uzbekistan. Red sandstones 7-17 m from the floor of the ravine. Upper Cretaceous, upper Turonian - Santonian. Specific type of shell** (Nessov and Kaznyshkin 1986: fig. 1A, A; Nessov, 1988b).

170. Arslanbob*, western outskirts of the settlement, Northeastern Fergana, Kirghizia. Yalovach Formation. Upper Cretaceous, Santonian. Smooth shell, 0.2 mm thick, similar to shell attributed to birds *Gobipteryx*** from the Campanian of Mongolia (Nessov, 1992c); crest-patterned shell, 0.4-1.6 mm thick, from elongated eggs (of hadrosaurids?)** (Nessov and Kaznyshkin, 1986; Nessov et al., 1990).

171. Charvak* left bank of the Karaungur River. Northeastern Fergana, Kyrgyzstan. Yalovach Formation. Upper Cretaceous, Santonian. Crest-patterned, knobbed shell of elongated eggs (belonging to hadrosaurid?)** (Nessov and Kaznyshkin, 1986; Nessov et al., 1990).

172. Balabansai III*, 4-5 km north-west of the city of Tashkumyr down the dry river bed from the locality noted in part 4.3.168, Kirghizia. **[113/114]** Clayey sandstones with gravel in the Yalovach Formation. Upper Cretaceous, Santonian. Several levels with shell of dinosaurian eggs of different types, including shell noted above, supposedly from hadrosaurs**, and also thin, angusticanaliculate shell, probably from small theropods**, and shell of the foveocanaliculate

variant of the prolatocanaliculate type (belonging to ceratopsids?)** (Nessov, 1985a; Nessov and Kaznyshkin, 1986).

173 and 174. Kichiachisai* and Karasai*, valleys 8-10 km north-west of the city of Tashkumyr, Northern Fergana, Kirghizia. Yalovach Formation. Upper Cretaceous, Santonian. Crest-patterned, knobbed shell of (hadrosaurs?)** and shell of dinosaurs with convex, rounded pustules on the outside**, other types of shell (Nessov and Kaznyshkin, 1986).

175. Balabansai IV*, 4-5 km north-west of the city of Tashkumyr, Northern Fergana, Kirghizia. Clays with gravel and sand in the lower part of the Nichkesai Formation. Upper Cretaceous, lower Campanian. Several levels with dinosaurian eggshell of different types (Nessov and Kaznyshkin, 1986) among which there are compact accumulations of chemically corroded shell (normally it is light) attributed by the author to hadrosaurids (?)** and possibly coming from pellets of consumers of eggs and clutches (theropods or ankylosaurs?).

176. Dzhiddasai II*, lower part of the basin of dry river beds, 6-7 km north-west of the city of Tashkumyr, Northern Fergana, Kirghizia. Lower part of the Nichkesai Formation. Upper Cretaceous, lower Campanian. Different types dinosaur eggshell (Nessov and Kaznyshkin, 1986; Nessov, 1992c).

177. Naryn*, right and left banks of the river in Tashkumyr city, accessible prior to inundation by the waters of the reservoir in 1992-1994, Northern Fergana, Kirghizia. Shell attributed to hadrosaurids(?)** (Nessov and Kaznyhskin, 1986).

178. Mountain pass* (more exactly, area in front of the mountain pass) along the road from Tashkumyr to Karavan, outcrops left of the road, Northern Fergana, Kirghizia. Lower part of the Nichkesai Formation. Upper Cretaceous, lower Campanian. Thin, smooth fragments of shell of the angusticanaliculate type (belonging to theropods or birds?)** (Nessov and Kaznyshkin, 1986).

179. Koshbolot* (=Shakaptar, =Shakhaptar) (Nessov, 1988a: 98) south of the Shakaptar settlement and east of the road, Northwestern Fergana, Kirghizia. Lower part of the Nichkesai Formation (Nessov and Kaznyshkin, 1986; Nessov, 1988a). Upper Cretaceous, lower Campanian.

Dominance of crest-patterned, knobbed shell of specific type (from hadrosaurids?)** and presence of a number of other types resembles associations of remains of eggs from the Zaisan Basin in Kazakhstan and from Hunan Province, People's Republic of China.

180. Taizhuzgen I (left bank of the river) (Bazhanov and Kozhmakulova, 1960; Bazhanov, 1961) south of Zaisan Basin, Kazakhstan. Three or four localities were noted: "2 km up the mouth of the river head of [r.] Sargamys" (Bazhanov 1973: 23), 1.5 km east of this location, 2.5 km up the mouth of Sargamys; a locality was also cited for the right bank, west of the mouth of the Taizhuzgen River (approximately 1 km south-west of deposit of bentonitic clays) (see also locality 4.1.3.153). Lower part of the Northaisan Formation (earlier called Manrak Formation). Upper Cretaceous, lower Campanian - ?Maastrichtian. Shell of two or three species of dinosaurs (Nurumov, 1964); currently no fewer than eight types of eggshell are known from this locality (Nessov and Kaznyshkin, 1986; Nessov, 1988a). Dominant here (Khozatsky et al., 1977; Verzilin and Rogozina, 1981) is knobbed shell of elongated eggs belonging to the form family Elongatoolithidae and form genus *Elongatoolithus* Zhao,1975. **[114/115]** Such shell apparently comes from advanced Asian hadrosaurids rather than theropods (Mikhailov, 1991) or protoceratopsids (Rozhdestvensky, 1971). This shell has received a new generic name *Dinosauriovum* Vialov, 1975, with form subgenera *Dinosauriovum*, *Grumuliovum,* and *Orantiovum* (Vialov, 1986). Diagnoses of a part of these subgeneric taxa contain characters in which characters of the external relief of the near-pole and equatorial parts of one egg differ. This shell from Taizhuzgen cannot be attributed to *Protoceratops* sp. (Rozhdestvensky 1971: 30) because it does not belong to the type attributed to this genus of dinosaurs in Mongolia (locality Bain-Dzak). The latter, in turn, cannot be attributed to hadrosaurids.

181. Area between the rivers Kusto and Taizhuzgen (Verzilin and Rogozina, 1981), southern part of Zaisan Basin, Kazakhstan. North Zaisan Formation, slightly higher level of formation than in Taizhuzgen (N. N. Verzilin, oral communication). Upper Cretaceous, lower Campanian - ?Maastrichtian. There are several types of shell: shell with crests on the equatorial regions of the

eggs and shell with knobs on the near-pole parts, which probably belonged to hadrosaurids*, are dominant (collections of N. N. Verzilin).

182. Chimkent, 20 km south-west of the city, South Kazakhstan. The level probably corresponds to the Temirchin Formation (O. A. Fedorenko, oral communication). Upper Cretaceous, upper Senonian. Two fragments of eggshell of dinosaurs from the core of a borehole (Bazhanov, 1961; Nurumov, 1964). One specimen belongs to crest-patterned morphotype (from hadrosaurids?)*, another has pustules on the external surface as does one of the types of the shell in the lower part of the Nichkesai Formation of the Fergana Depression.

Eastern Kyzylkum. Upper part of the Bosagin Formation, not Danian - lower Paleocene (Stratigraphic Dictionary, 1979), but Upper Cretaceous, Campanian - Maastrichtian. Because the Bosagin Formation is regarded as an analogue of the Temirichin Formation (Stratigraphic Dictionary, 1979), based on an oral communication of O. A. Fedorenko, this may be a incorrect reference to the same locality that had already been noted for the vicinity of Chikment (shell in borecore).

183. Glinovka, vicinity of the settlement, eastern Kazakhstan. Upper Cretaceous. Fragments of shell(?), possibly of dinosaurs, bones of large reptiles (E. G. Kordikova, oral communication; data require verification).

4.4. Tracks of dinosaurs

4.4.1. Jurassic

184. Ravat (=Rabat) settlement in the valley of the River Yagnob (=Yagnau), close to the right bank, near side of the former road from Dushanbe to Khodzhent, along the stretch from the Ravat bridge to Kugi-Malek mountain, Zeravshan Ridge, Tadjikistan. Lower part of the Dzhirukut Formation. Middle Jurassic rather than Upper Triassic (Rhaetian) as sometimes cited (Romanovsky, 1882; Yuryev, 1954a: 187 and fig. 1) and Upper Jurassic (Rozhdestvensky, 1964b). Tridactyl tracks (8 specimens) with long center digit. They were called *Brontozoum tianschanicum*

Rom. in the original description. Tracks were found by G. D. Romanovsky (1882: pl. X, 1; 1884, 1890) and P. A. Chuenko. The Latin binomen was initially given to an animal rather than to tracks. For three pairs of tracks, step length was determined by A. K. Rozhdestvensky **[115/116]** (1964a). L. K. Gabuniya and V. V. Kurbatov (1988) believed that the tracks were left by carnosaurs. During the reconstruction of the road, the tracks were destroyed. These were rediscovered close to that area, approximately 120 specimens; approximately 40 are now left. According to A. K. Rozhdestvensky (1964a, 1969: figs. A-C on p. 247), the prints from three track-bearing horizons (Amanniyazov et al., 1987) belong to bipedal carnosaurs and coelurosaurs and quadrupedal pentadactyl (based on the figures, tetradactyl and pentadactyl) stegosaurs(?) and bipedal camptosaurs. Recently, three horizons with tracks were discovered here (Novikov and Sapozhnikova, 1981; Baratov and Novikov, 1984). Tetradactyl and pentadactyl tracks were found. Described from here is *Ravatichnus kotshnevi* Gab. et Kurb. (left by a "foot-walking" quadruped with a pentadactyl foot, possibly a representative of sauropods). Tracks of the type noted by G. D. Romanovsky were redescribed on the basis of differences from type tracks of *Eubrontes* (=*Brontozoum*) as *Gabirutosaurus tianschanicus* (Rom.); later, the name was changed to *Gabirutosaurichnus* (because it is an ichnogenus) and the tracks were attributed to the Carnosauripodidae fam. nov. (Dzhalilov and Novikov, 1993). These tracks indicated a gregarious mode of life and also tetradactyl condition because of the small digit I that does not always touched the substrate (Gabuniya and Kurbatov, 1988: fig. 3). Described from here are also tracks of *Coelurosaurichnus romanovskyi* Gab. et Kurb. (Gabuniya and Kurbato, 1988), which were probably left by coelurosaurs. Also tracks of *Ravatosauropus rozhdestvenkyi* Dzhal. et Novik were named from this area; it was not possible to classify these tracks with any group and they were left as incertae sedis (Dzhalilov and Novikov, 1993). Tracks left by camptosaurs were called *Camptosauropus vialovi* Gab et Kurb.; they were attributed to the ichnofamily Iguanodontopodidae (Dzhalilov and Novikov, 1993).

185. Shirkent II (Novikov and Radililovsky, 1984; Amanniyazov et al., 1987; Gabuniya and Kurbatov, 1988; Novikov and Dzhalilov, 1988), upper reaches of the left tributary of the Shirkent

River, 4 km east of the settlement of Kyrgyzkishlak, Tadzhikistan. Lower part of the Kugitang Formation. Middle Upper Jurassic, middle upper Callovian - lower Oxfordian. Approximately 300 tracks in two track-bearing horizons (approximately 170 in the lower). Among these, there are distinct tridactyl tracks of *Shirkentosauropus shirkentensis* Dzhal. et Novik. (Dzhalilov and Novikov, 1993) with narrow, nearly parallel phalanges (sizes of tracks ranging from 48 x 34 to 52 x 36 cm, length of step approximately 1 m). Other tracks - *Regarosaurupus manovi* Dzhal. were also tridactyl, but smaller (26 x 16 cm) with pointed posterior part and broadly separated prints of side phalanges; the center digit tapers (presence of a long claw is possible). Both types of tracks were left by theropods. A third type of tracks, *Microsauropus tursunzadei* Dzhal. et Novik. (family incertae sedis) (Dzhalilov and Novikov, 1993) with imprints of three short phalanges, was possibly left by sauropods, but there are doubts concerning identity of the dinosaurs producing this particular type (Gabuniya and Kurbatov, 1988). Tracks at localities 184 and 185 may belong to the species of dinosaurs already known by remains of teeth and bones in parts 4.1.1.2.-4.1.1.9.

186. Kharkush, northern part of the basin of Shirkent River, Tadzhikistan. [Cover] of sandstones of the Karabil Formation. Upper Jurassic, Tithonian? Five trackways of 29 tridactyl imprints of large theropods (imprint of "pes" 72 cm in length, 60 cm in width), possibly of undescribed ichnospecies of *Megalosauropus* (Gabuniya and Kurbatov, 1988; Novikov and **[116/117]** Dzhalilov, 1988) or *Kharkushsauropus kharkushensis* Dzhal. et Novik. from the ichnofamily Iguanodontopodidae (Dzhalilov and Novikov, 1993).

187. Khodzhapil-Ata (= Khodzha-Efil-Ata, Gabuniya and Kurbatov, 1984; = Khodzhaipil, Sedletsky, 1983b), northwestern slope of Kugitangtau Ridge, southeastern Turkmenistan. Limestones. Upper Jurassic, middle Oxfordian (Amanniyazov, 1984; Amanniyazov et al., 1987), or Middle Jurassic, middle and upper Callovian, of the Kurek Formation of the Kugitang Series (Gabuniya and Kurbatov, 1988). The extent of the locality with discoveries of tracks is approximately 10 km. Based on 2,500 to 2,860 tracks have been discovered on 11 track-bearing surfaces, some dinosaurs were moving in groups of several individuals (Sedletsky, 1983a,b; Amanniyazov, 1985,

1986; Amanniyazov et al., 1988; Gabuniya and Kurbatov, 1988). Tracks of a large, bipedal theropod called *Turkmenosaurus kugitanensis* Aman. 1985, which had a short center digit. Another smaller theropod with a longer center digit left the tracks of *Chodhapileosaurus krimholzii* Aman., 1985. The tracks of a bipedal, tetradactyl, and digitigrade dinosaur are called *Gissarosaurus tetraphalangensis* Aman., 1985. It has an arc-shaped imprint behind the tracks of digits. These tracks, in our opinion, were possibly left by a segnosaur (Segnosauria)* or a closely related form (see also part 4.4.2.194). One should bear in mind that the remains of segnosaurs proper are so far known only from the Cretaceous, although the group was obviously related morphologically to relatively close Late Triassic - Early Jurassic ancestors, most probably among the prosauropods (see Part 1.1).

Names of ichnogenera established for this locality were also used in Cyrillic (Amanniyazov, 1986). The tracks are made in shallow water, showing, in some parts, ripple marks. L. K. Gabuniya and V. V. Kurbatov (1988) noted for one of the types of tracks from this locality very small differences from *Megalosauropus uzbekistanicus* Gab. et Kurb., already known from the Jurassic of Kharkush and Tashkurgan. The differences are so small that as the two aforementioned authors believe that such tracks from Khodzhapil-Aty can be identified with those already known (Gabuniya and Kurbatov, 1988: fig. 10). In the region of the settlement of Khodzhapil-Ata, tracks of animals have been observed; these were regarded by V. I. Sedletsky (1983b) to be more closely related to iguanodontids. They are reminiscent of *Camptosauropus* from Ravat (Gabuniya and Kurbatov, 1988: fig. 9), but are larger. Also other tracks of ornithopod type were noted, but these are of smaller size (length of tracks 30 cm, step length 100 cm).

188. Chagyl, locality in southern Turkmenistan (Tuarkyr Ridge). Continental, coal-bearing Chairlin Formation of the upper Salakhbek subseries. According to V. A. Prozorovsky (oral communication), the level probably belongs to the Middle Jurassic, Baiocian. One tridactyl track of a dinosaur (Elfimov et al., 1991); no cast was made, but a photo is available.

189. Bolshoi Balkhan, elevation in western Turkmenistan. Upper Jurassic (Amanniyazov et al., 1987: 3). Tracks of dinosaurs.

190. Tashkurgan, south-western part of Hissar Mountains (Akkabak Mountains), 3.5 km south-east of the settlement of Tashkurgan (Amanniyazov et al., 1987) up the left edge of sai [sai = creek] Amir-Temir near the place where it is joined by Mergandar brook, Uzbekistan. Uppermost layer of limestones of the Kurek Formation of the Kugitang Series. Upper Jurassic, Oxfordian - lower Kimmeridgian (Amanniyazov et al., 1987) or upper Oxfordian (as the uppermost layer of the Kugitang Formation?) (Gabuniya and Kurbatov, 1988). Tracks of *Megalosauropus uzbekistanicus* Gab. et Kurb., 1982 (Amanniyazov et al., 1988: fig. 12B; Martinson, 1990) - ichnospecies **[117/118]** of large, tridactyl carnosaur (more than 48 tracks) with a step length of 1.2-1.6 m. There are also smaller tracks (of young individuals or other, most probably carnivorous dinosaurs) in this area.

191. Khodzha-Karshavar (Tashmush), 100 km north-east of Tashkurgan. Coastal lagoonal deposits of the Upper Jurassic. Several dozens of poorly preserved tridactyl tracks similar to the tracks from Tashkurgan (Amanniyazov et al., 1987). This locality was referred to as Khodzha-Karshavar (Novoselsky and Novoselskaya, 1993) on the upper Tashmush River. Tracks in that area were observed in limestones of the Tupolang Formation on the southern slope of the Hissar Mountains, Surkhandarya Region, Tadzhikistan. These tracks, according to V. V. Kurbatov, are similar to those from Tashkurgan. A tooth of dinosaur (probably lost later) and two groups of tracks were noted: elongated (drop-shaped) and broad in the form of a triangle with smoothed vertices. In one of the sectors all tracks are three-toed. The locality is the second in size to Khodzhapil-Ata and, in the number of tracks, is comparable to Shirkent II, but is larger than the latter in size.

192. Khingou, river in the Ridge of Peter the Great, Tadzhikistan. Zarbuz Formation. Upper Jurassic. Tracks of dinosaurs (Dzhalilov and Novikov, 1993).

4.4.2. Cretaceous

193. Sataplia, mountain 6 km north-west of the city of Kutaisi, Georgia. Limestones of the lower Neocomian with marine pelecypods (Gabuniya, 1952; Chabukiani, 1960). Lower Cretaceous. *Satapliasaurus* [*Satapliasauropus*] *tschabukianii* Gab. (Gabuniya, 1951, 1952, 1956, 1958). Name (binominal, Latin) originally was formed for the animal that left tracks, but not for the tracks proper (Gabuniya, 1951). This name may be a senior synonym (Haubold 1971) for tracks described as *S. dsocenidzei* Gab. and *S.kandelakii* Gab. from the same locality. Tracks of *S. tschabukianii* belonged to bipedal dinosaurs with relatively sharp unguals on digits II-IV; the claw of digit I is turned backwards and situated above substrate surface. Their similarity to tracks of *Columbosauripus* from the Upper Cretaceous of Canada is noted. It is established that these animals were running fast and were intermediate in the structure and size of hindlimbs between coelurosaurs and the large Late Cretaceous predators (Gabuniya, 1956). Several versions of spelling of both parts of the binomen of the ichnospecies are on record, including those in combination with the generic name *Sathapliasaurus* (Gabuniya, 1956).

Two meters above the noted level, tridactyl tracks with short digits turned forward have been found; these were supposedly left by camptosaurs (Gabuniya, 1951, 1956). These tracks were compared to *Dakotosauripus* (Haubold, 1971: 104) (see also Part 4.1.2.35).

194. Shirkent I (Novikov and Radililovsky, 1984; Amanniyazov et al., 1987), 1.5 km north of the settlement of Shirkent, near the right bank of the lower Shirkent River, southern slope of the Hissar Mountains, Tadzhikistan. Lower part of the Shirabad Formation. Lower Cretaceous, upper Albian. Two trackways (7 tracks) of imprints (half meter in length, considering long claws), supposedly of tetradactyl hindlimbs with a step length of only 72-75 cm (Zakharov, 1964; Novikov and Dzhalilov, 1988). The first digit is short or, what seems probable, its ungual phalanx could have been turned upwards. The fourth digit is long. The dinosaurian nature of these tracks, which were considered to be nine, has been questioned (Rozhdestvensky and **[118/119]** Khozatsky, 1967). The author of the first description of the tracks believed that, based on these tracks, he could distinguish a new genus and a new species of theropods (rather than ichnogenus and ichnospecies) -

Macropodosaurus gravis Zakharov (Zakharov, 1964; Novikov and Dzhalilov, 1988). These tracks resemble those left by a segnosaur* (segnosaurs are characterized by the specific structure of a tetradactyl pes with strong, narrow unguals; Perle, 1981: fig. 9) although it can also be assumed that the tracks could have been left by representatives of megalosaurids (Amanniyazov et al., 1987: 44), primarily taking into account the extreme scarcity of information on the structure of the distal part of limbs of the latter (Weishampel et al., 1990a: 203, 204, figs. 6, 29K). The name *Macropodosaurus* was replaced by *Macropodosauropus*, and the track was attributed to the ichnofamily Megalosauripodidae Vialov, 1987 (Dzhalilov and Novikov, 1993).

In connection with the possibility of a segnosaurian nature of the tracks, it is curious to note that the author of their original description (Zakharov, 1964), written when the segnosaurs were not yet known, shrewdly made the following assumptions: there could have been unknown branches among dinosaurs; the theropod that left the tracks could have passed to omnivorous feeding and had a relatively short tail; the animal had to be placed into a separate family. Taking into account all this and the possibly segnosaurian nature of these tracks and also of those noted in Part 4.4.1.187, the ichnotaxon should be called Segnosauripodidae ichnofam. nov.

One track from the locality Shirkent I resembles the imprint of a tridactyl "pes" with rounded digital pads and without traces of unguals (Zakharov, 1964).

195. Babatag II (Bulin et al., 1981; Amanniyazov et al., 1987; Novikov and Dzhalilov, 1988). Left tributary of the upper part of the Chorroksai brook, 6 km northwest of the settlement of Akmechet', Tadzhikistan. The basis of the upper part of the Luchak Formation (stratigraphically 12 m below Babatag I). Lower Cretaceous, upper Albian. Seven (Dzhalilov and Novikov, 1984) or six trackways on limestone (more than 200 tracks on the area of 10,000 square meters), among which there are bipedal, oval, tridactyl tracks, 37 cm length and with weak traces of phalanges and step length of 83 cm; tetradactyl tracks with two trackways of the same animal (distance between them is 1.4 m). The tracks of forelimbs are broad (35 x 52 cm) and those of the hindlimbs are relatively narrower (80 x 70 cm). The ichnogenus *Kafirniganosauropus* n. gen. from this location was established without

indication of a type species; therefore, this name is invalid. Described from here are also tracks of *Chorrokhsauropus khakimovi* Dzhal. et Novik., attributed to the ichnoorder Sauropodina, but it still remains unclear if they belong to a particular ichnofamily. For the same locality, tracks of *Akmechetosauropus makhamovi* Dzhal. et Novik from the ichnofamily Hadrosauripodidae are reported (Dzhalilov and Novikov, 1993).

196. Babatag I (Amanniyazov et al., 1987), right bank of the middle part of current of the Chucheli brook (slope of Khokadzhulsun Mountains) 20 km northeast of Babatag II, 45 km southwest of the settlement of Hissar, Babatag Ridge, Tadzhikistan. Upper part of the Luchak Formation. Lower Cretaceous, upper Albian. Seven (Dzhalilov and Novikov, 1984) or eight tridactyl tracks in limestone; tracks 70-86 cm in length. Possibly they were left by a small, bipedal ornithopod; the tracks were called *Babatagosauropus bulini* Dzhal. et Novik. and attributed to Hadrosauripodidae (Dzhalilov and Novikov, 1993).

On the tracks in the Cenomanian in the vicinity of the Gumatag settlement see Part 4.5.199.

On the tracks from the locality Chermozak, see Part 4.5.203.

[119/120]

4.5. Remains that should no longer be attributed to dinosaurs and localities that should no longer be regarded as those where of dinosaurian remains were found in the CIS.

197. Rivers Sharzhenga, Vetluga, Yuga, Luza, Mezen', Tsilma, and Northern Dvina in the European part of Russia and River Donguz* (197a) on the left Asian part of the Ural River Basin. Triassic. Indications of discoveries in these and several other localities in the region (Tolmatschow, 1904; Tolmachoff, 1924; Tolmachoff, 1926; Yuryev, 1954a) of remains of prosauropods, *Thecodontosaurus*, apparently belong to thecodontians and other reptiles (Rozhdestvensky and Tatarinov, 1964: 541).

On non-dinosaurian remains from the Upper Triassic or, more likely, from the Lower Jurassic, see also data on Kadzhisai locality (Part 4.1.1).

198. Aulie*, locality near the settlement of Aktas, Karatau Ridge, Kazakhstan. Karabastaus Formation. Lower part of the Upper Jurassic. A fossil (Bazhanov and Shevchenko, 1948), 44 cm in length, 103 and 165 mm wide at the ends, with internal cavity, with a thickness of walls of approximately 45 mm, was completely replaced by limestone. In sections of the external, middle, and internal parts of the sample, spongy structure was noted, and, in some places, tracts of longitudinal vessels of different diameter, both straight and branching. Absence of even traces of phosphorus in the specimen was noted. Apparently these are not remains of a theropod dinosaur (*Megalosaurus*), as V. S. Bazhanov and V. V. Shevchenko (1948) believed, because phosphate of bones in carbonates of the noted formation is not subject to dissolution. On the contrary, the buffering action of carbonates should have prevented formation of acids dissolving the calcium phosphate of bones and teeth. The fossil discussed is apparently a part of a false stem of a hay-scented fern* with numerous thin stems stretching in dense mass with fibrils. Both tubules and spongy areas are noted for such false stems (e.g., fragments of false stems of the Early Cretaceous *Tempskya*).

The feather-like structure *Praeornis sharovi* Raut. from Aulie has been attributed to a bird (Rautian, 1978), reptile (Kurzanov, 1987: 78) or even dinosaur (Doludenko et al., 1990), but the remains are most likely a complex leaf of Cycadales (Nessov, 1992c). According to local inhabitants (Doludenko et al., 1990: 23), a skeleton of a relatively small dinosaur was once found in Aulie, but was not preserved and was not studied by any vertebrate specialist.

199. Gumatag, 300 m north of the settlement, 24 km from the Baisun settlement (southeastern Hissar Mountains), Uzbekistan. Upper part of the Tyubegatan Formation. Upper Cretaceous, Cenomanian. Horseshoe-like tracks of *Gumatagichnus* (=*Bipartitipes*) *unguliformes* (Gabuniya et al., 1988), normally not oriented on the surface of sandstone. Four areas contain 5, 13, 54, and 12 tracks, respectively. Each track is 7-12 cm in length and 10-12 cm in width. They

were interpreted (Amanniyazov et al., 1987; Gabuniya et al., 1988) as tracks of unknown dinosaurs, but are probably tracks of feeding on the sand sea bottom of relatively large, semi-burrowing arthropods: Chelicerates of the family Limulidae or crustaceans. Remains of organisms in adjacent layers are marine.

[120/121]

200. Karabulak ("Sopka Otpechatok"), Zaisan Basin, Eastern Kazakhstan. An imprint of dinosaurian skin from the Mesozoic noted by V. G. Tsekhovsky for the Konurkurin Formation of this locality (Bazhanov and Kozhamkulova, 1960) was reidentified as an imprint of the external surface of the carapace of a turtle of the family Trionychidae (Rozhdestvensky and Khozatsky, 1967; Russell and Zhai, 1987); this family is known from the end of the Early Cretaceous until the present. The age of the horizon, based on other data, is middle Eocene (Paleogene).

201. Kochkorka, depression southwest of Lake Issyk-Kul, Kirghizia. A. K. Rozhdestvensky (1964) noted bones of dinosaurs from here, but did not do so in his later works. Possibly these data referred to bones of large Tertiary mammals known here and in the northwestern Issyk-Kul Region (Tarasov, 1968; Russell and Zhai, 1987).

202. Sagibovo Boguchan* (mound) on the left(!) bank of the Amur River, near village of Sagibovo, Amur Region, Russia. Discoveries of dinosaurs here, on the Russian side of the Amur River (Krassilov, 1976; Bolotsky and Moisyeyenko, 1988), were reported erroneously. The error was caused by a wrong label in the exhibition of the Central Museum of Geological Exploration (Nessov and Golovneva, 1990) referring to the discovery at the beginning of the century. In reality, the bones come from the right bank of the Amur River, on the Chinese side.

Information on discoveries of dinosaurian bones on Kordon Mountain near Blagoveshchensk (Krassilov 1976) requires confirmation, because the location of this site has not been reidentified so far during fieldwork.

The locality with bones and teeth of dinosaurs on the right bank of the Amur River ("Bely'ye Kruchi") (Krishtofovich and Baikovskaya, 1966; Bolotsky and Moisyeyenko, 1988; Nessov and

Golovneva, 1990; references in these works) belongs to China, although it was frequently noted and cited in reviews of localities from the territory of our country (e.g., Yuryev, 1954a; Rozhdestvensky, 1957; Rozhdestvensky and Khozatsky, 1967).

Taking into account data on the geology of the Amur River basin, it is likely that information on discoveries of dinosaur bones 50 km below Blagoveshchensk (Riabinin, 1925) refers to "Bely'ye Kruchi", which is situated 265 km below this city.

203. Chermozak, locality in Tadzhikistan. Tracks (obscure, poorly preserved) noted originally (Khomizuri, 1972; photo of N. N. Kalandadze) as dinosaur tracks on Mesozoic sandstone, at Kilometer 31 on the highway from Dushanbe to Kulyab, 10 km east of the Chermozak mountain pass. They were reidentified (Amanniyazov et al., 1987) as belonging to a relatively small mammal (approximately size of a lynx) of the late Oligocene age (late Paleogene). The deposits belong to the Boldzhuan Formation, outcrop of which is observed at Kilometer 30 of the highway; 25 tracks are now known in that area.

204. Concerning a discovery identified as a spine of *Stegosaurus* sp. from the Jurassic of the Vilyui River, 80 km up from the Akhtaranda River (Tolmatschew, 1904), it was later noted as not belonging to dinosaurs (Tolmachoff, 1924; Tolmachev, 1926). See comments on locality 4.1.1.11.

205. Volyno-Podoliya, Ukraine. From this region, supposedly from the Jurassic, a problematic discovery has been reported. This was identified as a tooth of a theropod of the new genus *Macrodontophion*, without reference to a specific name (Zborzewski, 1834; Weishampel et al., 1990a: 77). An Early Devonian rather than Jurassic age is suggested by the general geology of the region, by the evidence **[121/122]** (Zborezewski, 1834) that the deposits are rich in teeth of "pangolins" and "snakes", and the direct reference in the text to the "ancient red sandstone" as the source of the fossil. According to A. O. Ivanov (oral communication), teeth of Crossopterygii of the genus *Porolepis*, rather than of snakes and pangolins, are quite common in the red strata of the Dniester Series of the Lower Devonian in Podolia. The evidence against the identification of these remains as those of a theropod is as follows: The bend is situated not in the plane where the

longitudinal external crest of the crown or two such crests are situated, but rather in the plane perpendicular to this direction (the bend is present in the lingual direction, towards the inside of the mouth), which is characteristic of many fishes, but not of theropod dinosaurs. This formation is not the tooth of a vertebrate, which is evidenced by the rounded rather than pointed outline of the apex on the cast of the cavity, which could be regarded as the pulp cavity. The narrowing on the cast and also the knob of the winding crest, the latter stretching along the plane of symmetry, provide evidence against interpreting this specimen as a tooth. Of the Devonian fossils, the distal end of the pectoral fin of fishes of the group Antiarchi is most similar to the object in question.

Supplement

206. After the manuscript was completed and prepared for printing, the author and his students A. V. Guba and A. A. Timofeyev found part of the diaphysis of a femur of a theropod** (with a total body height of approximately 3-3.5 m) and a small unworn tooth of a primitive duck-billed dinosaur** (height of the animal was approximately 2 m) in the upper Albian - Cenomanian phosphate-bearing sands of the Stoilen iron-ore mines* near the cities of Gubkin and Staryi Oskol in the northeast of the Belgorod Region, Russia, in June 1994. These discoveries were made within an assemblage of marine and coastal marine fauna including the sharks *Polyacrodus*, Hexanchidae, *Eorhincodon* of the family Rhincodontidae, *Paraorthacodus*, *Synechodu*s, *Cretolamna*, *Cretoxyrhina*, *Paraisurus*, chimaeras from the families Chimaeridae, Callorhynchidae, Edaphodontidae, Ganodiidae fam. nov., and others, and also Osteichthyes, specifically Holostei indet., *Belonostomu*s, bony fishes of the family Dercetidae(?), *Apateodus,* and Teleostei indet., turtles (Toxochelyinae indet. or Macrobaenidae indet.), *Teguliscaph*a (Protostegidae), Cheloniidae indet. or Desmatochelyidae indet., ichthyosaurs *Platypterygius* (probably two species -- a small, earlier one, from the late Albian, and a large, more recent one, from the Cenomanian), small plesiosaurs of the family Elasmosauridae and large *Polyptychodon* (Pliosauroidea). Marine vertebrates inhabited this bay of the Tethys Ocean, which formed a deep inlet from the Southeast

and possessed high bioproductivity due to wind upwelling. Dinosaurs inhabited the coastal plains with areas of sandy beaches and with coastal forests, which, in some areas, formed mangrove environments. The low coastal plain areas must have received nutrients from the sea during wind-tide action and during storms. The aforementioned dinosaurs are probably late Albian in age. They inhabited the territory of Fenno-Sarmatia, which soon afterwards (Sinitsin, 1966) became separated from Asia by a longitudinal strait. Possibly the hadrosaurids migrated to western Europe from that landmass. The locality noted is only the tenth locality with remains of dinosaurs for Russia. In Figs. 8-11, it is not designated as are the subsequent localities.

In September 1994, the author, O. I. Tsaruk (Institute of Zoology, Academy of Sciences of Uzbekistan), and J. D. Archibald (San Diego State University, California) **[122/123]** collected additional material during fieldwork in the Kyzylkum, at localities that were not indicated on the maps shown in Figs. 8-11.

207. Sheikhdzheili III*, Karakalpakistan. Base of the Khodzhakul Formation. Lower Cretaceous, Albian. Caudal vertebra of primitive Hadrosauridae**.

208. Kyzylkala I*, mound (level at one third of its height) 1.2 km north-east of the settlement of Kyzylkala, southeastern elevation of the Sultan-Uvais Ridge, Karakalpakistan. Lower part of the Beshtyubin Formation. Upper Cretaceous, lower Turonian. Bones of Dinosauria indet**.

209. Kyzylkala II*, shallow ravine 7 km east-north-east of the settlement of Kyzylkala, Karakalpakistan. Upper part of the Khodzhakul Formation or Beshtyubin Formation. Upper Cretaceous, Cenomanian - lower Turonian. Caudal vertebra of Theropoda indet.** with large internal cavity.

210. Karachadalysai*, ravine on the eastern edge of the Sultan-Uvais Ridge, Karakalpakistan. Yellow sands in the lower part of the Beshtyubin Formation. Upper Cretaceous, lower Turonian or lower part of the lower Turonian. Small Theropoda**, Tyrannosauridae cf. *Alectrosaurus* sp.**, Sauropoda cf. Diplodocidae**, Hadrosauridae Hadrosaurinae indet.**

At the same locality, but 1.5-2 m above the previous level*. Black, iron-rich sandstones in the lower part of the Beshtyubin Formation. Upper Cretaceous, lower Turonian or lower part of the lower Turonian. Large Theropoda**, Ankylosauria**, Hadrosauridae**. Discovery of associated turtles *Lindholmemys* and Carettochelyidae and skate *Myledaphus* supports independence of the assemblage noted in Part 4.1.3.58.

Based on the study of the composition of the assemblages of dinosaurian remains considered (Parts 2-4 of this review), we can distinguish faunal associations, sometimes spread over vast areas. Distinctly different associations of dinosaurian eggshell are established. Localities that were not included in the list given below may reflect other complexes (intermediate in time) or they are still insufficiently known. Listed below are the associations, designated by Roman numerals (questionable ones are indicated by a question mark), and the assemblages noted in text, which are shown with Arabic numerals. I? 1?; II. 2-4, 5?, 6-9; III. 11; IV. 14; V. 17-20, 21?; VI. 24; VII? 28?; VIII. 29, 31?; IX. 37?, 39-42; X. 58?, 210; XI. 62, 70, 72?; XII; 89, 91, 94, 97?; XIII. 99,106?; XIV. 127-133; XV. 136; XVI. 140; XVII. 142; XVIII. 151, 152?; XIX? 155? Based on remains of eggshell (...), at least three associations can be distinguished: I..., 167, 168; II..., 170-172; III... 175-177, 179. At least at one locality (4.3.172), one can separate a succession of associations that succeed each other in time.

Association IX (Sheikhdzheili et al.) is similar to one known from the region of the Tsondolein-Khuduk well in Gansu Province (China), and Association XI (Dzharakuduk II and others) is very similar in composition to that from the Iren Dabasu Formation of Inner Mongolia (China). This shows the real possibility for trans-Asiatic correlations of deposits and localities by remains of dinosaurs. The discovery of remains of theropods of the genus *Troodon* and similar hadrosaurids on both sides of the present-day Bering Sea permits us to hope for establishing correlations between the two continents in the future. Along the southwestern margin of Asia, in China, Mongolia, and southeast Asia, one can also expect a large shift in dinosaurian associations from the Cenomanian to the Turonian. Discovery of such a shift would permit separating the Bainshirein

Formation by remains of dinosaurs into two parts - a Cenomanian part (e.g., the earlier **[124/125]** of the faunas at Khara-Khutul, including the turtle *Kizylkumemys*) and the Turonian - Coniacian - ?Santonian one (fauna of Shiregin-Gashuna and other locations with turtle *Lindholmemys*).

Fauna I, as the only level associated with the Lower Jurassic with its known specific dinosaurian fauna (Weishampel et al., 1990a), in the future may appear to be peculiar in the composition of the dinosaurian fauna. Dinosaurian fauna II reflects the stage that is named here Sarykamsyshsaian, and associations III and IV may appear to be endemic. Fauna V corresponds to the stage named here Murtoian. Fauna VI probably belongs to the association known in Mongolia in the Khukhtyk Horizon. In faunal complex VII, sauropods are known only from the discovery of a single tooth, but this is the first appearance of slender-toothed sauropods in the Cretaceous of Asia, which distinguishes this fauna at least from the Murtoian assemblage. Dinosaur fauna VIII is very peculiar, and its corresponding stage is named Khodzhakulian. Fauna IX corresponds to the Sheikhdzheilian stage. Fauna X is very distinctive, but unfortunately is insufficiently known. Dinosaur fauna XI corresponds to the Bissektian stage, but the association with large hadrosaurs represented in the uppermost part of the Bissekty Formation is not included into this stage. Fauna XII represents the Kansaian stage. Associations XIII and XIV are possibly geographically distinct from the Kansaian fauna, but are close to it in age. Associations XV and XVI are insufficiently known, but are possibly distinct. Association XVII represents the fauna and the Greymesian stage, whereas XVIII corresponds to the Kakanautian fauna and stage. Discoveries at the level of fauna XIX are possibly distinct for the terminal Cretaceous.

It is possible to separate the following associations and stages by types of eggshell: I ... - Balabansaian, IIs - Arslanbobian, IIIs - Koshlobotian.

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[NON-RUSSIAN REFERENCES USING THE ROMAN ALPHABET, PP. 135-143]

[SUMMARIES IN ENGLISH, GERMAN, AND FRENCH, PP. 144-145]

[145/146]

LEGENDS FOR PLATES

Three-digit specimen numbers refer to the collection No. 12457 at the Central Museum of Geological Survey of St. Petersburg: e.g., the abbreviated number 431 correlates with 431/12457. Numbers of other collections housed in this museum were not abbreviated. Numbers with RO denote specimens deposited in the osteological collections of the Department of Ornithology at the Zoological Institute of the Russian Academy of Sciences.

Plate I. Remains of dinosaurs (1-14, 16-17, 19-22), pterosaur (18), dinosaur or bird (24) and lizards (25-27), from the lower Cenomanian, Upper Cretaceous, upper part of the Khodzhakul' Formation, Sheikhdzheili locality (here and below the northern extremity of the Sheikhdzheili ridge), Karakalpakistan (23), from the upper Turonian (1, 3-8, 10-14, 17, 21-22) and Coniacian (2, 9, 16, 18-20, 24-27), the Upper Cretaceous (Bissekty Formation) Dzharakuduk locality, Uzbekistan, and teeth of carnivorous dinosaurs from the Santonian - early Campanian, Upper Cretaceous (Bostobin Formation), locality Baibishe, Kazakhstan (15). 1 - ungual phalanx of (?)forelimb, possibly from *Alectrosaurus* sp., site CDZH-14a, No. 431, x 1; 2 - trunk vertebra, possibly from *Alectrosaurus* sp., site CBI-5a, No. 432, x 0.4; 3-12 - teeth of theropods (some of these – 5-6, 8 - may belong to *Alectrosaurus* sp.; of these, 8 - for the most typical specimen; 3, 7, 10-11 - long teeth with relatively thicker base may belong to a different theropod, possibly to the one that had a lesser trochanter of ornithomimid type); Nos. 433-442, 3, 8 - site CBI-28; 6-7, 10-11 - site CDZH 17; 4-5, 12 - site CDZH-17a; 9 - tooth has traces of weathering and polishing by sand that occurred before fossilization (Argast et al., 1987), site CBI-14; 3 – x 0.5.; 8 – x 0.75; 5, 11 – x 1; 4, 6-7, 10, 12, 15 – x 1.5; 9 - x 3; 13-14 - ungual phalanges: 13 - Segnosauria indet., 14 - theropod (?), site CDZH-17, No. 443, 444, x 0.33 and approximately x 0.5; 1 - relatively thick (labiolingually) tooth of Tyrannosauridae, site BAI-3, No. 485, x 1; 16 - metacarpal I of a theropod, possibly of a young *Alectrosaurus* sp. (view from above), site CBI-17, No. 445, x 0.66; 17 - phalanx of digit IV of hindlimb of a theropod, site CDZH-17a, No. 446, x 0.66; 18 - proximal part of phalanx 2 of digit IV of wing of pterosaur *Azhdarcho lancicollis* Ness., site CBI-14, No. 8/11915, x 1; 18a - from proximal end, 18b - from below; 19-20 - two astragali of theropods, possibly *Alectrosaurus*, site CBI-14 and CBI-17, Nos. 447, 448, x 0.5; 19a, 20a - from above, 19b, 20b - from below; 21 - phalanx of hindlimb of a theropod, site CBI-28, No. 449, x 0.75; 22 - part of braincase of a relatively large carnosaur, view from the front and slightly from the right (Malyeyev, 1965: fig. 2), site CBI-23, No. 450, x 0.33; 23 - tooth of a small theropod *Troodon* (=*Pectinodon*) *asiamericanus* sp. n., site SSHD-8, holotype No. 49/12176, x 6; 24 - vertebra of ?theropod or bird, site CBI-14, RO No. 4607, x 2.5; 25-27 - remains of lizards, site CBI-4c: 25 - dentary of *Sheikhia priscagama* Ness. (Priscagamidae), holotype No. 697, x8; 25a - from above, 25b - from the inside; 26-27 - dentary from the inside (No. 451) and maxilla (No. 452) from the outside (27a) and inside (27b), x 8.

Plate II. Remains of dinosaurs (1-6, 9-17, 19-21), dinosaurs and possibly birds (7-8, 18), mammal (22), lizards (23-27); from the lower Cenomanian, Upper Cretaceous, upper part of the Khodzhakul Formation, Sheikhdzheili locality, Karakalpakistan (6), upper Turonian (1, 2-4, 10, 13-14, 16, 18-19, 25-27) and Coniacian (5, 7-9, 11-12, 15, 17, 20-24), Upper Cretaceous (Bissekty Formation), Dzharakuduk locality, Uzbekistan: 1-3 - ungual phalanges of segnosaurs Segnosauria indet., 1, 2 - site CDZH-17a and CBI-16, No. 453 and No. 454, x 0.75 and x 0.5; 3 - site CDZH-17a, No. 455, x 1.1; 4 - tooth of a segnosaur, site CDZH-17a, No. 3/11822, x 6; 5 - vertebra (dorsolumbar?) of a segnosaur; site CBI-5, No. 456, x 0.75; 6 - ungual phalanx of a segnosaur, site SSHD-8a, No. 457, x 0.75; 7 - strongly (dorsoventrally) flattened centrum of a theropod(?) or a large non-flying bird (see also Fig. 18), site CBI-5a, No. 458, x 0.75; 8 - ungual phalanx, possibly from the forelimb of an oviraptorosaur or hindlimb of a bird?, site CBI-17, No. 459, x 4; 9 - tooth of a theropod or bony fish of family Saurodontidae(?), *Asiamerica asiatica* sp. n., site CBI-14, holotype No. 460, x 2; 10 - tooth of a small theropod, apparently of a peculiar species, site CDZH-16, No. 2/11822, x 3; 11 - tooth of a dromaeosaurid (deinonychosaur) (Ostrom, 1969: figs. 23-24), site CBI-14, No. 461, x 1.6; 12 - frontal of a segnosaur or theropod (?), site CBI-14, No. 462, x 0.5; 13, 14 - ungual phalanges **[146/147]** (viewed from above) of theropods, possibly *Alectrosaurus* sp., site CDZH-16, No. 463, 464, x 0.33; 15 - anterior part of sacrum of a small theropod, site CBI-5a, No. 1/12454, x 0.5; 16 - symphyseal part of mandible of theropod *Caenagnathasia martinsoni* Curr., Godfr. et Ness. (Caenagnathidae, Oviraptorosauria), site CDZH-17a, No. 401: 16a - from above, x 3; 16b - from the right, x 2; 17 - braincase of a relatively small theropod, possibly dromaeosaurid, but not *Itemirus medullaris* Kurz., site CBI-4, No. 466, x 0.75; 18 - centrum with long, slit-like pleurocoel, possibly from bird ?*Kuszholia* sp. or from a theropod or a segnosaur (see also Fig. 7), site CBI-16, No. 467, x 1; 19 - ungual phalanx of manus of ornithomimosaur (Marsh, 1896: figs. 49-52; Nicholls and Russell, 1985: fig. 8C; Barsbold, 1988: fig. 1), site CDZH-17, No. 468, x 1; 20 - distal part of humerus of a small theropod, site CBI-14, No. RO 4622, x3; 21 - supposedly opisthocoelous vertebra (possibly caudal), probably from a small theropod, site CBI-14, No. RO 4619: 21a - from below, x 2; 21b - back view(?), x 2.5; 21c - lateral view, x 2.2; 22 - upper molar (M1?) of a mammal ?*Aspanlestes* sp. (Mixotheridia), site CBI-14, No. 6/12455, x 10; 23 - frontal of a lizard, site CBI-4v, No. 469, x 3; 24 - dentary of lizard *Sheikhia* sp. (Priscagamidae), site CBI-14, No. 470, x 6: 24a - from above; 24b - from the inside; 25-27 - fragments of dentaries of lizards, one of these (26) possibly of Gekkota, another (27) from Teiidae, site CDZH-17a, Nos. 471-472, x 6.

Plate III. Remains of dinosaurs (1-7, 9-13) and crocodylian (8); from the upper Barremian - middle Aptian, Lower Cretaceous (Murtoi Formation), Mogoito site (Buryatia) (13), lower Cenomanian, Upper Cretaceous (upper part of Khodzhakul Formation), Sheikhszheili locality (10) and Chelpyk (11), Karakalpakistan from the upper Turonian (1, 5, 8) and Coniacian (2-4, 6-7, 9), Upper Cretaceous (Bissekty Formation), Dzharakuduk, Uzbekistan, from the lower Santonian, Upper Cretaceous (Yalovach Formation) Kyzyl ilyal', Tadzhikistan (12): 1 - anterior part of the sacrum of a small theropod (Oviraptorosauria? or cf. *Gallimimus* sp.), site CDZH-16, No. 474, x 1; 2-4 - caudal vertebrae Nos. 475-477: ornithomimid? (2), theropod (3), dinosaur (4): 2 - x 1.1; 3 - x1, 4 - x 0.75; 5 - proximal part of femur of a theropod, site CDZH-16, No. 479, x 0.75; 6 - caudal vertebra of a theropod (cf. *Dryptosaurus* sp.), segnosaur, or hadrosaurid? cf. *Hypsibema* sp., site CBI-14, No. 725, x 0.75 (see Baird and Horner, 1979: fig. 4a; Gallagher, 1990: fig. 11), 7 - femur of ornithomimid *Archaeornithomimus* (?) *bissektensis* sp. n., site CBI-4, holotype, No. 726: 7a - posterior view, x 0.7; 7b - from the lateral side and slightly from posterior side, x 0.65; 7v - from the distal end, x 0.75; 7g - from the anterior side, x 0.66; 7d - from the proximal end, x 0.66; 7e - from the medial side, x 0.7; 8 - cervical or dorsal osteoderm of a crocodylian, site CBI-28, No. 480, x 1; 9-11 - teeth of sauropods Titanosauridae or Diplodocidae; they are long, thin, and smooth or have notably weaker folds of enamel than *Alamosaurus* from the Upper Cretaceous of the USA (Kues et al., 1980: figs. 3-5), Nos. 481-483: 9 - site CBI-14, No. 41/12176, x 2; 10-11 – site SSHD-8, x 1.5, and site SCH-1, x 0.7; 12 - frontal of *Troodon isfarensis* sp. n., site FIS-2, holotype, No. 484, 12a – x 1 and 12b – x 1.5; 13 - tooth of sauropod cf. *Chiayusaurus* sp. (Nessov and Starkov, 1992: 10, 13), possibly from

Camarasauridae, discovery by A. I. Starkov, site "Promoina Klevenskogo," x 1.1: 13a - from the distal end; 13b - from the side; 13v - from the outside.

Plate IV. Remains of dinosaurs (1-17), turtles (18), aspidorhynchid fish (19); from the late Barremian - middle Aptian, Lower Cretaceous (Murtoi Formation), Mogoito locality, Buryatia (1), upper Albian, Lower Cretaceous (middle or lower part of the Khodzhakul Formation), Khodzhakul (2, 3, 12, 19), lower Cenomanian, Upper Cretaceous (Upper part of the Khodzhakul Formation), Sheikhdzheili (13-17) and Chelpyk (10, 18), Karakalpakistan, upper Turonian (6) and Coniacian (4, 5, 7, 9, 11), Upper Cretaceous (Bissekty Formation), Dzharakuduk, Uzbekistan, Santonian - lower Campanian, Upper Cretaceous (Bostobin Formation), Buroinak (8): 1 - procoelous caudal vertebra of a sauropod (Nessov and Starkov, 1992: 13), site "Promoina Klevenskogo," discovery by A. I. Starkov: 1a - from the left, x 0.3; 1b - from the front, x 0.33; 1v - from below, x 0.2; 2-6 - osteoderms of ankylosaurs: 2-3 - Shamosaurinae?, site SH-20; 4-6 - Ankylosaurinae: 4 - site CBI-4; 5 - site CBI-17, 6 - site CBI-28, Nos. 486-490; 2-3 – x 1.8 and 1.5 4-6 – x 1; 7-8 - terminal phalanges of ankylosaurs or ceratopsids, site CBI-14 and site 823-1k, Nos., 491, 492, x 0.5; 9 - vertebra of ceratopsid (cervical? 7-8) or ankylosaur, site CBI-5, No. 493, x 0.25; 10-11 - teeth of ankylosaurids, No. 12/12176 and No. 494, x 2 and x 4: 10 - site SCH-1 and 11 - site CBI-4; 12 - left maxilla of the early protoceratopsid *Kulceratops kulensis* gen. n., sp. n, site SH-20, holotype, No. 495, x 2: 12a - from below and somewhat from the outside; anterior part of the bone is oriented to the left; 12b - from above; anterior end of the bone is turned to the **[147/148]** right; 13-18 - remains of protoceratopsid *Asiaceratops salsopaludalis* Ness. et L. Kazn.: 13 - proximal part of the humerus, site SSHD-8a, No. 11, x 1.1; 14 - posteroventral part of the braincase, site SSHD-8a, No. 496: 14a - from above, x 2.2; 14b - from below, x 1.9; 14v - from behind and the left, x 1.5; 15 - posterior part of the braincase, from behind, site SSHD-8, No. 497, x 1.5; 16-17 - neurocentra: 16 - the largest of those found for the species, site SSHD-8a, No. 498, x 1.1; 17 - No. 499, x 1.5; 18 - vertebral plate of turtle *Kizylkumemys schultzi* Ness., No.96/11180, site SCH-1, x 0.8; 19 - part of jaw of Teleostei Aspidorhynchidae from the outside, site SH-20, No. 500, x 5.

Plate V. Remains of dinosaurs-protoceratopsids *Asiaceratops salsopaludalis* Ness. et L. Kazn. (1-19) from the lower Cenomanian, Upper Cretaceous (upper part of the Khodzhakul Formation, Chelpyk, site SCH-B (5), Sheikhdzheili, sites SSHD-8 and SSHD-8a (1, 3, 6-7, 10-13, 15-19), ravine Khodzhakulsai, site SH-5 and SH-25 (2, 4, 8-9), plateau between Khodzhakulsai and Sheikhdzheili, the bone was redeposited into the upper Paleocene (lower Paleogene) site SH-0 (14) of bony fish Elopomorpha from Sheikhdzheili, site SSHD-8, Karakalpakistan (21), and Protoceratopsidae indet., possibly belonging to as yet unknown genus (20) from the upper Turonian, Upper Cretaceous, lower part of the Bissekty Formation: 1-2 - maxilla, No. 13: 1a - from below, x 1; 1b - from above, x 1.2 and holotype No. 9: 2a - from above, x 1.3; 2b - from the outside, x 1; 3 - premaxilla (mirror image), No. 12: 3a - from the inside, x 1.8; 3b -from the outside, x 1.9; 4 - fragment of postorbital(?), No. 501, x 1.5; 5 - fragment of jaw bone with functional and replacing teeth, inside and outside view, No. 502, x 2; 6 - part of maxilla of a young individual, inside view and outside view, No. 503, x 1.5; 7-9 - dentaries, No. 504, 14, and 505: 7 - from the inside, 8-9 - from the outside and inside, x 1; 10 - rostral(?) bone, No. 15, x 3; 11-12 - distal parts of quadrates from behind, Nos. 506, 507, x 2; 13-14 - parts of frontals, Nos. 508, 509, x 1.5 and x 2; 15-19 - teeth, Nos. 510, 23, 511-513, 2; 2 - part of maxilla (mirror image), No. 514, x 2; 21 - one of the two pterygoid bones of fish with teeth, No. 515, x 5.

Plate VI. Remains of dinosaurs - protoceratopsids *Asiaceratops salsopaludalis* Ness. et L. Kazn. (1-15, 19-37), remains doubtfully attributed to this species (16-18, 38), from the lower Cenomanian, Upper Cretaceous (upper part of the Khodzhakul Formation), Sheikhdzheili, sites SSHD-8 and SSHD-8a (1, 3, 10-12, 14-23, 25-37) and Khodzhakulsai ravine, site SH-5 (39) and Chelpyk, site SCH-1 (11, 13, 24), Karakalpakistan: 1 - surangular, No. 17: 1a - from the outside, x 1.3; 1b - from the inside, x 1.2; 2 - a part of the small "frill" of squamosal(?), No. 516, x 2: 2a - from the outside, 2b - from the inside; 3-4 - parts of frontals from the inside, Nos. 517, 518, x 2; 5 - vertebra, side view, No. 519, x 2; 6 - scapula, No. 520, x 2; 7-8 - ungual phalanges, No. 10 and No. 521, x 2; 9-12, 14-17 - phalanges (10, 14 - anomalous fusion of phalanges in pairs), Nos. 522, 529, 9, 10, x 2; 11, x 1.8; 12, x 2.1; 14-17, x 2; 13, 18 - metapodia, Nos. 530, 531, x 2; 19-37 - teeth (21 - from the front and from behind and slightly from the side of wear facet, 23 - section through the pulp cavity, 35 - from the front and from behind), 19-27 - Nos. 532-540; 28 - No. 21, 29-31 - Nos. 541-543, 32 - No.16, 33-35 - Nos. 544-546, 36 - No. 22; 19-23, 25-37, x 2.1; 24 - x 4; 38 - pubis(?), No. 547, x 2; 39 - phalanx, No. 548, x 2.

Plate VII. Remains of dinosaurs - ceratopsids *Turanoceratops tardabilis* Ness. et L. Kazn. (1-8, 15-21), tooth and jaws doubtfully attributed with doubts to ceratopsids (9, 11-14), remains of hadrosaurids (10, 22) and bone of gar *Atractosteus turanensis* Ness.(23); from the upper Turonian (2, 4, 12-16, 18, 19, 21) and Coniacian (1, 3, 5-11, 17, 20, 22, 23), Upper Cretaceous (Bissekty Formation), Dzharakuduk, Uzbekistan: 1-9 - teeth (9 - strongly worn), 2, 4 - sites CDZH-17...; 5-9 - site CBI-14, Nos. 252, 549-551, 25 , 552-555; 1, 2, 4-7, x 1; 10 - fragment of mandible of a hadrosaurid, site CBI-14, No. 556, x 1; 11 - vertebra, site CBI-14, 557; 12-13 - fragments of jaws of hadrosaurids or ceratopsids(?), site CDZH-17a and CDZH-16, Nos. 558, 559, x 1; 14 - anterior part of the lower jaw of a ceratopsid or a hadrosaurid(?), site CBI-27, No. 560, x 0.5; 15 - nasal horn, site CDZH-16, No. 254, x 0.33: 15a - from the right side; 15b - from behind; 16-18 - supraorbital horns, site CDZH-16,CBI-28, and CBI-27, Nos. 256, 561, 562 16, 17 - x 0.4; 18 - x 0.75; 19 - predentary from the right, from above, and from below, site CBI-4, No. 727; x 0.33; 20 - fragment of the frill(?), site CBI-14, No. 563, x 0.75; 21 - left maxilla from below and from outside, site CBI-27 (level 1 m above the base of the Bissekty Formation), holotype, No. 251, x 0.4; 22 - front part of the mandible of a hadrosaurid, site CBI-14, **[148/149]** x 0.8; 23 - premaxilla of gar *Atractosteus turanensis* Ness., site CBI-14, No. 564, x 3: 23a - from above, 23b - from the right.

Plate VIII. Remains of dinosaurs - hadrosaurids *Gilmoreosaurus arkhangelskyi* Ness et L. Kazn., sp. n. (1-2, 6-7), of the same species or a different hadrosaurid (3, 8, 10) and a large bony fish, possibly *Aidachar* sp., belonging to Ichthyodectiformes; from the upper Turonian (2-3, 6-7, 9, 11) and Coniacian (1, 8, 10), Upper Cretaceous (Bissekty Formation), Dzharakuduk, Uzbekistan and hadrosaurid *Gilmoreosaurus* sp. cf. *G. arkhangelskyi* from the upper Turonian - Coniacian, Upper Cretaceous (Zhirkindek Formation), Kankazgan (=Tyulkeli), Kazakhstan (4-5): 1 - braincase, site CBI-14, No. 565, x 0.75: 1a - from above and slightly from behind; 1b - from the front and slightly from the left, part of parietal bone and anterior areas of the lateral wall were removed before photography; 1v - side view, anterodorsal wall of the braincase is oriented down and to the left; 1g - from behind and partly from the right; 1d - from behind and from below; 2 - upper part of the braincase from above and slightly from behind, site CDZH-17a, No. 566: 2a - x 0.75; 2b - x 0.5; 3 - major occipital bone, site CDZH-17a, No. 567; 3a - from above; 3b - from below; 4-5 - parietals (4 - from above, 5 - from below and slightly from behind), site TUL-7 and CBI-14, Nos. 568, 565 (see Pl. VIII, fig. 1), x 0.5; 6-7 - frontals (6, 7a - from above; 7b - from below), site CBI-28 and CDZH-16, Nos. 570, 571, x 0.33; 8 - parietal of a young individual from above and from the front, site CBI-14, No. 572, x 1; 9-10 - teeth, site CDZH-16 and CBI-14, Nos. 573, 574, x 1.5; 11 - vertebra of fish, somewhat anomalous in outline (asymmetrical in cross-section), site CDZH-17a, No. 575, x 0.75.

Plate IX. Remains of dinosaurs - hadrosaurids, including *Gilmoreosaurus arkhangelskyi* sp. n. (2, 3?, 4-10, 12?, 17), *Bactrosaurus kysylkumensis* (Riab.) (11?, 13, 14?, 16), of Teleostei or bony fishes, (23), crocodylian? (24), Teleostei *Lepidotes* sp. (25), bony fishes Ichthyodectiformes (26); from the upper Albian, Lower Cretaceous (lower or middle part of the Khodzhakul Formation), Khodzhakul (1), lower Cenomanian, Upper Cretaceous (upper part of the Khodzhakul Formation), Chelpyk Horizon (25) and Sheikhdzheili (26) Karakalpakistan, of the upper Turonian (2, 4, 7-10, 13, 14, 18-21) and Coniacian (3, 5-6, 11-12, 15-17, 23, 24), Upper Cretaceous (Bissekty Formation) site Dzharakuduk, Uzbekistan, Santonian - early Campanian, Upper Cretaceous (Bostobin Formation), Baibishe, Kazakhstan (22): 1 - tooth of one of the oldest known hadrosaurids, *Gilmoreosaurus* (?) *atavus* sp. n., site SH-20, No. 576: 1a - x 2.5; 1b - x 2.4; 2 - anterior part of sacrum, site CDZH-16, No. 577, x 0.3; 3 - atlas+epistropheus from the left, site CBI-5, No. 578, x 0.28; 4 - left maxilla from the outside and from below, site CBI-23, No. 579, x 0.4; 5-8 - dentaries of specimens of different ages from the inside (5 - site CBI-5a, No. 580, x 1; 6 - site CBI-14, No. 10/12454; 7 - site CDZH-24, No. 581, x 0.52; 8 - site CDZH-16, No. 582, x 0.4); 9. 10 - postorbital, site CDZH-16, Nos. 584, 585, x 0.5; 11-14 - vertebrae (11 - site CBI-17a, x 0.33; 12 - site CBI-40, x 0.33; 13-14 - site CDZH-14, x 0.25; 14 - Nos. 586-589); 15-21 - teeth (15, 17 - site CBI-14, x 1.8 and x 2, Nos. 590, 591; 16 - site CBI-17, No. 17.12176, x 0.5; 18-21 - site CDZH-17a, x 1.5, Nos. 592-595); 22 - one of posterior cervical vertebrae, from behind and from the right, site BAI-3k, specimen from the Paleontological Museum of University of Oslo, x 0.33; 23 - scales, site CBI-4v, No. 596, x 5; 24 - tooth on the stage of early resorption of the root, site CBI-4, No. 597, x 6; 25 scales, site SCH-1, No. 598, x 1.5; 26 - fragment of a jaw with thecodont teeth and alveoli, site SSHD-8, No. 599, x 4.

Plate X. Remains of a moderate-sized carnosaur, *Tarbosaurus* sp. (1), of hadrosaurid dinosaurs (2?, 3-4, 6, 7?, 8, 11?, 12?, 13, 14?, 25), in part probably from *Gilmoreosaurus arkhangelskyi* sp. n. (3-4, 13-14) or most likely from this species (5), theropods (9-10), of dinosaurs that cannot be identified, but possibly hadrosaurids, apparently with tracks of inflammation of periosteum probably spread inside the bone (15), bone tumor (osteoma) (16) and bone corn after fracture and fusion of bones (17) (Rothschild, 1987, 1988; Tanke, 1989), of a small ornithischian dinosaur that cannot be identified (18), teeth of young hadrosaurids or other dinosaurs of very primitive ornithopods of hypsilophodontid type or even similar to heterodontosaurs (19-23), sauropod (24); from the upper Turonian (2, 4-11, 13, 17, 19-23) and Coniacian (3, 12, 18, 24), Upper Cretaceous (Bissekty Formation), Dzharakuduk locality, Uzbekistan; upper Turonian, Upper Cretaceous (Zhirkindek Formation), Kankazgan (=Tyu'keli) locality, Kazakhstan (25) and Santonian - lower Campanian, Upper Cretaceous (Bostobin Formation) (1) Baibishe site, Kazakhstan (1): 1 - femur, site BAI-3k, No. 601: 1a - posteriorly, x 0.18; 1b - **[149/150]** from the front, x 0.13; 2 - fragment of ulna (?), site CDZH-16, No. 602, x 0.33; 3-4 - humeri, site CBI-2, x 0.25, and site CDZH-23, x 0.5, Nos. 603, 604; 5 - caudal vertebra, site CDZH-16, No. 605, x 0.75; 6-8, "ungual" phalanges: 6-7 - site CBI-28, x 0.45; 8 - site CDZH-14, x 0.5, Nos. 606-608; 9-10 - ungual phalanges of hindlimb of theropods, possibly *Alectrosaurus* sp. (Mader and Bradley, 1989: fig. 4), site CBI-1, x 1.1, and CDZH-17g, x 1, Nos. 609, 610; 11-12 - phalanges of digits of ornithischians, site CDZH-17a and site CBI-19, Nos. 611, 612 x 0.75; 13-14 - surangulars from the inside, site CDZH-17a, x 0.75, and site CDZH-24, x 0.5, Nos. 613, 614; 15-17 - bones with traces of disease and injuries (15 - site CBI-28, x 0.33; 16-17 - CDZH-16, x 0.75 and x 0.5, Nos. 615-617); 18 - vertebra from the side, site CBI-14, No. 618, x 0.75; 19-23 - teeth (19 - site CDZH-17a, x 2; 20-22 - site CDZH-17g, x 2, x 4, and x 1.5; 23 - site CBI-4v, x 6; 19-20 - Nos. 619, 620; 21 - No. 4/11822; 22, 23 - Nos. 621, 622); 24 - "lying" ungual phalanx (Rozhdestvensky, 1978: 64), ungual phalanx possibly inverted when on substrate (Gallup, 1989), relatively sharp (Marsh, 1896: pl. 37), site CBI-40, No. 663, x 0.36; 25 - "ungual" phalanx, site TUL-5, No. 465, x 0.75.

Plate XI. Remains of dinosaurs - hadrosaurids (1-4), including (1-2) *Gilmoreosaurus arkhangelskyi* sp. n. and (4) *Bactrosaurus kizylkumensis* (Riab.), mammals: Multituberculata *Uzbekbaatar kisylkumensis* Kielan-Jawor. et Ness. (5) condylarth cf. Periptychidae gen. et sp. nov. (6), Proteutheria gen. et sp. nov. (7), birds: ichthyornithiform or enantiornithiform *Zhyraornis logunovi* Ness. (8) and enantiornine *Sazavis prisca* Ness. (9), anuran amphibian *Gobiates kizylkumensis* Roc. et Ness. (10), caudate amphibian, apparently *Mynbulakia surgayi* Ness. (11), elopomorph bony fishes gen. et sp. nov. (12-14), Teleostei Aspidorhynchidae spp. n. (15-16), gar (17), Teleostei Pholidophoroidei, very late in the record (18), bony fish Enchodontoidei (19), ray *Myledaphus tritus* Ness. (20), Araucariaceae (21) and Cupressaceae (22); from the upper Albian, Lower Cretaceous (lower or middle part of the Khodzhakul Formation), Khodzhakul locality (21) and

Lower Cenomanian, Upper Cretaceous (upper part of the Khodzhakul Formation), Sheikhdzheili locality (15, 22), Karakalpakistan; upper Turonian (1, 3, 11, 17, 20) and Coniacian (2, 4-10, 12-14, 18-19), Upper Cretaceous of Dzharakuduk locality, Uzbekistan, and lower Santonian, Upper Cretaceous (Yalovach Formation) of Kansai locality (Kyzylbulak), Tadzhikistan (16): 1-2 - frontals (1, 2b - from above, 2a - from below) site CDZH-16 and CBI-5, holotype No. 664 and No. 665, x 0.5; 3 - posterior part of the dentary, site CDZH-16, No. 666, x 0.5; 4 - maxilla, site C I-14, No. 667, x 0.4; 5 - tooth p4 from different sides, site CBI-14, No. 100/12455, x 10; 6 - tooth M1 from below and behind, site CBI-14, No. 2/12455, x 8.5; 7 - skull in the same form as it was found; view from above (from the left and from behind; phosphatized soft tissues have been preserved, apparently skin with subcutaneous cellular tissue and muscles) and view from the right, site CBI-5a, No. C.79066 (Zoological Institute, RAS), x 4.2; 8 - sacrum from the right, site CBI-5a, No. RO 4600, x 2; 9 - tibiotarsus from the front, site CBI-5a, No. RO 3472, x 2.25; 10 - squamosal, site CBI-4v, No. 668, x 4; 11 - atlas from the front, site CDZH-17a, No. 104/12177, x 6; 12 - premaxilla from below, site CBI-17, No.16/12454, x 2; 13 - ?one of the anterior pterygoid bones or palatine, site CBI-14, No. 669, x 4; 14 - parasphenoid from below, site CBI-5a, No. 670, x 2; 15, 16 - parts of mandible, site SSHD-8a, x 2.2, and site FKA-7a, x 8, Nos. 671, 672; 17 - tooth, site CDZH-17a, No. 7/11822, x 3; 18 - bone of skull roof, site CBI-4, x 2; 20 - from behind and from the front, No. 675, x 10; 21-22 - cones (given to S. G. Zhilin for deposit in the collection of the Botanical Institute, RAS) site SH-20, x 1, and site SSHD-8a, x 1.5.

Plate XII. Remains of dinosaur *Psittacosaurus mongoliensis* Osborn (identification by A. K. Rozhdestvensky) (1), bony fishes *Eurypholis* spp. (2-3), sharks: Heterodontoidea *Glickmanodus rarus* Ness. et Mert. (4)) and Hybodontoidea *Polyacrodus* ex gr. *illingworthi* (Dixon) (5), *Polyacrodus torosus* Ness. et Mert. (6) Hybodontoidea that cannot be identified (16, 17) and *Acrodus levis* Woodw. (30), ... fishes - polyodontids (7) bony fishes - enchodontids (8), lizards Gekkota (9), Teleostei - aspidorhynchids (10, 15), wood with tracks of boring by brackish-water pelecypods

Martesiinae or Xylophaginae (11), coprolite of cartilaginous fish (12), remains of Teleostei - amiids *Amia semimarina* Ness. (13-14), turtles (18), bony fish - Elopomorpha sp. n. (19), Teleostei *Lepidotes* sp. (20-25) and *Anomaeodus splendidus* Ness. (26-27), crocodylians (28-29), sturgeon-like fish (31), Teleostei *Amia limosa* Ness. (32), bony fish with mobile fin spine (33) and lizard (34); **[150/151]** these remains come from the Aptian-Albian (most probably from the upper Aptian), Lower Cretaceous, of Ulan-Osh locality, Mongolia (1), upper Albian, Lower Cretaceous (lower or middle part of the Khodzhakul Formation), site SH-20 (2-10), Khodzhakul locality, from the lower Cenomanian (upper part of the Khodzhakul Formation), site SSHD-8 and SSHD-8a (11-15, 18-29) Sheikhdzheili locality and Cenomanian (upper part of the same formation) of Chelpyk, site SCH-1 (17, 30), Karakalpakistan, from the Cenomanian (Dzharakuduk locality), site CDZH-3 (16 , locality Itemir, Uzbekistan, upper Turonian (31) and Coniacian (32-34), Upper Cretaceous (Bissekty Formation), Dzharakuduk locality, Uzbekistan: 1 - maxilla, collection of Vertebrate Zoology Department of St. Petersburg University, x 2; 2-3 - dorsal and lateral plates, No. 31/12177, x 6, and No. 676, x 5; 4-6 - teeth: No. 677: 4a - x 7.5; 4b - x 5; No. 81/12178, x 3; No. 76/12178, x 3; 7 - scales, No. 32/12177, x 8; 8 - part of bone (palatine?) with tooth, No. 728, x3; 9 - part of a jaw, No. 678, x 6; 10 - mandible, No. 679, x 3; 11 - silicified wood with tracks of mollusk vital activity, No. 680, x 1.5; 12 - phosphatized material reflecting spiral structure of midgut of cartilaginous fish, No. 729, x 1.5; 13, 14 - anterior parts of maxillae and dentaries, Nos. 28/12176 and 1/12000, x 1; 15 - maxilla, No. 681, x 6; 16 - dorsal fin spine, No. 682, x 1; 17 - lateral head spine of male, No. 683, x 1.5; 18 - ungual phalanx, No. 684, x 1.5; 19 - premaxilla, No. 685, x 4; 20-21 - tooth apices with acrodine covering; Nos. 48a-48b/12176, x 2; 22-23 - skull bones, Nos. 686, 687, x 1.5; 24-25 - scales and vertebra, Nos. 688, 689, x 2; 26-27 - vomerine dental plate with tooth at the edge of the jaw, Nos. 690, 691, x 3 and x 4; 28-29 - teeth, Nos. 692, 693, x 1.5; 30 - tooth, No. 34/12176, x 2; 31 - lateral plate, site CBI-4v, No. 72/11914, x 6; 32 - maxilla, site CBI-14, No. 694, x 2; 33-34 - fin spine, dentary, site CBI-4v, Nos. 695, 696, x 4 and x 10.

Plate XIII. Dense tree stand buried in place on the coast of ancient interbasin channels and liman basins of the Coniacian (first half of the Late Cretaceous, middle to upper part of the Bissekty Formation at Dzharakuduk). Found in the same area were imprints of leaves of Platanaceae (probably dominant in the plant community), laurel trees, magnolias, and other angiosperms, buried at a level of soil that was considerably sideritized during diagenesis and retained in some parts remains of the leaf litter.

Plate XIV. Residual mountain Chelpyk (Cholpyk) in Karakalpakistan, consisting of sandstones of the upper part of the Khodzhakul Formation (Cenomanian) and containing remains of dinosaurs and other vertebrates slightly above the middle of the slope. A fortress dating to the second millennium BC is situated on the top formed by a thick lens of ferruginous sandstones (sideritized during diagenesis).

The upper part of ravines near the settlement Kodzhakul in Karakalpakistan are formed by sandstones of the middle part of the Khodzhakul Formation (upper Albian). Found here (at site SH-20, marked by crosses) were a maxilla of the protoceratopsid *Kulceratops kulensis* g. n., sp. n. and remains of other dinosaurs, as well as other vertebrates (including fishes, amphibians, lizards, pterosaurs, birds, and mammals).

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