Correlation of Late Cretaceous Continental Vertebrate Assemblages in Middle and Central Asia

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Abstract  The relative stratigraphic positions of the better-known assemblages of Late Cretaceous continental vertebrates from Middle and Central Asia are assessed by parsimony analysis of the presence/absence of 26 proposed biostatigraphic marker taxa. The oldest assemblage in the region is Khodzhakul from the Kyzylkum Desert of Uzbekistan (early Cenomanian). The next stage includes assemblages from the lower and upper parts of the Bayn Shire Formation of the eastern Gobi Desert, Mongolia (Cenomanian to Santonian). The Iren Dabasu fauna from Inner Mongolia, China, clusters with the Turonian-Santonian faunas from Middle Asia based on the shared presence of the trionychid turtle Khunuchelys, and is likely Santonian in age. Three Middle Asian assemblages (Bissekty, Yalovach, and Bostobe) are endemic in the presence of two crocodyliform taxa (Kansajsuchus and Tadzhikosuchus) and share another crocodyliform

Key Words: C. gobiensis, Gobio, M. mongolica, N. nemegti, S. lancia, S. mongoliensis, S. saurolophus, T. barunensis, T. yalovachi, T. bostobiensis, K. kansaiensis, K. nemegtensis, K. shamosiensis

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(Shamosuchus) with the Gobi assemblages. The Campanian-Maastrichtian assemblages from the Gobi Desert cluster with coeval North American faunas. The Campanian vertebrate assemblages from the Djadokhta and Barun Goyot formations are highly endemic, reflecting semi-arid paleoenvironments. The assemblage from the Nemegt Formation, which existed under more mesic conditions, is similar in composition to those from other fluvial depositional environments (Bissekty, Iren Dabasu, and North American Judithian and Lancian assemblages). The presence of the crested hadrosaurine Saurolophus supports a Maastrichtian age for the Nemegt assemblage. Three Gobi assemblages (Djadokhta, Barun Goyot, and Nemegt) are grouped together based on the shared presence of the endemic turtle Mongolemys and parvicursorine theropods. The Campanian to Maastrichtian assemblages of Central Asia and North America differ from the older assemblages in Asia in the presence of derived Tyrannosauridae, Pachycephalosauria, and Hadrosauridae. In Middle Asia, continental vertebrate assemblages from this time interval remain largely unknown due to regional marine transgressions.

Key words biostratigraphy, vertebrates, Late Cretaceous, Middle Asia, Central Asia

1 Introduction

Correlation of the Late Cretaceous continental deposits of Central Asia to the Standard Global Chronostratigraphic Scale is difficult due to the absence of biostratigraphically useful fossils. However, the continental Late Cretaceous strata in Middle Asia are sometimes intercalated with marine deposits that do contain such fossils. This permits more precise age assessments for these units (King, personal communication). Furthermore, the Late Cretaceous deposits of Middle Asia contain dinosaurian assemblages similar to some extent to the better-known diverse assemblages from the Gobi Desert and other regions of Central Asia (Nessov, 1995, 1997; Averianov, 2007b; Sues & Averianov, 2009b). This combination of factors provides a unique opportunity for assessing the ages of the assemblages of Late Cretaceous continental vertebrates from Central Asia.

We follow the geographic usage of the term "Middle Asia" to specifically denote the region within "Central Asia" that comprises Kazakhstan, Kyrgyzstan, Tajikistan, Turkmenistan, and Uzbekistan (Dani & Masson, 1992).

In this paper we review biostratigraphic markers that are useful for dating the assemblages of Late Cretaceous continental vertebrates in Asia. Selected marker taxa are employed for a quantitative (parsimony) biostratigraphic analysis of the principal vertebrate assemblages. The recovered pattern of correlation between the analyzed assemblages is used to assess the relative temporal succession of the various faunas of continental vertebrates from the Late Cretaceous of Central Asia.

Abbreviations. BM-biostratigraphic marker; PIN-Paleontological Institute, Russian Academy of Sciences, Moscow.

2 Methods

There are a number of quantitative approaches for identifying areas of endemity in biogeography (see Simpson, 1960; Cheetham & Hazel, 1969; Raup & Crick, 1979; Holtz et al., 2004). Notably fewer methods are available for biostratigraphic analysis. These methods, reviewed by Makovicky (2008), fall into two categories. Most are based on quantitative analysis of either taxon occurrences or their stratigraphic ranges (e.g., Alroy, 1994, 2000; Fortelius et al., 2006). Other methods employ the phylogenetic relationships between taxa (Martinez, 1995). The cladistic biochronologic analysis developed by Makovicky (2008) is a further elaboration of the latter approach. It is of particular interest to us because it was applied to the chronological ordering of the assemblages of Late Cretaceous continental vertebrates from the Gobi Desert of Mongolia and northern China (Makovicky, 2008). Here we employed a different method, based on the more traditional "stage of evolution" approach to analyzing evolutionary transformations within selected groups of vertebrates. This approach has issues that were reviewed by Makovicky (2008), but it remains the basic approach for intra- and intercontinental biostratigraphic correlations. There are still significant
obstacles to developing a more rigorous approach because many vertebrate assemblages, such as the Middle Asian examples discussed here, are documented for the most part by fragmentary skeletal remains, greatly limiting their utility for phylogenetic analysis at lower taxonomic levels.

First, we review the principal groups of the Late Cretaceous continental vertebrates of Asia and their potential utility for biostratigraphic purposes. Taxa selected as biostratigraphic markers should satisfy four criteria: 1) wide geographic range, being at least found in more than one locality; 2) at least one transformation event should have occurred within the particular lineage during the Late Cretaceous; 3) represented by abundant material; 4) and identifiable even from fragmentary remains, such as isolated chondrichthyan or dinosaurian teeth or parts of turtle shells. The taxa included in the present study are individual genera or lower-level clades. We review 12 assemblages of Late Cretaceous continental vertebrates in this paper. The assemblages constitute the rows in the data matrix, and the columns in the data matrix list the biostratigraphic markers (Tab. 1). All multi-state biostratigraphic markers were treated as ordered. This dataset was subjected to parsimony analysis.

The following assemblages of Late Cretaceous continental vertebrates were selected for this analysis (Fig. 1).


2) Bissekty Formation, central Kyzylkum Desert, Uzbekistan. Principal locality: Dzharakuduk.

3) Yalovach Formation, Fergana Depression, Tajikistan. Principal locality: Kansai.

4) Bostobe Formation, northeastern Aral Sea region, Kazakhstan. Principal localities: Shahk Shakh, Buroinak, Akkurgan, Baibishe, and Egizkara.

5) Iren Dabasu Formation, Gobi Desert, Inner Mongolia, China. Principal locality: Iren Nor.

6) Lower part of Bayn Shire Formation, Gobi Desert, Mongolia. Principal localities: Shine Us Khuduk, Khara Khutul, and Amtgai.

7) Upper part of Bayn Shire Formation, Gobi Desert, Mongolia. Principal localities: Bayn Shire, Bayshin Tsav, and Burkhant.


9) Barun Goyot Formation, Gobi Desert, Mongolia. Principal localities: Khulsan, Khermeen Tsav (red beds), Udan Sayr, and Shara Tsav.


11-12) Vertebrate assemblages of the Judithian and Lancian land-mammal “ages” in North America (Russell, 1975; Cifelli et al., 2004; Kielan-Jaworowska et al., 2004).

The outgroup fauna is a hypothetical assemblage with state ‘0’ for all biostratigraphic markers.

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**Tab. 1** Data matrix of 12 Late Cretaceous vertebrate assemblages and 26 biostratigraphic markers used (for the parsimony analysis. For description of biostratigraphic markers see text)

<table>
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**Fig. 1** Approximate geographic locations of the assemblages of Late Cretaceous continental vertebrates in Middle and Central Asia discussed in this paper

3 Biostratigraphic Markers

3.1 Chondrichthyans

Teeth of sharks and rays are among the most common elements in Late Cretaceous microvertebrate assemblages. Freshwater deposits typically yield few chondrichthyan species (Estes, 1964; Beavan & Russell, 1999). Nessov (1997) presented a long list of shark species for the fluvi al Bissekty Formation of Uzbekistan, but the majority of these identifications were based on surface-collected specimens derived from the overlying marine Aitym Formation in the section at Dzharakuduk (Archibald et al., 1998). In Middle Asia, two chondrichthyan lineages appear most suitable for the correlation of the Late Cretaceous continental deposits: the hybodont shark *Hybodus* and the rhinobatoid ray *Myleadaphus* (Mertinene & Nessov, 1985; Nessov & Mertinene, 1986; Nessov et al., 1994).

BM 1) *Hybodus*: 0) absent [outgroup only]; 1) *H. hodzhakulensis* [Khodzhakul]; 2) *H. kansaiensis* [Bissekty, Iren Dabasu, Upper Bayn Shire]; 3) *H. montanensis* [Judithian]; 4) extinct [Lancian]; ?) microvertebrates not known or not sampled [Lower Bayn Shire, Djadokhta, Barun Goyot, Nemegt].

*H. kansaiensis* is cited for the Iren Dabasu Formation based on Currie & Eberth (1993: 136). Shuvalov & Trusova (1979: 85) listed "*H. asiaticus*" [nomen nudum] for the upper part of the Bayn Shire Formation at Bayshin Tsav. According to L.S. Glickman (cited by Shuvalov & Trusova, 1979: 87) this species is "quite similar to some species of *Hybodus* known from the Santonian of Kazakhstan". Currently the material of *Hybodus* from the Bostobe Formation of Kazakhstan is referred to *H. kansaiensis* (Nessov & Mertinene, 1986; Nessov, 1988, 1997), so the record for the Upper Bayn Shire assemblage is here assigned to that species. In North America *Hybodus* apparently became extinct prior to the Lancian (Estes, 1964; Bryant, 1989; Becker et al., 2004).

BM 2) *Myleadaphus*: 0) absent [outgroup, Khodzhakul]; 1) *M. tritus* (Bissekty, Iren Dabasu); 2) *M. glickmani* [Yalovach, Bostobe]; 3) *M. bipartitus* [Judithian, Lancian]; ?) microvertebrates not known or not sampled [Lower and Upper Bayn Shire, Djadokhta, Barun Goyot, Nemegt].

*Myleadaphus* is the most common freshwater elasmodbranch in the Campanian and Maastrichtian continental strata of North America, where it is represented by the type species, *M. bipartitus* (Estes, 1964; Bryant, 1989; Beavan & Russell, 1999; Neuman & Brinkman, 2005). In Middle Asia *Myleadaphus* first appeared in the uppermost (upper Cenomanian or lower Turonian) portion of the Khodzhakul Formation (Khachardalaysai; Nessov, 1997; AA, unpublished data). These teeth are referable to *M. tritus*, which is also known from the Turonian Bissekty Formation (Nessov & Udovichenko, 1986; Nessov, 1988, 1997). Currie & Eberth (1993: 136) cited a similar species for the Iren Dabasu Formation. In Middle Asia this species is replaced by *M. glickmani* in the Santonian Yalovach and Bostobe formations (*Parapalaeobates glickmani* of Nessov & Udovichenko, 1986; generic attribution based on Cappetta [1992]). The teeth of the three species of *Myleadaphus* show successive changes in the sculpture on the occlusal surface and increase in size and may represent a single evolutionary lineage.

3.2 Osteichthyans

Isolated osteichthyan bones are common in Late Cretaceous fluvial deposits but are rarely identified and reported in the literature (Estes, 1964; Nessov, 1985, 1997; Bryant, 1989; Nessov & Panteleeva, 1999; Peng et al., 2001; Neuman & Brinkman, 2005). The dominant groups (Lepisosteidae, Amiidae, and Aspidorhynchidae) do not exhibit marked changes during the entire Late Cretaceous and are represented by very similar species in Middle Asia and North America. For example, certain fish scales dubbed "Holostean B" from the Turonian Bissekty Formation of Uzbekistan and the Campanian Dinosaur Park Formation of Alberta are virtually indistinguishable (Neuman & Brinkman, 2005; A A, unpublished data). The Cenomanian Khodzhakul Formation has a larger proportion of osteichthyans with crushing dentitions, including pycnodontiforms and the semionotid *Lepidotes* (Nessov & Golovneva, 1983; Nessov, 1985), which are not known from the younger, Turonian and Santonian formations of Middle Asia. However, it is unclear if this difference is due to local extinctions of these taxa or reflects greater marine influence during the deposition of the Khodzhakul Formation. The fish remains
from the Gobi Desert have not been studied, although they are known from the Bayn Shire, Iren Dabasu, Barun Goyot, and Nemegt formations. The lack of osteichthyan remains in the Djadokhta Formation, which include extensive eolian deposits (Dashzeveg et al., 2005), may reflect unfavorable environmental conditions for these animals.

3.3 Amphibians

The composition of Late Cretaceous amphibian assemblages is quite different between North America and Middle Asia. In North America, the enigmatic Albanerpetidae are quite common throughout the Late Cretaceous (Gardner & Böhme, 2008). In Asia this group is known only from rare specimens from the Cenomanian Khodzhakul Formation and possibly a single specimen from the Turonian Bisskety Formation (Gardner & Averianov, 1998; Skutschas, 2007). Salamanders from the Late Cretaceous of North America comprise Amphiumidae, Batrachosauroididae, Scapherpetidae and Sirenidae, whereas all Cretaceous salamanders known to date from Middle Asia are Cryptobranchidae or Cryptobranchoidea (Skutschas, 2009). In Central Asia, Late Cretaceous salamanders are unknown; this is either a sampling artifact or an indication of unfavorable environments. The Middle Asian cryptobranchid *Eoscapherpeton* is potentially important for both biostratigraphy and biogeography (Nessov, 1997; Skutschas, personal communication).

**BM 3) Eoscapherpeton:** 0) absent [outgroup, Iren Dabasu, Lower and Upper Bayn Shire, Djadokhta, Barun Goyot, Nemegt, Judithian, Lancian]; 1) *E. gracilis* [Khodzhakul]; 2) *E. asiaticum* [Bisskety]; 3) *E. superum* [Yalovach, Bostobe].

Late Cretaceous frogs are known mostly from isolated bones in North America and Middle Asia (Estes, 1964; Roček & Nessov, 1993; Sanchiz, 1998; Gardner, 2008; Roček et al., 2010), whereas more complete anuran skeletal remains have been reported from the Gobi Desert (Borsuk-Bialynicka, 1978; Špinar & Tatarinov, 1986; Gubin, 1999; Roček, 2008). The discomoglossid (or gobiatid) genus *Gobiates*, which is known from the Bisskety and Barun Goyot formations (Roček & Nessov, 1993; Roček, 2008), is potentially important for interregional correlations, but additional anuran records from the other formations are needed for a more comprehensive biostratigraphic assessment of this group.

3.4 Testudines

Turtles arguably are the most common group of vertebrates in Late Cretaceous continental deposits. Even isolated shell elements are usually diagnostic to the generic level based on characteristic sculpture and patterns of the keratinous scutes. Furthermore, during the Late Cretaceous several phyletic lineages of turtles from different clades underwent considerable evolutionary change in Asia (Sukhanov, 2000). Together these factors make turtles one of the most important vertebrate groups for Late Cretaceous continental biostratigraphy.

**BM 4) Kizylkumemys:** 0) present [outgroup, Khodzhakul, Lower and Upper Bayn Shire]; 1) absent [other assemblages].

*Kizylkumemys* is a pitted-shell turtle (Carettochelyidae) first described from the Cenomanian Khodzhakul Formation of the southwestern Kyzylkum Desert of Uzbekistan (Nessov, 1977). It is also known from the Cenomanian Dzharakuduk Formation of the central Kyzylkum Desert (Nessov, 1997) and from the Early Cretaceous Sao Khua and Khok Kruat formations of Thailand (Tong et al., 2009). In Middle Asia, Carettochelyidae became extinct during the early Turonian (Nessov & Golovneva, 1983). In Mongolia *Kizylkumemys* is known only from the Bayn Shire Formation, from both the lower (Shine Us Khuduk, Khara Khutul) and upper (Bayshin Tsav) parts (Nessov, 1981; Sukhanov, 2000; Sukhanov et al., 2008).

**BM 5) Shachemydinae:** 0) absent [outgroup, Iren Dabasu, Lower and Upper Bayn Shire, Djadokhta, Barun Goyot, Nemegt, Judithian, Lancian]; 1) *Ferganemys* [Khodzhakul]; 2) *Shachemys ancestralis* [Bisskety]; 3) *Shachemys baibolatica* [Yalovach, Bostobe].

Shachemydinae is a subfamily of Adocidae, which, together with Nanhsiungchelyidae, constitutes the clade Adocusia, which is a sister-group to the clade comprising the soft-shelled turtles (Trionychia) (Syromyatnikova & Danilov, 2009). Shachemydinae is endemic to Asia, where it ranges back to the Early Cretaceous (Lapparent de Broin, 2004). In the Late Cretaceous this group is known exclusively from
Middle Asia, where it appears to be useful for regional biostratigraphy (Danilov et al., 2007).

BM 6) Nanhsiungchelyidae: 0) absent [outgroup, Bissetkty, Yalovach, Bostobe]; 1) Hanbogdemys [Lower and Upper Bayn Shire, Djadokhta]; Zangerlia [Djadokhta, Barun Goyot]; Basilemys [Judithian, Lancian]; ?) Nanhsiungchelyidae indet. [Khodzhakul, Iren Dabasu, Nemegt].

The distributional pattern of Nanhsiungchelyidae mirrors that of Schachemydinae. In Middle Asia Nanhsiungchelyidae is known only from rather uninformative remains from the Cenomanian Khodzhakul Formation (Danilov & Syromyatnikova, 2008). In Central Asia and Japan, the group extends back to the Early Cretaceous and was moderately diverse and abundant during the Late Cretaceous (Sukhanov, 2000; Danilov & Syromyatnikova, 2008; Sukhanov et al., 2008). In North America Nanhsiungchelyidae was represented only by Basilemys, a common element of Late Cretaceous continental assemblages starting in the Coniacian (Hutchison, 2000; Brinkman, 2003). Makovicky (2008: Fig. 5F) identified Basilemys in the Iren Dabasu fauna based on an earlier identification in Currie & Eberth (1993). Currently, however, there are no indisputable records of Basilemys from Asia, and earlier identifications should be treated as indeterminate Nanhsiungchelyidae until the material has been properly evaluated (Sukhanov, 2000; Danilov & Syromyatnikova, 2008).

BM 7) Khunnuchelys: 0) absent [outgroup, Khodzhakul, Lower and Upper Bayn Shire, Djadokhta, Barun Goyot, Nemegt, Judithian, Lancian]; 1) present [Bissekty, Yalovach, Bostobe, Iren Dabasu].

Khunnuchelys is a large soft-shelled turtle (Trionychidae) first reported on the basis of cranial remains from the Iren Dabasu and Bissetky formations (Brinkman et al., 1994). Recently a skull of Khunnuchelys was described from the Bostobe Formation of Uzbekistan (Vitek & Danilov, 2010). According to Vitek & Danilov (2010) this genus is possibly also represented by shell material in the Yalovach Formation of Tajikistan. A trionychid taxon of potential importance for intercontinental correlation is Aspidereotoides, which is known from the Campanian to Maastrichtian of North America and the Santonian to Campanian of Middle Asia (Gardner et al., 1995; Vitek & Danilov, 2010).

BM 8) Lindholmemydidae: 0) absent [outgroup, Judithian, Lancian]; 1) Lindholmemydys [Khodzhakul, Bissetky, Yalovach, Bostobe, Iren Dabasu, Lower and Upper Bayn Shire]; 2) Mongolemys [Djadokhta, Barun Goyot, Nemegt].

Lindholmemydidae is a group of freshwater turtles known exclusively from the Late Cretaceous and Paleogene of Asia (Sukhanov, 2000). Its monophyly remains to be demonstrated; it possibly represents a paraphyletic grouping of stem taxa to the crown clade Testudinoidea. Lindholmemydys is known from Middle Asia and from the Iren Dabasu and Bayn Shire formations of the Gobi Desert (Danilov & Sukhanov, 2001), whereas Mongolemys occurs in the younger formations of the Gobi Desert. A lindholmemydid turtle from the Khodzhakul Formation of Uzbekistan was previously identified as Mongolemys (Nessov & Krassovskaya, 1984) or Khodzhakulemys (Danilov, 1999). It has now been reassigned to Lindholmemydys (Danilov, personal communication). A published record of Mongolemys from the Lower Cretaceous of Mongolia (Sukhanov, 2000) is probably derived from the Upper Cretaceous, possibly from the Nemegt Formation (Danilov, personal communication).

3.5 Squamates

Snakes apparently originated in Gondwana and are currently known only from sparse remains from the Late Cretaceous of Europe and North America (Fox, 1975; Gardner & Cifelli, 1999). There are no records to date from the Mesozoic of Middle and Central Asia. Amphisbaenians are predominantly Gondwanan in distribution but have a modest fossil record in Europe and North America (Kearney, 2003). Gao & Nessov (1998) referred the enigmatic Hodzhakulia from the Khodzhakul Formation of Uzbekistan to Amphisbaenia, but this assignment was not accepted by later studies (Alifanov, 2000; Kearney, 2003). Hodzhakulia could be useful for interregional correlations because it is also occurs in the Lower Cretaceous, possibly Albian, of Mongolia (Alifanov, 2000). Isolated lizard bones are often quite common in the Late Cretaceous fluvial deposits from Middle Asia and North America (Gao & Fox, 1996; Nessov, 1997). The Djadokhta and Barun...
Goyot formations of the Gobi Desert have yielded a remarkable diversity of lizards, the majority of which are represented by articulated skulls and skeletons (Alifanov, 2000; Gao & Norell, 2000). This diversity, however, appears to have been overestimated, and certain taxa are in urgent need of taxonomic revision. By contrast, the fossil record for lizards from the fluvial strata of the Nemegt Formation is much less extensive (Alifanov, 2000), and only a single lizard bone has been reported to date from the fluvial deposits of the Iren Dabasu Formation (Currie & Eberth, 1993). Lizards could be useful for the biostratigraphic correlations among the Late Cretaceous localities from the Gobi Desert (Gao & Norell, 2000; Makovicky, 2008), but considerable endemism of the known assemblages currently restricts their utility for interregional correlation.

3.6 Choristoderes

The superficially crocodile-like choristoderes were a common element of continental aquatic ecosystems in Asia during the Early Cretaceous. They were especially diverse and successful in ecosystems lacking crocodyliform archosaurs (Matsumoto & Evans, 2010). Surprisingly, there is not a single record of choristoderes from the Late Cretaceous of Asia, whereas these reptiles were quite common (if less diverse) in North America during this time interval and survived the end-Cretaceous extinction event (Gao & Fox, 1998). In Asia, choristoderes briefly reappeared during the Paleocene, possibly by dispersal from Europe (Averianov, 2005).

3.7 Crocodyliforms

Isolated crocodyliform teeth and osteoderms are fairly common in most Late Cretaceous fluvial deposits from Asia and North America, but these materials are often insufficient for lower-level taxonomic identification. In Asia partial or complete crocodyliform skulls and partial skeletons are known from the Gobi Desert (Efimov, 1988; Osmólska et al., 1997; Storrs & Efimov, 2000; Pol & Norell, 2004a, b; Pol et al., 2009), but there are also some (mostly as yet unpublished) cranial remains from sites in Middle Asia. The latter material is currently under study by P.P. Skutschas and A.S. Rezvyi, and we rely on their personal communications for its identification. The Djadokhta and (to a lesser extent) Barun Goyot formations have yielded terrestrially adapted "protosuchian" crocodyliforms (Gobiosuchus, Zarassuchus, Zosuchus). Unidentified "protosuchians" are also known from the Bissekty Formation in Middle Asia. Neosuchian crocodyliforms are represented by Shamosuchus in both Central and Middle Asia and Kansajsuchus in Middle Asia. Late Cretaceous eusuchians in Asia are represented to date only by rare records of Tadzhikosuchus from the Bissekty, Yalovach, and Bostobe formations. This archaic faunal composition of Late Cretaceous crocodyliform assemblages of Asia, with the presence of "protosuchians" and dominance of non-eusuchian neosuchians, is in striking contrast to the composition of the Campanian and Maastrichtian assemblages of North America, which comprise only eusuchians (Wu, 2005). The following crocodyliform taxa seem to be useful for intra- and interregional biostratigraphy:

| BM 9) | Shamosuchus: | 0) absent [outgroup, Judithian, Lancian]; | 1) present [all other assemblages]. |
| BM 10) | Kansajsuchus; | 0) absent [outgroup, Khodzhakul, Iren Dabasu, Lower and Upper Bayn Shire, Djadokhta, Barun Goyot, Nemegt, Judithian, Lancian]; | 1) present [Bissekty, Yalovach, Bostobe]. |
| BM 11) | Eusuchia: | 0) absent [outgroup, Khodzhakul, Iren Dabasu, Lower and Upper Bayn Shire, Djadokhta, Barun Goyot, Nemegt]; | 1) Tadzhikosuchus [Bissekty, Yalovach, Bostobe]; | 2) Leidyosuchus [Judithian, Lancian]. |

3.8 Pterosaurs

The diversity of pterodactyloid pterosaurs reached its peak during the Early Cretaceous and steadily declined during the Late Cretaceous (Butler et al., 2009). There are three principal groups of Late Cretaceous pterodactyloids: Pteranodontidae and Nyctosauridae, restricted to the Western Hemisphere, and Azhdarchidae, almost worldwide in distribution. Remarkably, all of these last surviving clades of pterosaurs are toothless. But teeth of Ornithocheiridae are still common in the majority of nearshore marine environments during the Cenomanian (Barrett et al., 2008). Their presence in microvertebrate assemblages is usually well documented by isolated teeth (Wellnhofer & Buffetaut, 1999; Averianov, 2007a; Vullo & Neraudeau, 2009).

| BM 12) Pterosauria: | 1) Ornithocheiridae + Azhdarchidae |
Pterosaurian bones are known from the Iren Dabasu Formation but have not yet been identified (Currie & Eberth, 1993: 136). Azhdarchid remains have recently been recovered from the Upper Bayn Shire Formation (Burkhant & Bayshin Tsav; Watabe et al., 2009), and thus their absence in the Lower Bayn Shire is possibly a sampling artifact. But the absence of these and any other pterosaurs in the semi-arid depositional environments of the Djadokhta and Barun Goyot formation is puzzling. Perhaps these settings were not favorable to pterosaurs. By Nemegt times pterosaurs may have finally vanished in Asia, as there is no known Maastrichtian record of this group for that continent (Barrett et al., 2008; note that these authors mistakenly placed localities from European Russia in Asia).

3.9 Dinosaurs

An abundance of excellently preserved dinosaurian specimens has been recovered from Late Cretaceous sites in North America and Central Asia, whereas dinosaurian material from Middle Asia typically comprises only incomplete, dissociated bones. However, isolated teeth of a variety of dinosaurs are common at most of the Late Cretaceous microvertebrate sites and can be used for biostratigraphic correlations. Some distinctive dinosaurian dental morphotypes appear to have a wide stratigraphic and geographic range. For example, the teeth of enigmatic theropod *Richar-doestesia isosceles* from the Campanian and Maastrichtian of North America (Sankey et al., 2002; Sankey, 2008) are virtually identical to those of *"Asiameicana" asiatica* from the Turonian of Middle Asia (Nessov, 1995; Sues & Averianov, unpublished data). Among the isolated theropod teeth, those of tyranosauroids and troodontids are most useful for correlation purposes.

BM 13) Tyrannosauroidea: 0) basal tyranosauroids with labiolingually compressed teeth [outgroup, Khodzhakul, Bissekty, Yalovach, Bostobe, Iren Dabasu, Upper Bayn Shire]; 1) more derived tyranosauroids with labiolingually thick (incrassate) teeth [Nemegt, Judithian, Lancian]; ?) unknown [Lower Bayn Shire, Djadokhta, Barun Goyot].

The biostratigraphic marker is based on character 201 listed by Brusatte et al. (2010). The derived state was independently acquired by two tyrannosaurid clades of Campanian to Maastrichtian age: Albertosauirinae and 

\[(Dasperosaurus + (Tarbosaurus + Tyrannosaurus)).\]

The absence of tyranosauroids in the Lower Bayn Shire is possibly a sampling artifact. Large theropods are known from the Djadokhta Formation at Ukhaa Tolgod (Dingus et al., 2008), but, at the present time, it is unknown if they are tyranosauroids and what kind of teeth they have.

BM 14) Troodontidae: 0) dental morphotype similar to *Saurornithoides* [outgroup, Khodzhakul]; 1) dental morphotype similar to *Saurornithoides* [Yalovach, Djadokhta, Nemegt]; 2) dental morphotype similar to *Troodon* [Judithian, Lancian]; ?) unknown [Bissekty, Bostobe, Iren Dabasu, Lower and Upper Bayn Shire, Barun Goyot].

The absence of troodontid teeth in the lower and upper parts of the Bayn Shire Formation and the Barun Goyot Formation of the Gobi Desert, which have not been systematically prospected for microvertebrate remains, possibly represents a sampling artifact. But their absence in the microvertebrate samples from the Bostobe Formation of Kazakhstan (Averianov, 2007b) is puzzling. Troodontids with serrated teeth are not known from the Cenomanian and Turonian of the central Kyzylkum Desert where *Urbacodon*, a taxon with unserrated teeth, is present (Averianov & Sues, 2007).

According to Currie & Eberth (1993: 136), in the Iren Dabasu Formation "troodontid bones are rare, but include distinctive third metatarsals […] in which the distal articulation extends onto the posterior surface of the bone in a broad tongue. A femur (PIN 2549/100, Kurzanov, 1987) collected by the Sino-Soviet expedition is probably from a troodontid. These bones are provisionally referred to *Saurornithoides*..." Subsequently, the presence of *Saurornithoides* sp. has been cited for the Iren Dabasu assemblage (e.g., Weishampel et al., 2004). However, Currie & Dong (2001: 1763-1764) later noted that the metatarsal III of the Iren Dabasu troodontid is more similar to that of *Troodon* and other troodontids rather than *Saurornithoides*. "The Iren Dabasu troodontid, therefore, can-
not be identified further without additional material...” (Currie & Dong, 2001: 1764). A femur from Iren Nor figured by Kurzanov (1987, Fig. 36) is probably troodontid but cannot be definitely referred to Saurornithoides. Thus, Saurornithoides should be removed from the faunal list of the Iren Dabasu Formation, and the material from this unit should be listed as Troodontidae indet.

BM 15) Ornithomimosauria: 0) non-arctometatarsalian [outgroup, Upper Bayn Shire]; 1) arctometatarsalian, with ginglymoid distal condyle of metacarpal I [Bissekty, Iren Dabasu]; 2) arctometatarsalian, with ball-like distal condyle of metacarpal I [Nemegt, Judithian, Lancian]; ?) unknown [Khodzhakul, Yalovach, Bostobe, Lower Bayn Shire, Djadokhta, Barun Goyot].

The biostratigraphic marker is based on apomorphic characters established by Kobayashi & Lü (2003) and Kobayashi & Barsbold (2005). Ornithomimosauria from the Khodzhakul, Yalovach, Bostobe, Djadokhta, and Barun Goyot formations are known from incomplete specimens that do not permit more precise identification (Ksepka & Norell, 2004; Alifanov & Averianov, 2006; Averianov, 2007b). The first state characterizes Garudimimus and more basal ornithomimosauria, the second Archaeornithomimus, Sinornithomimus, and the ornithomimosaur from the Bissekty Formation, and the third characterizes taxa from the Nemegt Formation (Anserimimus, Gallimimus) and North America (Ornithomimus, Struthiomimus).

Currie & Eberth (1993: 137) noted that “at least some of Archaeornithomimus specimens [from Iren Dabasu Formation] are actually Garudimimus”, which is known from the Upper Bayn Shire Formation (Bayshin Tsav & Barsbold, 1981; Kobayashi & Barsbold, 2005). Identification of Garudimimus in the Iren Dabasu fauna was based on the putative presence of the first pedal digit in a single arctometatarsalian metatarsal. The presence of a first pedal digit was inferred from a concave facet on the medial side of the second metatarsal (Smith & Galton, 1990). However, as was shown by Kobayashi & Barsbold (2005), the pes of Garudimimus, unlike that of Archaeornithomimus, is not arctometatarsalian. Furthermore, the contact surface for the first metatarsal in Garudimimus is located on the posterior rather than the medial surface of the second metatarsal (Kobayashi & Barsbold, 2005). Consequently, Garudimimus should be removed from the faunal list for the Iren Dabasu Formation.

BM 16) Alvarezsauridae: 0) absent [outgroup, Khodzhakul, Bissekty, Yalovach, Bostobe, Lower and Upper Bayn Shire, Judithian]; 1) basal Alvarezsauridae [Lancian]; 2) Parvicursorinae [Djadokhta, Barun Goyot, Nemegt].

We have adopted the phylogeny of Alvarezsauridae by Longrich & Currie (2009), but we follow Xu et al. (2010a) in using Parvicursorinae for the clade comprising the Mongolian alvarezsaurids. Chiappe et al. (2002: fig. 4.26A, B) referred an isolated fibula from Iren Dabasu to Alvarezsauridae, but this bone more likely belongs to Avimimus (Longrich & Currie 2009: 240). In China parvicursorines are known from strata older than the Djadokhta Formation (Xu et al., 2010a).

BM 17) Oviraptorosauria: 0) absent [outgroup, Khodzhakul, Yalovach, Lower and Upper Bayn Shire]; 1) Oviraptorosauria stem to Oviraptoridae [Bissekty, Bostobe, Iren Dabasu, Barun Goyot, Nemegt, Judithian, Lancian]; 2) Oviraptoridae (Oviraptorinae + Ingeniinae) [Djadokhta, Barun Goyot, Nemegt].

The phylogeny of Oviraptorosauria is based on Longrich et al. (2010). Stem Oviraptorosauria includes Avimimus, Gigantoraptor, and Caenagnathidae (including Elmisauridae).

BM 18) Therizinosauroidea: absent [outgroup, Djadokhta, Barun Goyot]; Therizinosauroidea basal to Therizinosauridae [Khodzhakul, Bissekty, Yalovach, Bostobe, Iren Dabasu, Lower Bayn Shire]; 2) Therizinosauridae [Lower and Upper Bayn Shire, Nemegt]; ?) unknown [Judithian, Lancian].

We have adopted the phylogeny of Therizinosauroidea by Zanno (2010). The semi-arid environments of the Djadokhta and Barun Goyot may not have been favorable for therizinosauroids. The status of alleged records of therizinosaurids from the Campanian and Maastrichtian of North America is uncertain (Zanno, 2010).

BM 19) Hadrosauroidea: 0) absent [outgroup]; 1) basal Hadrosauroidea [Khodzhakul, Bissekty, Yalovach, Bostobe, Iren Dabasu, Upper and Lower Bayn Shire]; 2) Hadrosauridae [Nemegt, Judithian, Lancian]; ?) unknown [Djadokhta, Barun Goyot].
The phylogeny of Hadrosauroidea is based on the analysis by Sues & Averianov (2009b), with Aralosaurus placed outside Hadrosauridae. Hadrosaurid remains from the Djadokhta and Barun Goyot formations are rare, fragmentary, and currently indeterminate. The single exception to date is an occurrence of several juvenile hadrosaurid skeletons at Tugrugyin Shireh (Barsbold & Perle, 1983). Perhaps hadrosaurids used these semi-arid environments for nesting, but preferred feeding in more humid, more richly vegetated settings. Hadrosaurid remains are common in the fluvial strata of the Bayn Shire, Bissekty, Iren Dabasu, and Nemegt formations.

BM 20) Saurolophus: 0) absent [outgroup, Khodzhakul, Bissekty, Yalovach, Bostobe, Iren Dabasu, Lower and Upper Bayn Shire, Djadokhta, Barun Goyot, Judithian]; 1) present [Nemegt, Lancian].

The crested hadrosaurine Saurolophus, from the Nemegt Formation of Mongolia and from unit 4 of the Horseshoe Canyon Formation of Alberta, Canada, is the only known Late Cretaceous dinosaurian genus definitely shared between Asia and western North America (Bell, 2011, in press). It provides important evidence for dating the Nemegt Formation as Maastrichtian.

BM 21) Pachycephalosauria: 0) absent [outgroup, Khodzhakul, Bissekty, Yalovach, Bostobe, Iren Dabasu, Lower and Upper Bayn Shire, Djadokhta, Barun Goyot, Judithian]; 1) present [Djadokhta, Barun Goyot, Nemegt, Judithian, Lancian].

In Mongolia, Pachycephalosauria is represented by rare but rather complete skeletal remains (Maryańska et al., 2004). In North America pachycephalosaurs are mostly known by isolated frontoparietals as well as teeth from the fluvial strata of Judithian and Lancian age (Baszio, 1997). Not a single tooth of this morphotype has been identified to date in any of the extensive microvertebrate assemblages from the Late Cretaceous of Middle Asia. Possibly pachycephalosaurs were not present in Asia prior to the Campanian.

BM 22) Hesperornithiformes: 0) absent [outgroup, Khodzhakul, Bissekty, Yalovach, Bostobe, Iren Dabasu, Lower and Upper Bayn Shire, Djadokhta, Barun Goyot]; 1) present [Nemegt, Judithian, Lancian].

3.11 Mammalia

The rapid evolution of many mammalian groups, the abundance of their fossil remains, and easy identification of taxa from dental remains were the main reasons for the development of the land mammal "ages" or biozones on most continents (e.g., Lindsay, 2003). Three principal land mammal ages have been proposed for the Late Cretaceous of North America: Aquilan (late Santonian to early Campanian), Judithian (middle Campanian), and Lancian (late Maastrichtian) (Russell, 1975; Cifelli et al., 2004; Kielan-Jaworowska et al., 2004). The mammalian taxa from these ages are mostly endemic and unknown outside North America, except for the eutherian Paranyctoides, which is also known from the Bissekty and Aitym formations (Turonian and ?Coniacian) in Middle Asia (Archibald & Averianov, 2001; Averianov & Archibald, 2003). The mammalian assemblages from Mongolia are for the most part endemic, but allow correlation among the various localities in the Gobi Desert (Kielan-Jaworowska, 1974; Kielan-Jaworowska et al., 2004).
2003). One Mongolian multituberculate, Bulganbaatar, is known also from the early Campanian nearshore strata with marine fossils in Kazakhstan (Darbasa Formation; Averianov, 1997), which would indicate a Campanian date for the Djadokhta Formation (which is supported by magnetostratigraphic data; Dashzeveg et al., 2005).

BM 23) Cimolodonta: 0) absent [outgroup only]; 1) Uzbekbaatar [Bissekt]; 2) Djadokthatheroidea [Djadokhta, Barun Goyot]; Cimolomyidae [Nemegt, Judithian, Lancian]; ?) unknown [Khozhakul, Yalovach, Bostobe, Iren Dabasu, Lower and Upper Bayn Shire].

Multituberculates were the most diverse and abundant group of mammals in the Late Cretaceous of North America and Central Asia. In the latter region this group is represented by numerous well-preserved skulls and skeletons (Kielan-Jaworowska et al., 2004). On the contrary, multituberculates are absent or very rare in the eutherian-dominated Late Cretaceous mammalian assemblages of Middle Asia. In the extensively sampled Bissekt fauna they represent about 1% of all mammalian fossils recovered to date (Archibald & Averianov, 2005; Averianov & Archibald, 2006). In the latter multituberculates are represented only by the archaic cimolodontan Uzbekbaatar, the phylogenetic position of which is unresolved (Kielan-Jaworowska et al., 2004; Averianov & Archibald, 2006). The relationships of Buginbaatar, the only multituberculate taxon from the Nemegt Formation, are also uncertain. It has provisionally been referred to Cimolomyidae (Kielan-Jaworowska et al., 2004; Averianov & Archibald, 2006). The multituberculates from the Nemegt have potential for biostratigraphic correlation between Late Cretaceous continental vertebrate localities in Asia. Additional discoveries of asioryctitherians from the fluvial formations of the Gobi Desert may be helpful in constraining the stratigraphic positions of these units.

BM 24) Deltatheridiidae: 0) absent [outgroup, Khodzhakul]; 1) Sulestes [Bissekt]; 2) Deltatheridium or Deltatheroides [Djadokhta, Barun Goyot, Judithian, Lancian]; ?) unknown [Yalovach, Bostobe, Iren Dabasu, Lower and Upper Bayn Shire].

The metatherian clade Deltatheridiidae is a clade of Late Cretaceous eutherians endemic to Asia and also has potential for biostratigraphic correlation. In the Khodzhakul Formation Deltatheridiidae is represented only by a single isolated petrosal to date (Averianov & Archibald, 2005). Kulbeckia is best known from the Bissekt Formation of Uzbekistan, but some teeth have also been recovered from the Yalovach Formation of Tajikistan (Archibald & Averianov, 2003). Kulbeckia is close to the Bissekt Formation of Uzbekistan, but some teeth have also been recovered from the Yalovach Formation of Tajikistan (Archibald & Averianov, 2003). Kulbeckia is more similar to Kulbeckia than to any of the Mongolian zalambdalestids (Averianov & Nessov, 1995). Beleutinus, a poorly known zalambdalestid taxon from the Bostobe Formation of Kazakhstan, is more comparable in its "stage of evolution" to Kulbeckia than to any of the Mongolian zalambdalestids (AA, personal observation). Alymolestes from the Campanian of Kazakhstan has a derived structure of the lower molars similar to that of the Mongolian zalambdalestids (Averianov & Nessov, 1995).

4 Parsimony analysis

The data matrix comprises 13 vertebrate assem-
blages and 26 biostratigraphic markers (Table 1) and was analyzed using three parsimony programs. Implementation of the branch and bound search algorithm of PAUP, version 4.0b10 (Swofford, 2002), produced five trees, each with a length of 65 steps, a consistency index of 0.80, and a retention index of 0.83. TNT (Goloboff et al., 2003; new technology search algorithm) and NONA version 2.0 (Goloboff, 1999; 1,000 repetitions of the parsimony ratchet algorithm) run with the Winclada version 1.00.08 interface (Nixon, 1999) both produced two trees, each with a length of 59 steps, a consistency index of 0.88, and retention index of 0.87. The latter result, requiring fewer transformations, is accepted here. Both most parsimonious trees are illustrated in Fig. 2. Only unambiguously optimized apomorphic biostratigraphic markers are shown in Fig. 2 and discussed here.

The two most parsimonious trees differ in the topology of segment A (Fig. 2), with the North American faunas either basal (tree 1) or apical (tree 2) to the assemblage from the Nemegt Formation.

The most basal of the vertebrate assemblages discussed in this paper is Khodzhakul. Its marker taxa are Eoscapherpeton gracilis (3[1]) and Ferganemys (5[1]). The more apical assemblages are united by the absence of ornithocheirid pterosaurs (12[1]) and presence of Hybodus kansaiensis (1[2]). The cluster next branching off unites the two Bayn Shire assemblages based on the shared presence of Hanbogdemys (6[1]). The more apical assemblages are united by the absence of Kizylkumemys (4[1]) and the presence of Oviraptorosauria stem to Oviraptoridae (17[1]). These assemblages are divided into two groups, a Middle Asian one plus Iren Dabasu and a variable segment A. The first group is supported by the shared presence of Khunnuchelys (7[1]). The Middle Asiatic assemblages share the presence of the crocodyliforms Kansajsuchus (10[1]) and Tadzhikosuchus (11[1]). The Yalovach and Bostobe assemblages share the presence of Myledaphus glickmani (2[2]).

The Gobi and North American assemblages are united either by the presence of tyrannosaurids with halosauria and Mongolemys (8[2]) (tree 2). On Tree 1 the North American complexes share the absence of Shamosuchus (9[0]) and the presence of Leidyosuchus (11[2]) and Troodon (14[2]). The presence of Parvencerorinae (16[2]) unites the Gobi faunas, and the pachycephalosaurian teeth (13[1]), Hadrosauridae (19[2]), and Pachycephalosauria (21[1]) (tree 1) or by Pachycephalosauria presence of Djadokthatheroidea (23[2]) unites the

![Fig. 2](image-url)  
**Fig. 2** Two most parsimonious trees produced by the parsimony ratchet algorithm of NONA version 2.0 using the data matrix present in Tab. 1

The trees differ in the topology of segment A. Only unambiguous biostratigraphic markers are shown (black circles represent nonhomoplasies and white circles represent homoplasies). The numbers at the circles are biostratigraphic markers (above) and states (below).
Pachycephalosauria (21[1]) (tree 1) or by Pachycephalosauria (23[2]) unites the Djarakuduk and Barun Goyot assemblages. On Tree 2 the Nemegt and North American faunas are grouped together by the presence of Hesperornithiformes (22[1]), and the North American faunas share the absence of Lindholmemys (8[0]) and Shamosuchus (9[0]) and the presence of Leidyosuchus (11[2]) and Troodon (14[2]).

5 Succession of the Late Cretaceous vertebrate assemblages in Middle and Central Asia

5.1 Middle Asia

In the Kyzylkum Desert there are two principal Late Cretaceous vertebrate-bearing formations: the early Cenomanian Khodzhakul Formation in the southwestern Kyzylkum and the middle to late Turonian Bissekty Formation in the central Kyzylkum. Archibald & Averianov (2005) named the vertebrate assemblages from these stratigraphic units the Sheikhdzheili and Bissekty local faunas, respectively. However, the first fauna is named after the most important locality and the second name is derived from a stratigraphic unit. For the sake of consistency, we here use only names for vertebrate local faunas that are derived from their respective stratigraphic units rather than the principal localities. Thus, we now refer to the Sheikhdzheili local fauna of Archibald & Averianov (2005) as the Khodzhakul local fauna.

The turtle assemblage of the Khodzhakul Formation is characterized by the presence of Ferganemys and Kizylkumemys, which are absent from younger faunal assemblages in Middle Asia. Ferganemys was originally described from the Lower Cretaceous of Kyrgyzstan (Nessov & Khozatsky, 1977). Syromyatnikova (2011) has recently questioned the referral of the Kyzylkum species, F. itemirensis, to the same genus. Ferganemys itemirensis was first described from the Cenomanian of the central Kyzylkum Desert (Nessov, 1981). Kizylkumemys and Ferganemys appear to be useful taxa for correlating pre-Turonian vertebrate assemblages in Middle Asia.

The dinosauromorph assemblages from the Khodzhakul and Bissekty formations are remarkably similar at the family level. This is not surprising in view of their geographic proximity and similar ages (both faunas are separated by an interval of only five to eight million years). The most conspicuous difference between the two faunas is the presence of the basal neoceratopsian Asiaceratops in the Khodzhakul assemblage, where it was one of most common herbivorous dinosaurs. In the Bissekty local fauna basin neoceratopsians are apparently represented by a rare, distinct taxon. In this fauna there is also a second ceratopsian, the stem ceratopsid Turanoceratops (Sues & Averianov, 2009a). Turanoceratops is not common in the Bissekty local fauna and unknown from the Khodzhakul local fauna to date. There are some minor morphological differences between the ornithomimids, therizinosaurids, and hadrosauroids from these faunas. However, it is difficult to evaluate these differences because of the fragmentary nature of the available Khodzhakul dinosaurian remains.

Only eutherians are known from the Khodzhakul mammalian assemblage: the stem eutherian Bobolestes, plesiomorphic zhelestids, and a possible zalambdalestid (Averianov & Archibald, 2005). Zhelestids are represented by taxa less derived than those from the Bissekty local fauna.

A vertebrate assemblage from the Cenomanian Dzharkuduk Formation at Itemir in the Itemir-Dzharkuduk Depression of the central Kyzylkum closely resembles the Khodzhakul local fauna in its composition. It includes five taxa of dinosaurs: Tyrannosauridae indet., Urbacodon itemirensis (Troodontidae), Neosauropoda indet., Haddosauropoidea indet., and Asiaceratops salsopaludalis (Neoceratopsia). Skeletal remains of Asiaceratops are common at this locality and indistinguishable from those from sites in Karakalpakistan. The latter have yielded a troodontid with un serrated teeth, whereas the Khodzhakul fauna has a troodontid with serrated teeth. A similar taxon with un serrated teeth, Urbacodon sp., is present in the younger Bissekty local fauna of the same region (Averianov & Sues, 2007). Currently it is unclear if this similarity is due to the close geographic proximity of the two localities or the younger geological age of the Itemir local fauna relative to the Khodzhakul local fauna. The presence of Ferganemys and Kizylkumemys as well as ornithocheirid pterosaurs in the Dzhara-
The only Cenomanian vertebrate assemblages known in Middle Asia outside the Kyzylkum Desert are those from the Sharikhan and other formations in the Fergana Depression of Kyrgyzstan. These units have yielded only incomplete dinosaurian remains, including large Theropoda indet. (Tyrannosauroidea?), Ornithomimosauria indet., Sauropoda indet., and Hadrosauridea indet. (Nessov, 1995; Averianov, 2006).

In the Itemir-Dzharakuduk Depression the Cenomanian and Turonian dinosaur-bearing fluvial deposits are separated by a thick marine section deposited during the early Turonian transgression (Uchkuduk and Dzhairantan formations; Pyatkov et al., 1967; King, personal communication). Similarly, the fluvial deposits of the Cenomanian Khodzhakul Formation in Karakalpakstan are overlain by the early Turonian marine strata of the Beshtyube Formation (Schultz, 1972; King, personal communication). During this early Turonian transgression a significant faunal turnover took place among marine vertebrates and freshwater turtles (Nessov & Golovneva, 1983; Nessov, 1997). However, terrestrial vertebrates, including dinosaurs, seem to have been little affected by this turnover. A notable exception is the disappearance of ornithocheirid pterosaurs in the region after the Cenomanian (Averianov, 2007a), which may have been related to changes in the fish fauna.

The vertebrates from the Aitym Formation at Dzharakuduk (Aitym local fauna) come from nearshore marine deposits with numerous remains of a diversity of chondrichthyan and other fishes. This stratigraphic unit marks a transgression following the deposition of the fluvial Biszekty Formation, possibly during the latest Turonian or Coniacian (King, personal communication). The few dinosaurian teeth recovered to date from the Aitym Formation are indistinguishable from those from the underlying Biszekty Formation. The mammalian fauna is also very similar, except for the presence of a slightly more derived species of the multituberculate *Uzbekbaatar*, which also appears to be more common here (Averianov & Archibald, 2003).

The marine transgression continued in the Kyzylkum region during the Santonian and Campanian and reached its peak in the Maastrichtian (Pyatkov et al., 1967; King, personal communication). This explains the rarity of dinosaur occurrences in the Kyzylkum Desert for this time interval.

The Turonian Zhirkindek Formation in the Aral Sea region of Kazakhstan is coeval with the Biszekty Formation of Uzbekistan. Its poorly known dinosaurian assemblage includes Tyrannosauroidea indet., Ornithomimosauria indet., Therizinosauroida indet., Dromaeosauridae indet., Sauropoda indet., Hadrosauridea indet., and Neoceratopsia indet. (Nessov, 1995; Kordikova et al., 2001; Averianov, 2007b; Averianov & Sues, 2009). The hadrosaurid bones from the Zhirkindek Formation are very similar to those of *Levnesovia* from the Biszekty local fauna (Sues & Averianov, 2009b). The only difference between the two faunas is the presence of a large basal neoceratopsian in the Zhirkindek fauna (Averianov & Sues, 2009). Other vertebrates from the Zhirkindek Formation include fishes, turtles, lizards, and crocodyliforms (Kordikova et al., 2001) but these materials have not yet been studied in detail.

Younger, Santonian vertebrate faunas are known in Middle Asia from regions unaffected by the post-Turonian marine transgression. These are the Yalovach local fauna in the Fergana Depression of Tajikistan and the Bostobe local fauna in the Aral Sea region of Kazakhstan. All common groups of dinosaurs in the Biszekty local fauna are also present in the Santonian faunas. The Bostobe hadrosaurid *Aralosaurus* is distinctly more derived than the Biszekty hadrosaurid *Levnesovia* (Sues & Averianov, 2009b), which is consistent with a younger, Santonian or possibly even early Campanian age for the Bostobe Formation. Troodontids are currently unknown from the Bostobe local fauna, but are represented in the Yalovach local fauna by a taxon with serrated teeth (Averianov & Sues, 2007), unlike *Urbacodon* with unserrated teeth from the Biszekty local fauna. Rich microvertebrate samples have been recovered from both the Yalovach and Bostobe formations (Nessov, 1997; Kordikova et al., 2001), but these materials have not yet been fully documented.

The Turonian-Santonian vertebrate faunas of Middle Asia are set apart biogeographically from the Cen-
Central Asian Late Cretaceous faunas by the presence of the endemic crocodyliforms *Kansajsuchus* and *Tadzhikosuchus*. Eusuchians are unknown in the Late Cretaceous of Central Asia, but are present in North America (*Leidyosuchus*). The crocodyliform *Shamosuchus* is common in the Late Cretaceous faunas of Middle and Central Asia, but is unknown in North America. The other distinct taxon for the Turonian-Santonian vertebrate assemblages of Middle Asia is the trionychid turtle *Khunnuchelys*. In Central Asia it is known only from the Iren Dabasu fauna (Brinkman et al., 1994).

Campanian vertebrates in Middle Asia are known from a microvertebrate sample obtained from nearshore marine strata of the Darbasa Formation in southern Kazakhstan. Only the mammal and troodontid teeth from this sample have been described to date (Averianov & Nessov, 1995; Averianov, 1997; Averianov & Sues, 2007). This fauna is notable for the presence of the multituberculate mammal *Bulganbaatar*, which was originally reported from the Djadokhta Formation of Mongolia. The zalambdalestid mammal *Alymlestes* from the Darbasa Formation is similar in its "stage of evolution" to the Campanian zalambdalestids from Mongolia and clearly more derived than *Kulbeckia* from the Turonian Bissekty fauna.

Only marine vertebrates, mostly sharks and mosasaurs, are currently known from the Maastrichtian of Middle Asia (Nessov, 1997).

### 5.2 Central Asia

Nessov's pioneering work on the Cretaceous vertebrates from the Kyzylkum Desert suggested that the Bissekty fauna most closely resembles that from the Iren Dabasu Formation of Inner Mongolia, China (Nessov, 1995, 1997). This correlation led to Nessov to refer certain dinosaurs from the Bissekty local fauna to genera previously reported from the Iren Dabasu fauna: *Alectrosaurus* sp., *Archaeornithomimus* (?) *bissektensis*, *Gilmoreosaurus arkhangelskyi*, and *Bactrosaurus kysylkumensis* (Nessov, 1995). The practice of attribution of fragmentary materials to taxa known from more complete specimens in a different locality leads to circular reasoning when the relative age of localities is considered. Based on our own work we have reidentified these Bissekty dinosaurs as Tyranosauroida indet., Ornithomimosauria indet., and *Levesnovia transoxiana* or Hadrosauroida indet. Nevertheless, the Iren Dabasu local fauna appears to be quite similar to the Bissekty local fauna in composition and evolutionary level of the taxa concerned.

The hadrosauroids *Levesnovia* and *Bactrosaurus* are certainly closely related (Sues & Averianov, 2009b). The principal difference between the dinosaurs from the two faunas is the presence of different groups of oviraptorosaurs. In the Bissekty there is the small caenagnathid *Caenagnathasia*, whereas the Iren Dabasu local fauna includes an avimimid and the large oviraptorosaur *Gigantoraptor*. Caenagnathidae are currently known only from the Late Cretaceous of North America and Middle Asia, but *Elmisaurus* and *Nomingia* from the Nemegt Formation of Gobi Desert are probably additional representatives of this clade in Central Asia (Osmólska et al., 2004). This faunal difference may reflect the different environmental and paleogeographic positions of the two faunas (coastal plains of Middle Asia versus inland areas of Central Asia) rather than a difference in stratigraphic age. The similarities between the Iren Dabasu and Nemegt biotas in the charophytes and freshwater ostracodes (Van Itterbeeck et al., 2005) and the shared presence of *Avimimus* (or Avimimidae) probably reflect fluvial depositional settings and mesic climatic conditions (Jerzykiewicz & Russell, 1991) rather than similarity in age. This is especially evident when these assemblages are compared with those from the Djadokhta Formation, which represent semi-arid settings (Jerzykiewicz & Russell, 1991). The presence in the Iren Dabasu fauna of the turtle *Khunnuchelys*, which is otherwise known only from the Turonian to Santonian of Middle Asia (Brinkman et al., 2004; Vitek & Danilov, 2010), also suggests a pre-Campanian age for this assemblage.

The poorly known Shireegiin Gashuun local fauna of the Gobi Desert of Mongolia with the small basal neoceratopsian *Graciliceratops* is similar in its composition to the Cenomanian Khodzhakul and Dzharakuduk faunas of Middle Asia, which are dominated by the small basal neoceratopsian *Asiaceratops*. However, the presence of the turtle *Lindholmemys* in this forma-
tion (Danilov & Sukhanov, 2001) suggests a younger, possibly Turonian to Santonian age for this unit.

The Bayn Shire Formation in the eastern Gobi Desert of Mongolia has been traditionally correlated with the Iren Dabasu Formation of Inner Mongolia (Currie & Eberth, 1993; Nessov, 1995, 1997; Hicks et al., 1999; Averianov, 2002). Based on the stratigraphic ranges of the turtles, this unit can be divided into a lower, Cenomanian to early Turonian part with *Kizylkumemys* and an upper, late Turonian to Santonian part with *Lindholmemys* (Nessov, 1997; Sukhanov et al., 2008). Based on magnetostratigraphic data, Hicks et al. (1999) argued that the Bayn Shire Formation was most likely deposited no later than the latest Santonian. Sukhanov (2000) also reported *Kizylkumemys* from the upper part of the Bayn Shire Formation. *Lindholmemys* is known also from the Iren Dabasu Formation but is absent from the younger, Campanian to Maastrichtian faunas of the Gobi Desert, where it is replaced by *Mongolemys* (Currie & Eberth, 1993; Danilov & Sukhanov, 2001). There are no dinosaurian genera known to be shared between the lower and upper parts of the Bayn Shire Formation.

Based on the occurrences of turtles and dinosaurs, Nessov (1997) correlated the lower and upper parts of the Bayn Shire Formation with the Khodzhakul and Bissekty formations in Middle Asia, respectively. Although these stratigraphic units share no dinosaurian genera, this correlation is plausible given the similar evolutionary levels of the dinosaurs, notably the therizinosaurids and ankylosaurs. The Bissekty therizinosauroid closely resembles *Erlikosaurus* from the upper Bay Shire fauna. The postcranial elements of *Bissektipelta* from the Bissekty Formation are almost identical to those of *Talarurus* from the upper Bay Shire and differ from those of more derived, stratigraphically younger ankylosaurs.

The remarkably diverse faunas known from the Djadokhta and Barun Goyot formations document the next (Campanian) stage of vertebrate evolution in the Gobi Desert. The dinosaurs from these units differ considerably from those of the Bissekty fauna in 1) the rarity of tyrannosaurs, ornithomimids, and hadrosaurs; 2) presence of diverse alvarezsaurids and oviraptorids, which are not known in Middle Asia; 3) presence of pachycephalosaurs; and 4) abundance of basal neoceratopsians ("protoceratopsids"), which are very rare in the Bissekty fauna. The highly diverse lizard faunas of the Djadokhta and Barun Goyot formations do not have direct parallels in other regions. A dentary fragment of a lizard from the Bostobe Formation of Kazakhstan, identified as *Slavoia* by Kordikova et al. (2001), is best referred to as Scinicomorpha indet. Multituberculate mammals are represented by an endemic clade Djadokhtatherioidea, which is unknown in other regions except for *Bulganbaatar* from Kazakhstan (Averianov, 1997). The therian mammals from the Gobi assemblages show more similarities with the faunas from Middle Asia. Deltatheridiidae, Asio-ryctitheria, and Zalambdalestidae are present in both regions, but the Mongolian taxa are clearly more derived than those from the Turonian of Uzbekistan (Archibald & Averianov, 2006; Averianov et al., 2010). However, the most remarkable difference between the Late Cretaceous mammalian faunas of Middle and Central Asia is the dominance of Zhelestidae in the former and their complete absence in the latter.

In the Maastrichtian the faunas of the Djadokhta and Barun Goyot formations were replaced by the fauna of the fluvial strata of the Nemegt Formation. The Nemegt dinosaurian assemblage differs markedly from those of the Djadokhta and Barun Goyot formations in the abundance of ornithomimids (*Gallimimus*), dominance of tyrannosaurs (*Tarbosaurus*) and hadrosaurs (*Saurolophus*), and the absence of "protoceratopsids". In this respect the Nemegt fauna resembles the Bissekty fauna, but this similarity, for the most part, probably reflects similar floodplain depositional environments rather than geological age. The tyrannosaurs, ornithomimids, therizinosaurids, and hadrosaurs of the Nemegt fauna all are distinctly more derived than related taxa from the Bissekty fauna. The Nemegt dinosaurian fauna is also ecologically similar to the assemblage from the Iren Dabasu Formation, which sometimes has led to the mistaken impression that these two faunas are comparable in age.

The stratigraphic correlation of the principal Late Cretaceous vertebrate faunas of Middle and Central Asia proposed in this paper is illustrated in Fig. 3.
6 Discussion

Jerzykiewicz & Russell (1991) proposed a succession of seven Cretaceous Mongolian Land Vertebrate "Ages" ("MOLVAs"), including four for the Late Cretaceous: Saynshandian, Baynshirenian, Barungoyotian, and Nemegtian. All these "ages" were modified versions of the biostratigraphic horizons used by Soviet geologists (see Barsbold, 1983). This explains appearance of the earliest Late Cretaceous Saynshandian "MOLVA" for which no actual vertebrate fossils were known (Jerzykiewicz & Russell, 1991) but which is characterized by a distinct assemblage of freshwater mollusks (Martinson, 1982). In Inner Mongolia (China), the Iren Dabasu and Bayan Mandachu formations could be easily referred to the Baynshirenian and Barungoyotian MOLVAs, respectively (Lucas & Estep, 1998). Less certain is the reference of the vertebrate assemblage from the Wangshi Series of Shandong (China) to the Barungoyotian MOLVA (Lucas & Estep, 2008). The only shared taxon between Gobi and Shandong dinosaurian assemblages is the ankylosaurid *Pinacosaurus* (Buffetaut, 1995). However, the lack of cranial material for the Shandong ankylosaurid renders this identification questionable. In contrast to the Barungoyotian faunas of Gobi, the Shandong dinosaurian assemblage is dominated by hadrosauroids, including the basal hadrosaurid *Tanius*, the giant saurolophine *Shantungosaurus*, and the lambeosaurine *Tsintaosaurus* (Prieto-Márquez, 2010). Ceratopsia is represented by *Sinoceratops*, identified as the most basal centrosaurine ceratopsid, and the leptoceratopsid *Zhuchengceratops* (Xu et al., 2010b, c). There is also a tyrannosaurid *Zhuchengtyrannus*, which closely resembles the Nemegtian *Tarbosaurus* (Hone et al., 2011). Currently there are no non-dinosaurian vertebrates recorded from the Wangshi Series, and thus this vertebrate assemblage was not included into our analysis. The Wangshi Series is possibly Campanian in age, and its dinosaurian assemblage resembles contemporaneous dinosaurian faunas from North America more closely than the Gobi faunas (Prieto-Márquez, 2010; Xu et al., 2010b, c). Lucas & Estep (1998) also referred to the Nemegtian MOLVA several poorly known dinosaur assemblages in Xinjiang and Guandong provinces of China.

The concept "Land Vertebrate Ages" is potentially useful for correlation of the assemblages of Late Cretaceous continental vertebrates in Asia, but "Mongo-
lian Land Vertebrates Ages" ("MOLVAs") should be transformed to "Asian Land Vertebrate Ages" ("ALVAs") and formally defined. The paucity of data concerning non-dinosaurian vertebrates in many East Asian localities makes such a zonation scheme premature at present.

Acknowledgments We thank Igor Danilov, Chris King, Pavel Skutschas, and Elena Syromyatnikova for information and advice. We gratefully acknowledge financial support of the National Science Foundation (EAR-9804771 and EAR-0207004 to J.D. Archibald and H.-D. Sues), the National Geographic Society (#5901-97 and #6281-98 to J.D. Archibald and H.-D. Sues), the Civilian Research and Development Foundation (RU-G1-2571-ST-04 and RUB1-2860-ST-07), and the Russian Fund of Basic Research (07-04-91110-AFGIRa). Averianov also received research support from the President's of Russia grant MD 255, 2003.04 and the Russian Fund of Basic Research grants 04-04-49113, 04-04-49637, 07-04-00393, and 10-04-01350, by the Ministry of Education and Science of Russian Federation (contract 16.518.11.7070), and from a Paleontological Museum grant of Saint Petersburg State University. We thank Benjamin Sames and Spencer Lucas for constructive reviews of the manuscript.

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