

中亚与亚洲中部晚白垩世的陆生脊椎动物组合对比^①

A. AVERIANOV¹⁾ H.-D. SUES²⁾

1) 俄罗斯科学院动物研究所 俄罗斯圣彼得堡 199034;

2) 史密森森协会自然历史博物馆古生物学部 美国华盛顿特区 20013-7012

摘要: 通过对前人建议的 26 个生物地层标志化石存在与否的简约分析, 中亚与亚洲中部晚白垩世的陆生脊椎动物组合的相对层位得到了更清楚的揭示。此区最古老的组合是乌兹别克斯坦克孜勒库姆沙漠的 Khodzhakul 组合(早塞诺曼期), 其次为蒙古戈壁沙漠东部 Bayn Shire 组的下部和上部的组合(塞诺曼期至桑顿期)。中国内蒙古二连达布苏动物群与中亚的土伦期—桑顿期动物群属于同一类群, 因为它们均具龟鳖类 *Khunnuchelys*, 前者时代可能为桑顿期。三个中亚的组合(Bissekty、Yalovach 和 Bostobe 组合)中有两个地方性的鳄形类(*Kansajsuchus* 和 *Tadzhikosuchus*)和一个出现于戈壁沙漠的鳄形类(*Shamosuchus*)化石。戈壁沙漠的坎潘期至马斯特里赫特期组合与北美同期动物群为同一类群。Djadokhta 组与 Barun Goyot 组的坎潘期脊椎动物组合具有高度的地方性, 并反应了半干旱的古环境。产自 Nemegt 组的组合生存于比较潮湿的环境。在组成上, 这一组合与其他河流相沉积环境(Bissekty、二连达布苏以及北美 Judithian 期和 Lancian 期的组合)相似。具顶饰的鸭嘴龙 *Saurolophus* 的存在, 支持了 Nemegt 组合为马斯特里赫特期时代。戈壁沙漠的这三个组合(Djadokhta、Barun Goyot 和 Nemegt 组合)被归为一类, 因为它们共同拥有地方性的龟类 *Mongolemys* 和兽脚亚目的小驰龙类。亚洲中部和北美的坎潘期至马斯特里赫特期组合与亚洲更加古老的组合不同在于存有暴龙科、肿头龙亚目和鸭嘴龙科。在中亚, 由于地区性的海侵, 这一时间段内的陆生脊椎动物组合多不清楚。

关键词: 生物地层学, 脊椎动物, 晚白垩世, 中亚, 亚洲中部

中图法分类号: P 534.53

文献标识码: A

文章编号: 0253-4959 (2012) 02-0462-24

CORRELATION OF LATE CRETACEOUS CONTINENTAL VERTEBRATE ASSEMBLAGES IN MIDDLE AND CENTRAL ASIA

A. AVERIANOV¹⁾ and H.-D. SUES²⁾

1) Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, Saint Petersburg 199034, Russia, e-mail: dzharakuduk@mail.ru;

2) Department of Paleobiology, National Museum of Natural History, Smithsonian Institution MRC 121, P.O. Box 37012, Washington, DC 20013-7012, U.S.A.

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 biostratigraphic 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 *Khunnuchelys* 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*) but share another crocodyliform

国家自然科学基金(No.91114201)和国家重点基础研究发展计划(2012CB821906)资助出版。

文稿接受日期: 2011-08-17; 修改稿收到日期: 2012-03-31。

第一作者简介: 博士, 研究员, 主要从事古脊椎动物和地层研究; E-mail: dzharakuduk@mail.ru

(*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 as-

sess 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 endemism 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).

1) Khodzshakul Formation, southwestern Kyzylkum Desert, Uzbekistan. Principal localities: Khodzshakul, Sheikhdzheili, and Chelpyk.

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)

	0	1	2
outgroup	12345678901234567890123456		
Khodzshakul	000000000000000000000000		
Bissekty	10101?0110000?0011000?00?		
Yalovach	2121201111110?101110001111		
Bostobe	22313011111101?0011000???1		
Iren Dabasu	21010?11100?0?10111000????		
Bayn Shire Lower	??000101100?????00?1000????		
Bayn Shire Upper	2?00010110010?00021000????		
Djadokhta	??010?02100??1?220?0102222		
Barun Goyot	??010202100?????2?0?0102233		
Nemegt	??010?02100?1122?221113???		
Judithian	33010300002112201?20113200		
Lancian	43010300002112211?21113200		

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: Shakh 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 Burkhan.

8) Djadokhta Formation, Gobi Desert, Mongolia and China. Principal localities: Bayn Dzak, Ukhaa Tolgod, Baga Tarjach, Alag Teer, Boro Khovil, Tugrugen Shire, and Bayan Mandahu.

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

10) Nemegt Formation, Gobi Desert, Mongolia. Principal localities: Nemegt, Altan Ula I-IV, Bugiin Tsav, Khermeen Tsav (white beds), Gurileen Tsav, Nogon Tsav, Tsagan Khushu, and Naran Bulak.

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.

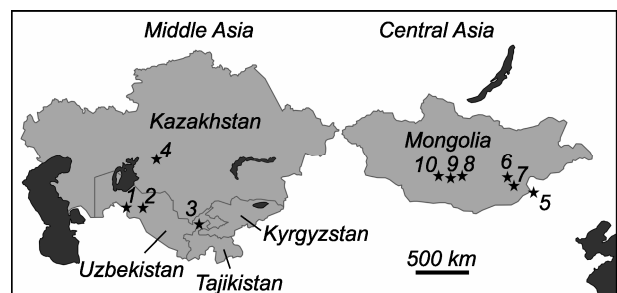


Fig. 1 Approximate geographic locations of the assemblages of Late Cretaceous continental vertebrates in Middle and Central Asia discussed in this paper

1. Khodzshakul; 2. Bissekty; 3. Yalovach; 4. Bostobe; 5. Iren Dabasu; 6. Lower Bayn Shire; 7. Upper Bayn Shire; 8. Djadokhta; 9. Barun Goyot; 10. Nemegt

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). Nessonov (1997) presented a long list of shark species for the fluvial 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 *Myledaphus* (Mertinene & Nessonov, 1985; Nessonov & Mertinene, 1986; Nessonov et al., 1994).

BM 1) *Hybodus*: 0) absent [outgroup only]; 1) *H. hodzhakulensis* [Khodzhakul]; 2) *H. kansaiensis* [Bissekty, Yalovach, Bostobe, 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* (Nessonov & Mertinene, 1986; Nessonov, 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) *Myledaphus*: 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].

Myledaphus is the most common freshwater elasmobranch 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 *Myledaphus* first appeared in the uppermost (upper Cenomanian or lower Turonian) portion of the Khodzhakul Formation (Karachadalysai; Nessonov, 1997; AA, unpublished data). These teeth are referable to *M. tritus*, which is also known from the Turonian Bissekty Formation (Nessonov & Udovichenko, 1986; Nessonov, 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 Nessonov & Udovichenko, 1986; generic attribution based on Cappetta [1992]). The teeth of the three species of *Myledaphus* 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; Nessonov, 1985, 1997; Bryant, 1989; Nessonov & 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* (Nessonov & Golovneva, 1983; Nessonov, 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 Khodzhaikul Formation and possibly a single specimen from the Turonian Bissekty 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* [Khodzhaikul]; 2) *E. asiaticum* [Bissekty]; 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-Białynicka, 1978; Špinar & Tatarinov, 1986; Gubin, 1999; Roček, 2008). The discoglossid (or gobiatid) genus *Gobiates*, which is known from the Bissekty 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, Khodzhaikul, Lower and Upper Bayn Shire]; 1) absent [other assemblages].

Kizylkumemys is a pitted-shell turtle (Carettochelyidae) first described from the Cenomanian Khodzhaikul Formation of the southwestern Kizylkum Desert of Uzbekistan (Nessov, 1977). It is also known from the Cenomanian Dzharakuduk Formation of the central Kizylkum 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* [Khodzhaikul]; 2) *Shachemys ancestralis* [Bissekty]; 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, Bissekty, 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 *Shachemydinae*. 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 Bissekty 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 *Aspideretoides*, which is known from the Campanian to Maastichtian of North America and the Santonian to Cam-

panian of Middle Asia (Gardner et al., 1995; Vitek & Danilov, 2010).

BM 8) *Lindholmemydidae*: 0) absent [outgroup, Judithian, Lancian]; 1) *Lindholmemyd* [Khodzhakul, Bissekty, 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. *Lindholmemyd* 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 *Lindholmemyd* (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*, *Zaraasuchus*, *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

[outgroup, Khodzhakul]; 2) Azhdarchidae only [Bissekty, Yalovach, Bostobe, Upper Bayn Shire, Judithian, Lancian]; ?) no pterosaur records [Iren Dabasu, Lower Bayn Shire, Djadokhta, Barun Goyot, Nemegt].

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 *Richardoestesia isosceles* from the Campanian and Maastrichtian of North America (Sankey et al., 2002; Sankey, 2008) are virtually identical to those of "*Asiamericana*" *asiatica* from the Turonian of Middle Asia (Nessov, 1995; Sues & Averianov, unpublished data). Among the isolated theropod teeth, those of tyrannosauroids and troodontids are most useful for correlation purposes.

BM 13) Tyrannosauroidea: 0) basal tyrannosauroids with labiolingually compressed teeth [outgroup, Khodzhakul, Bissekty, Yalovach, Bostobe, Iren Dabasu, Upper Bayn Shire]; 1) more derived tyrannosauroids 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: Albertosaurinae and (*Daspletosaurus* + (*Tarbosaurus* + *Tyrannosaurus*)). The absence of tyrannosauroids 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 tyrannosauroids and what kind of teeth they have.

BM 14) Troodontidae: 0) dental morphotype similar to *Sinornithoides* [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). Ornithomimosaur 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 ornithomimosaur, 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 metatarsus. 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 Elmsauridae).

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 semiarid environments of the Djadokhta and Barun Goyot may not have been favorable for therizinosauroids. The status of alleged records of therizinosaur 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. Hadrosauroid 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 hadrosauroid skeletons at Tugrugyin Shireh (Barsbold & Perle, 1983). Perhaps hadrosauroids used these semi-arid environments for nesting, but preferred feeding in more humid, more richly vegetated settings. Hadrosauroid 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]; 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.

3.10 Aves

The fossil record of Late Cretaceous birds is generally sparse but a number of rather complete specimens have been recovered from the Gobi Desert (Elzanowski, 1977; Kurochkin, 1996, 2000; Chiappe et al., 2001; Clarke & Norell, 2002). In Middle Asia,

Enantiornithiformes and taxa of uncertain affinities are known from isolated bones or bone fragments (Kurochkin, 2000; Chiappe & Walker, 2002). In Mongolia, both enantiornithiform and ornithuran birds were present, whereas ornithurans predominate in the Judithian and Lancian of North America (Kurochkin, 2000; Hope, 2002; Clarke & Norell, 2004; Longrich, 2009). The majority of the Late Cretaceous taxa of Enantiornithiformes and Ornithurae from Asia are endemic and thus not useful for interregional correlations. However, one group, Hesperornithiformes, is potentially important for biostratigraphy. In North America this group ranges from the Cenomanian to the Maastrichtian (Tokaryk et al., 1997; Everhart & Bell, 2009; Wilson et al., 2011). In Europe Hesperornithiformes are present during the Campanian (Nessov & Yarkov, 1993; Panteleyev et al., 2004; Rees & Lindgren, 2005). In Asia all known records of Hesperornithiformes appear to be Maastrichtian in age (Nessov & Borkin, 1983; Nessov & Prizemlin, 1991; Kurochkin, 2000; Dyke et al., 2006).

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.,

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* [Bissekty]; 2) Djadokhtatheroidea [Djadokhta, Barun Goyot]; Cimolomyidae [Nemegt, Judithian, Lancian]; ?) unknown [Khodzhakul, 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 Bissekty 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), and is more similar to certain North American taxa than to any other multituberculate taxon from the Gobi Desert.

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

The metatherian clade Deltatheridiidae is known in North America from the Early Cretaceous and from a few records from the Judithian and Lancian faunas (Fox, 1974; Davis et al., 2003; Kielan-Jaworowska et al., 2004; Rougier et al., 2004). The latter records possibly represent dispersals from Asia. In Asia this group is represented by well-preserved specimens

from Mongolia and more fragmentary material from Uzbekistan and Kazakhstan (Averianov, 1997; Rougier et al., 1998, 2004; Averianov et al., 2010). The absence of this group from other formations in Middle and Central Asia possibly represents sampling artifacts.

BM 25) Asioryctitheria: 0) absent [outgroup, Khodzhakul, Judithian, Lancian]; 1) *Daulestes* [Bissekty]; 2) *Kennalestes* [Djadokhta]; 3) *Asioryctes* [Barun Goyot]; ?) unknown [Yalovach, Bostobe, Iren Dabasu, Lower and Upper Bayn Shire, Nemegt].

The endemic Asian eutherian clade Asioryctitheria is well known from the Bissekty Formation of Middle Asia and the Djadokhta and Barun Goyot formations of Central Asia (Archibald & Averianov, 2006). This group of rapidly evolving mammals has 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 26) Zalambdalestidae: 0) absent [outgroup, Judithian, Lancian]; 1) *Kulbeckia* [Bissekty, Yalovach, Bostobe]; 2) *Zalambdalestes* [Djadokhta]; 3) *Barunlestes* [Barun Goyot]; ?) unknown [Khodzhakul, Iren Dabasu, Lower and Upper Bayn Shire, Nemegt].

This is another clade of Late Cretaceous eutherians endemic to Asia and also has potential for biostratigraphic correlation. In the Khodzhakul Formation Zalambdalestidae is represented only by a single isolated petrosal to date (Averianov & Archibald, 2005). *Kulbeckia* is best known from the Bissekty Formation of Uzbekistan, but some teeth have also been recovered from the Yalovach Formation of Tajikistan (Archibald & Averianov, 2003). *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). *Alymlestes* from the Campanian of Kazakhstan has a derived structure of the lower molars similar to that of the Mongolian zalambdalestids (Averianov & Nessonov, 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 ab-

sence 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 Parvicursorinae (16[2]) unites the Gobi faunas, and their crassate teeth (13[1]), Hadrosauridae (19[2]), and Pachycephalosauria (21[1]) (tree 1) or by Pachycep-

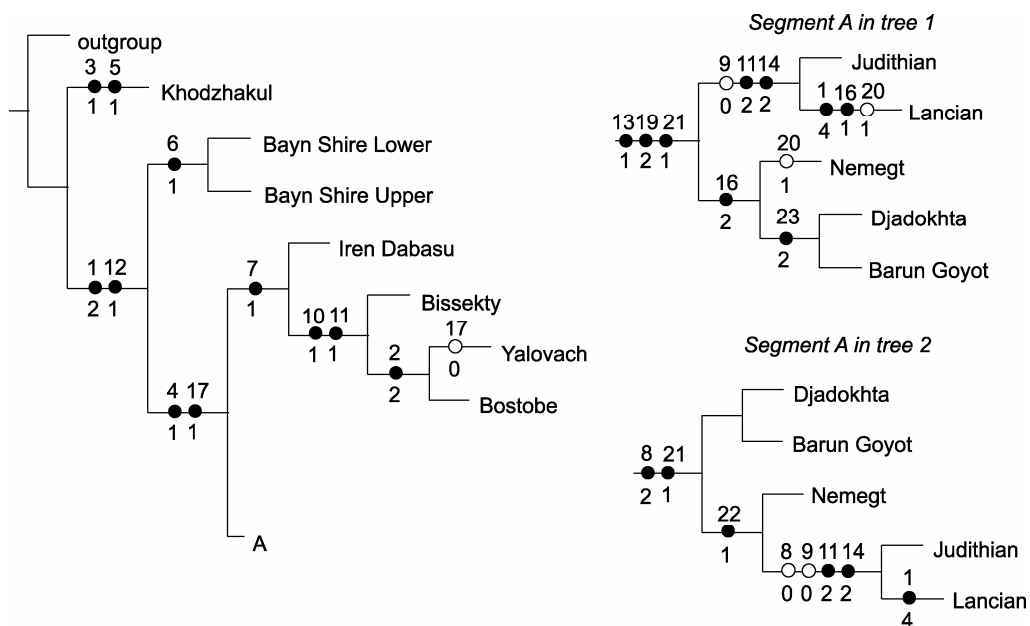


Fig. 2 Two most parsimonious trees produced by the parsimony ratchet algorithm of NONA version 2.0 using the data matrix present in Tab. 1

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)

kuduk Formation support its Cenomanian age.

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. (Tyrannosauroida?), Ornithomimosauria indet., Sauropoda indet., and Hadrosauroida 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 Dzheirantau formations; Pyatkov et al., 1967; King, personal communication). Similarly, the fluvial deposits of the Cenomanian Khodzhakul Formation in Karakalpakistan 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 near-shore 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 Bissekty 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 Bissekty 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 Bissekty Formation of Uzbekistan. Its poorly known dinosaurian assemblage includes Tyrannosauroida indet., Ornithomimosauria indet., Therizinosauroida indet., Dromaeosauridae indet., Sauropoda indet., Hadrosauroida indet., and Neoceratopsia indet. (Nessov, 1995; Kordikova et al., 2001; Averianov, 2007b; Averianov & Sues, 2009). The hadrosauroid bones from the Zhirkindek Formation are very similar to those of *Levnesovia* from the Bissekty 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 Bissekty local fauna are also present in the Santonian faunas. The Bostobe hadrosauroid *Aralosaurus* is distinctly more derived than the Bissekty hadrosauroid *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 Bissekty 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-

tral 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 near-shore marine strata of the Darbasa Formation in southern Kazakhstan. Only the mammal and troodontid teeth from this sample have been described to date (Averianov & Nessonov, 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 (Nessonov, 1997).

5.2 Central Asia

Nessonov'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 (Nessonov, 1995, 1997). This correlation led to Nessonov to refer certain dinosaurs from the Bissekty local fauna to genera previously reported from the Iren Dabasu fauna: *Alectrosaurus* sp., *Archaeornithomimus* (?) *bissektensis*, *Gilmoresaurus arkhangelskyi*, and *Bactrosaurus kysylkumensis* (Nessonov, 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 *Tyrannosauroida* indet., *Ornithomimosauria* indet., and *Levnesovia 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 *Levnesovia* 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 Khodzhaikul and Dzharakuduk faunas of Middle Asia, which are dominated by the small basal neoceratopsian *Asiaceratops*. However, the presence of the turtle *Lindholmemyx* 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 therizinosauroids and ankylosaurids. The Bissekty therizinosauroid closely resembles *Erlikosaurus* from the upper Bayn Shire fauna. The postcranial elements of *Bissektipelta* from the Bissekty Formation are almost identical to those of *Talarurus* from the upper Bayn 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 tyrannosauroids, ornithomimids, and hadrosauroids; 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 *Scincomorpha* indet. Multituberculate mammals are represented by an endemic clade Djadokhtatheroidea, 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 tyrannosaurids (*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 tyrannosaurids, ornithomimids, therizinosaurids, and hadrosaurids 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.

Ma	Age	Kyzylkum	Kazakhstan	Fergana	Gobi	
					Mongolia	Inner Mongolia
70	Maastrichtian				Nemegt	
75	Campanian				Barun Goyot	
80			Darbasa		Djadokhta	Bayan Mandahu
85	Santonian		Bostobc/Syuk Syuk	Yalovach		Iren Dabasu
90	Coniacian	Aitym			Upper Bayn Shire	
95	Turonian	Bissekty	Zhirkindek		lower Bayn Shire	
100	Cenomanian	Khodzhakul		Sharikhan		
	Albian					

Fig. 3 Attempted stratigraphic correlation of the assemblages of Late Cretaceous continental vertebrates in Middle and Central Asia discussed in this paper

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 hadrosauroid *Taninus*, 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 "Mongolian

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.

References

- Alifanov V R. 2000. The fossil record of Cretaceous lizards from Mongolia. In: Benton M J, Shishkin M A, Unwin D M & Kurochkin E N eds. The age of dinosaurs in Russia and Mongolia. Cambridge: Cambridge University Press. 368-389
- Alifanov V R & Averianov A O. 2006. On the finding of ornithomimid dinosaurs (Saurischia, Ornithomimosauria) in the Upper Cretaceous beds of Tajikistan. *Paleontological Journal*, **40**(1): 103-108
- Alroy J. 1994. Appearance event ordination: a new biochronologic method. *Paleobiology*, **20**(2): 191-207
- Alroy J. 2000. New methods for quantifying macroevolutionary patterns and processes. *Paleobiology*, **26**(4): 707-733
- Archibald J D & Averianov A O. 2001. *Paranyctoides* and allies from the Late Cretaceous of North America and Asia. *Acta Palaeontologica Polonica*, **46**(4): 533-551
- Archibald J D & Averianov A O. 2003. The Late Cretaceous placental mammal *Kulbeckia*. *Journal of Vertebrate Paleontology*, **23**(2): 404-419
- Archibald J D & Averianov A O. 2005. Mammalian faunal succession in the Cretaceous of the Kyzylkum Desert. *Journal of Mammalian Evolution*, **12**(1-2): 9-22
- Archibald J D & Averianov A O. 2006. Late Cretaceous asioryctitherian eutherian mammals from Uzbekistan and phylogenetic analysis of Asioryctitheria. *Acta Palaeontologica Polonica*, **51**(2): 351-376
- Archibald J D, Sues H-D, Averianov A O, King C, Ward D J, Tsaruk O I, Danilov I G, Rezvyi A S, Veretennikov B G & Khodjaev A. 1998. Précis of the Cretaceous paleontology, biostratigraphy and sedimentology at Dzharakuduk (Turonian?-Santonian), Kyzylkum Desert, Uzbekistan. *Bulletin of the New Mexico Museum of Natural History and Science*, **14**: 21-28
- Averianov A O. 1997. New Late Cretaceous mammals of southern Kazakhstan. *Acta Palaeontologica Polonica*, **42**(2): 243-256
- Averianov A O. 2002. An ankylosaurid (Ornithischia: Ankylosauria) braincase from the Upper Cretaceous Bissekty Formation of Uzbekistan. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre*, **72**(1): 97-110
- Averianov A O. 2005. The first choristoderes (Diapsida, Choristodera) from the Paleogene of Asia. *Paleontological Journal*, **39**(1): 79-84
- Averianov A O. 2006. On an ornithomimid dinosaur (Saurischia, Ornithomimosauria) from the Cenomanian of Fergan. *Paleontologicheskii Zhurnal*, (3): 88-92
- Averianov A O. 2007a. Mid-Cretaceous ornithocheirids (Pterosauria, Ornithocheiridae) from Russia and Uzbekistan. *Paleontological Journal*, **41**(1): 79-86
- Averianov A O. 2007b. Theropod dinosaurs from the Late Cretaceous of North-East Aral Sea area, Kazakhstan. *Cretaceous Research*, **28**(3): 532-544
- Averianov A O & Archibald J D. 2003. Mammals from the Upper Cretaceous Aitym Formation, Kyzylkum Desert, Uzbekistan. *Cretaceous Research*, **24**(2): 171-191
- Averianov A O & Archibald J D. 2005. Mammals from the mid-Cretaceous Khodzhaikul Formation, Kyzylkum Desert, Uzbekistan. *Cretaceous Research*, **26**(4): 593-608
- Averianov A O & Archibald J D. 2006. New specimens of the multituberculate mammal *Uzbekbaatar* from the Late Cretaceous of Uzbekistan. *Acta Palaeontologica Polonica*, **51**(2): 377-380
- Averianov A O, Archibald J D & Ekdale E G. 2010. New material of the Late Cretaceous deltatheroidan mammal *Sulestes* from Uzbekistan and phylogenetic reassessment of the metatherian-eutherian dichotomy. *Journal of Systematic Palaeontology*, **8**(3): 301-330
- Averianov A O & Nessov L A. 1995. A new Cretaceous mammal from the Campanian of Kazakhstan. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* (1): 65-74
- Averianov A O & Sues H-D. 2007. A new troodontid (Dinosauria: Theropoda) from the Cenomanian of Uzbekistan, with a review of troodontid records from the territories of the former Soviet Union. *Journal of Vertebrate Paleontology*, **27**(1): 87-98
- Averianov A O & Sues H-D. 2009. First record of a basal neoceratopsian dinosaur from the Late Cretaceous of Kazakhstan. *Acta Palaeontologica Polonica*, **54**(3): 553-556

- Barrett P M, Butler R J, Edwards N P & Milner A R. 2008. Pterosaur distribution in time and space: an atlas. *Zitteliana*, **B28**: 61-107
- Barsbold R. 1981. Toothless carnivorous dinosaurs of Mongolia. *Trudy Sovmestnoi Sovetsko-Mongol'skoi Paleontologicheskoi Ekspeditsii*, **15**: 28-39
- Barsbold R. 1983. Carnivorous dinosaurs from the Cretaceous of Mongolia. *Trudy Sovmestnoi Sovetsko-Mongol'skoi Paleontologicheskoi Ekspeditsii*, **19**: 1-120
- Barsbold R & Perle A. 1983. On the taphonomy of joint burial of juvenile dinosaurs and some aspects of their ecology. *Trudy Sovmestnoi Sovetsko-Mongol'skoi Paleontologicheskoi Ekspeditsii*, **24**: 121-125
- Baszio S. 1997. Systematic palaeontology of isolated dinosaur teeth from the latest Cretaceous of south Alberta, Canada. *Courier Forschungsinstitut Senckenberg*, **196**: 33-77
- Beavan N R & Russell A P. 1999. An elasmobranch assemblage from the terrestrial-marine transitional Lethbridge Coal Zone (Dinosaur Park Formation: upper Campanian), Alberta, Canada. *Journal of Paleontology*, **73**(3): 494-503
- Becker M A, Chamberlain J A & Terry D O Jr. 2004. Chondrichthyans from the Fairpoint Member of the Fox Hills Formation (Maastrichtian), Meade County, South Dakota. *Journal of Vertebrate Paleontology*, **24**(4): 780-793
- Bell P R. 2011. Redescription of the skull of *Saurolophus osborni* Brown 1912 (Ornithischia: Hadrosauridae). *Cretaceous Research*, **32**(1): 30-44
- Bell P R (in press). Cranial osteology and ontogeny of *Saurolophus angustirostris* from the Late Cretaceous of Mongolia with comments on *Saurolophus osborni* from Canada. *Acta Palaeontologica Polonica*, **56**
- Borsuk-Białynicka M. 1978. *Eopelobates leptocolaptus* sp.n. : the first Upper Cretaceous pelobatid frog from Asia. *Palaeontologia Polonica*, **38**: 57-63
- Brinkman D B. 2003. A review of nonmarine turtles from the Late Cretaceous of Alberta. *Canadian Journal of Earth Sciences*, **40**(4): 557-571
- Brinkman D B, Nessov L A & Peng J-H. 1994. *Khummuchelys* gen. nov., a new trionychid (Testudines: Trionychidae) from the Late Cretaceous of Inner Mongolia and Uzbekistan. *Canadian Journal of Earth Sciences*, **30**(10-11): 2214-2223
- Brusatte S L, Norell M A, Carr T D, Erickson G M, Hutchinson J R, Balanoff A M, Bever G S, Choiniere J N, Makovicky P J & Xu X. 2010. Tyrannosaur paleobiology: new research on ancient exemplar organisms. *Science*, **329**(5998): 1481-1485
- Bryant L J. 1989. Non-dinosaurian lower vertebrates across the Cretaceous-Tertiary boundary in northeastern Montana. *University of California Publications in Geological Sciences*, **134**: 1-107
- Buffetaut E. 1995. An ankylosaurid dinosaur from the Upper Cretaceous of Shandong (China). *Geological Magazine*, **132**(6): 683-692
- Butler R J, Barrett P M, Nowbath S & Upchurch P. 2009. Estimating the effects of sampling biases on pterosaur diversity patterns: implications for hypotheses of bird/pterosaur competitive replacement. *Paleobiology*, **35**(3): 432-446
- Cappetta H. 1992. Nouveaux Rhinobatoidei (Neoselachii, Rajiformes) à denture spécialisée du Maastrichtien du Maroc. Remarques sur l'évolution dentaire des Rajiformes et des Myliobatiformes. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **187**(1): 31-52
- Cheetham A H & Hazel J E. 1969. Binary (presence-absence) similarity coefficients. *Journal of Paleontology*, **43**(5): 1130-1136
- Chiappe L M, Norell M A & Clark J M. 2001. A new skull of *Gobipteryx minuta* (Aves: Enantiornithes) from the Cretaceous of the Gobi Desert. *American Museum Novitates*, (3346): 1-15
- Chiappe L M, Norell M A & Clark J M. 2002. The Cretaceous, short-armed Alvarezsauridae: *Mononykus* and its kin. In: Chiappe L M & Witmer L M eds. *Mesozoic birds: above the heads of dinosaurs*. Berkeley: University of California Press. 87-120
- Chiappe L M & Walker C A. 2002. Skeletal morphology and systematics of the Cretaceous Euenantiornithes (Ornithothoraces: Enantiornithes). In: Chiappe L M & Witmer L M eds. *Mesozoic birds, above the heads of dinosaurs*. Berkeley: University of California Press. 240-267
- Cifelli R L, Eberle J J, Lofgren D L, Lillegraven J A & Clemens W A. 2004. Mammalian biochronology of the latest Cretaceous. In: Woodburne M O ed. *Late Cretaceous and Cenozoic Mammals of North America: biostratigraphy and geochronology*. New York: Columbia University Press. 21-42
- Clarke J A & Norell M A. 2002. The morphology and phylogenetic position of *Apsaravis ukhaana* from the Late Cretaceous of Mongolia. *American Museum Novitates*, (3387): 1-46
- Clarke J A & Norell M A. 2004. New avialan remains and a review of the known avifauna from the Late Cretaceous Nemegt Formation of Mongolia. *American Museum Novitates*, (3447): 1-12
- Currie P J & Dong Z M. 2001. New information on Cretaceous troodontids (Dinosauria, Theropoda) from the People's Republic of China. *Canadian Journal of Earth Sciences*, **38**(12): 1753-1766
- Currie P J & Eberth D A. 1993. Palaeontology, sedimentology and palaeoecology of the Iren Dabasu Formation (Upper Cretaceous), Inner Mongolia, People's Republic of China. *Cretaceous Research*, **14**(2): 127-144
- Dani A H & Masson V M. 1992. History of civilizations of Central Asia. Volume 1. Paris: UNESCO
- Danilov I G. 1999. A new lindholmemydid genus (*Testudines*: Lindholmemydidae) from the mid-Cretaceous of Uzbekistan. *Russian Journal of Herpetology*, **6**(2): 63-71
- Danilov I G & Sukhanov V B. 2001. New data on lindholmemydid turtle *Lindholmemyd* from the Late Cretaceous of Mongolia. *Acta Palaeontologica Polonica*, **46**(1): 125-131
- Danilov I G & Syromyatnikova E V. 2008. New materials on turtles of the family Nanhsiungchelyidae from the Creta-

- ceous of Uzbekistan and Mongolia, with a review of the nanhsiungchelyid record in Asia. *Proceedings of the Zoological Institute of the Russian Academy of Sciences*, **312**(1/2): 3-25
- Danilov I G., Syromyatnikova E V & Sukhanov V B. 2007. Turtles of the genus *Shachemys* from the Upper Cretaceous of Asia. In: Rozanov A Y, Lopatin A V & Parkhaev P Y eds. *Modern paleontology: classical and new methods*. Moscow: Paleontological Institute of the Russian Academy of Sciences. 59-72
- Dashzeveg D, Dingus L, Loope D B, Swisher C C III, Dulam T & Sweeney M R. 2005. New stratigraphic subdivision, depositional environment, and age estimate for the Upper Cretaceous Djadokhta Formation, southern Ulan Nur Basin, Mongolia. *American Museum Novitates*, (3498): 1-31
- Davis B M, Cifelli R L & Kielan-Jaworowska Z. 2008. Earliest evidence of Deltatheroidea (Mammalia: Metatheria) from the Early Cretaceous of North America. In: Sargis E J & Dagosto M eds. *Mammalian evolutionary morphology. A Tribute to Frederick S. Szalay*. Berlin: Springer. 3-24
- Dingus L, Loope D B, Dashzeveg D, Swisher C C III, Minjin C, Novacek M J & Norell M A. 2008. The geology of Ukhaa Tolgod (Djadokhta Formation, Upper Cretaceous, Nemegt Basin, Mongolia). *American Museum Novitates*, (3616): 1-40
- Dyke G J, Malakhov D V & Chiappe L M. 2006. A re-analysis of the marine bird *Asiahesperornis* from northern Kazakhstan. *Cretaceous Research*, **27**(6): 947-953
- Efimov M B. 1988. On the fossil crocodiles of Mongolia and the USSR. *Trudy Sovmestnoi Sovetsko-Mongol'skoi Paleontologicheskoi Ekspeditsii*, **34**: 81-90
- Elzanowski A. 1977. Skulls of *Gobipteryx* (Aves) from the Upper Cretaceous of Mongolia. *Palaeontologia Polonica*, **37**: 153-165
- Estes R. 1964. Fossil vertebrates from the Late Cretaceous Lance Formation, eastern Wyoming. *University of California Publications in Geological Sciences*, **49**: 1-180
- Everhart M J & Bell A. 2009. A hesperornithiform limb bone from the basal Greenhorn Formation (Late Cretaceous; middle Cenomanian) of North Central Kansas. *Journal of Vertebrate Paleontology*, **29**(3): 952-956
- Fortelius M, Gionis A, Jernvall J & Mannila H. 2006. Spectral ordering and biochronology of European fossil mammals. *Paleobiology*, **32**(2): 206-214
- Fox R C. 1974. *Deltatheroidea*-like mammals from the Upper Cretaceous of North America. *Nature*, **249**(5455): 392
- Fox R C. 1975. Fossil snakes from the upper Milk River Formation (Upper Cretaceous), Alberta. *Canadian Journal of Earth Sciences*, **12**(9): 1557-1563
- Gao K. & Fox R C. 1996. Taxonomy and evolution of Late Cretaceous lizards (Reptilia: Squamata) from western Canada. *Bulletin of Carnegie Museum of Natural History*, **33**: 1-107
- Gao K & Fox R C. 1998. New choristoderes (Reptilia: Diapsida) from the Upper Cretaceous and Palaeocene, Alberta and Saskatchewan, Canada, and phylogenetic relationships of Choristodera. *Zoological Journal of the Linnean Society*, **124**(4): 303-353
- Gao K & Nessov L A. 1998. Early Cretaceous squamates from the Kyzylkum Desert, Uzbekistan. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **207**: 289-309
- Gao K & Norell M A. 2000. Taxonomic composition and systematics of Late Cretaceous lizard assemblages from Ukhaa Tolgod and adjacent localities, Mongolian Gobi Desert. *Bulletin of the American Museum of Natural History*, **249**: 1-118
- Gardner J D. 2008. New information on frogs (Lissamphibia: Anura) from the Lance Formation (Late Maastrichtian) and Bug Creek Anthills (late Maastrichtian and early Paleocene), Hell Creek Formation, USA. In: Sankey J T & Baszio S eds. *Vertebrate microfossil assemblages: their role in paleoecology and paleobiogeography*. Bloomington: Indiana University Press. 219-249
- Gardner J D & Averianov A O. 1998. Albanerpetontid amphibians from the Upper Cretaceous of Middle Asia. *Acta Palaeontologica Polonica*, **43**(3): 453-467
- Gardner J D & Böhme M. 2008. Review of Albanerpetontidae (Lissamphibia), with comments on the paleoecological preferences of European Tertiary albanerpetontids. *Vertebrate Microfossil Assemblages*. In: Sankey J T & Baszio S eds. *Their Role in Paleoecology and Paleobiogeography*. Bloomington: Indiana University Press. 178-218
- Gardner J D & Cifelli R L. 1999. A primitive snake from the Cretaceous of Utah. *Special Papers in Palaeontology*, **60**: 87-100
- Gardner J D, Russell A P & Brinkman D B. 1995. Systematics and taxonomy of soft-shelled turtles (Family Trionychidae) from the Judith River Group (mid-Campanian) of North America. *Canadian Journal of Earth Sciences*, **32**(5): 631-643
- Goloboff P. 1999. NONA (ver. 1.9). Software published by the author, San Miguel de Tucumán, Argentina. Available online at www.cladistics.org
- Goloboff P, Farris J S & Nixon K C. 2003. Tree analysis using new technology. Program and documentation available from the authors (and online at www.zmuc.dk/public/phylogeny)
- Gubin Y M. 1999. Gobiatis (Anura) from the Upper Cretaceous locality Khermeen Tsav (Gobi Desert, Mongolia). *Paleontologicheskii Zhurnal*, (1): 76-87
- Hicks J F, Brinkman D L, Nichols D L & Watabe M. 1999. Paleomagnetic and palynologic analyses of Albian to Santonian strata at Bayn Shireh, Burkhan, and Khuren Dukh, eastern Gobi Desert, Mongolia. *Cretaceous Research*, **20**(6): 829-850
- Holtz T R, Chapman R E Jr & Lamanna M C. 2004. Mesozoic biogeography of dinosauria. In: Weishampel D B, Dodson P & Osmólska H eds. *The dinosauria* (Second edition). Berkeley: University of California Press. 627-642

- Hone D W E, Wang K, Sullivan C, Zhao X, Chen S, Li D, Ji S, Ji Q, & Xu X. 2011. A new, large tyrannosaurine theropod from the Upper Cretaceous of China. *Cretaceous Research*, **32**(4): 495-503
- Hope S. 2002. The Mesozoic radiation of Neornithes. In: Chiappe L M & Witmer L M eds. *Mesozoic birds, above the heads of dinosaurs*. Berkeley: University of California Press. 339-388
- Hutchison J H. 2000. Diversity of Cretaceous turtle faunas of eastern Asia and their contribution to the turtle faunas of North America. *Paleontological Society of Korea Special Publication*, **4**: 27-38
- Jerzykiewicz T & Russell D A. 1991. Late Mesozoic stratigraphy and vertebrates of the Gobi Basin. *Cretaceous Research*, **12**(4): 345-377
- Kielan-Jaworowska Z. 1974. Multituberculate succession in the Late Cretaceous of the Gobi Desert (Mongolia). *Palaeontologia Polonica*, **30**: 23-44
- Kielan-Jaworowska Z, Cifelli R L & Luo Z-X. 2004. Mammals from the age of dinosaurs: origins, evolution, and structure. New York : Columbia University Press. 1-630
- Kielan-Jaworowska Z, Hurum J H & Badamgarav D. 2003. An extended range of multituberculate *Kryptobaatar* and distribution of mammals in the Upper Cretaceous of the Gobi Desert. *Acta Palaeontologica Polonica*, **48**(2): 273-278
- Kearney M. 2003. Systematics of the Amphisbaenia (Lepidosauria: Squamata) based on morphological evidence from recent and fossil forms. *Herpetological Monographs*, **17**(1): 1-74
- Kobayashi Y & Barsbold R. 2005. Reexamination of a primitive ornithomimosaur, *Garudimimus brevipes* Barsbold, 1981 (Dinosauria: Theropoda), from the Late Cretaceous of Mongolia. *Canadian Journal of Earth Sciences*, **42**(9): 1501-1521
- Kobayashi Y & Lü J-C. 2003. A new ornithomimid dinosaur with gregarious habits from the Late Cretaceous of China. *Acta Palaeontologica Polonica*, **48**(2): 235-259
- Kordikova E G, Polly D P, Alifanov V R, Roček Z, Gunnell G F & Averianov A O. 2001. Small vertebrates from the Late Cretaceous and Early Tertiary of the northeastern Aral Sea Region, Kazakhstan. *Journal of Paleontology*, **75**(2): 390-400
- Ksepka D T & Norell M A. 2004. Ornithomimosaur cranial material from Ukhaa Tolgod (Omnogov, Mongolia). *American Museum Novitates*, (3448): 1-4
- Kurochkin E N. 1996. A new enantiornithid of the Mongolian Late Cretaceous, and a general appraisal of the infraclass Enantiornithes (Aves). Moscow, Paleontological Institute, Special Issue. 60
- Kurochkin E N. 2000. Mesozoic birds of Mongolia and the former USSR. In: Benton M J, Shishkin M A, Unwin D M & Kurochkin E N eds. *The age of dinosaurs in Russia and Mongolia*. Cambridge: Cambridge University Press. 533-559
- Kurzanov S M. 1987. Avimimididae and the problem of the origin of birds. *Trudy Sovmestnoi Sovetsko-Mongol'skoi Paleontologicheskoi Ekspeditsii*, **31**: 1-92
- Lapparent de Broin F de. 2004. A new Shachemydinae (Chelonii, Cryptodira) from the Lower Cretaceous of Laos: preliminary data. *Comptes Rendus Palevol*, **3**(5): 387-396
- Lindsay E H. 2003. Chronostratigraphy, biochronology, datum events, land mammal ages, stage of evolution, and appearance event ordination. *Bulletin of the American Museum of Natural History*, **279**: 212-230
- Longrich N R. 2009. An ornithurine-dominated avifauna from the Belly River Group (Campanian, Upper Cretaceous) of Alberta, Canada. *Cretaceous Research*, **30**(1): 161-177
- Longrich N R & Currie P J. 2009. *Albertonykus borealis*, a new alvarezsaur (Dinosauria: Theropoda) from the early Maastriichtian of Alberta, Canada: implications for the systematics and ecology of the Alvarezsauridae. *Cretaceous Research*, **30**(1): 239-252
- Longrich N R, Currie P J & Dong Z-M. 2010. A new oviraptorid (Dinosauria: Theropoda) from the Upper Cretaceous of Bayan Mandahu, Inner Mongolia. *Palaeontology*, **53**(5): 945-960
- Lucas S G. & Estep J W. 1998. Vertebrate biostratigraphy and biochronology of the Cretaceous of China. *New Mexico Museum of Natural History and Science Bulletin*, **14**: 1-20
- Makovicky P J. 2008. Telling time from fossils: a phylogeny-based approach to chronological ordering of paleobiotas. *Cladistics*, **24**(3): 350-371
- Martinez J N. 1995. Biochronology and parsimony methods. *Bulletin de la Société géologique de France*, **166**(5): 517-526
- Martinson G G. 1982. Late Cretaceous mollusks of Mongolia. *Trudy Sovmestnoi Sovetsko-Mongol'skoi Paleontologicheskoi Ekspeditsii*, **17**: 1-84
- Maryańska T, Chapman R E & Weishampel D B. 2004. Pachycephalosauria. In: Weishampel D B, Dodson P & Osmólska H eds. *The dinosauria* (Second edition). Berkeley: University of California Press. 464-477
- Matsumoto R & Evans S E. 2010. Choristoderes and the freshwater assemblages of Laurasia. *Journal of Iberian Geology*, **36**(2): 253-274
- Mertinene R A & Nessov L A. 1985. Hybodont sharks from the Cretaceous of Middle Asia. *Doklady Akademii Nauk Tadzhikskoi SSR*, **28**(1): 588-592
- Nessov L A. 1977. A new genus of two-clawed turtle from the Upper Cretaceous of Karakalpakia. *Paleontologicheskii Zhurnal*, (1): 103-114
- Nessov L A. 1981. On a turtle of the family of the Dermatemydidae from the Cretaceous of the Amur River Basin, and some other rare finds of ancient turtle remains of Asia. *Herpetological Investigations in Siberia and Far East*. L Y Borkin. Leningrad: Zoologicheskii Institut AN SSSR. 69-73
- Nessov L A. 1985. Rare bony fishes, terrestrial lizards and mammals from the zone of estuaries and coastal plains of the Cretaceous of Kizylkum. *Ezhegodnik Vsesoyuznogo Paleontologicheskogo Obshchestva*, **28**: 199-219
- Nessov L A. 1988. Assemblages of late Mesozoic and Paleo-

- cene vertebrates of Middle Asia. In: Bogdanova T N & Oshurkova M V eds. Formation and evolution of the continental biotas. Leningrad: Izdatel'stvo Nauka. 93-101
- Nessov L A. 1995. Dinosaurs of Northern Eurasia: new data about assemblages, ecology and paleobiogeography. Saint Petersburg: Izdatel'stvo Sankt-Peterburgskogo Universiteta. 1-156
- Nessov L A. 1997. Cretaceous nonmarine vertebrates of northern Eurasia. In: Golovneva L B & Averianov A O eds. Saint Petersburg: Izdatel'stvo Sankt-Peterburgskogo Universiteta. 1-218
- Nessov L A & Borkin L Y. 1983. New findings of bird bones from the Cretaceous of Mongolia and Middle Asia. Trudy Zoologicheskogo Instituta AN SSSR, **116**: 108-110
- Nessov L A & Golovneva L B. 1983. Changes of vertebrate complexes of Cenomanian-Santonian (Late Cretaceous) of Kyzylkum. In: Oleinikov A N ed. Paleontology and evolution of biosphere. Transactions of XXV Session of the All-Union Paleontological Society. Leningrad: Nauka. 126-134
- Nessov L A & Khozatsky L I. 1977. Freshwater turtle from the Early Cretaceous of Fergana. Ezhegodnik Vsesoyuznogo Paleontologicheskogo Obshchestva, **20**: 248-262
- Nessov L A & Krassovskaya T B. 1984. [Transformations in the composition of turtle assemblages of the Late Cretaceous of Middle Asia]. Vestnik Leningradskogo Universiteta (Seriya Biologiya), **1**(3): 15-25
- Nessov L A & Mertinene R A. 1986. Remains of chondrichthyan fishes from the Cretaceous of Middle Asia and Kazakhstan as a source of information on the age and origin of the deposits. In: Krymgoltz G Y & Belenkova V S eds. Paleontology and detailed stratigraphic correlation. Leningrad: Nauka. 35-41
- Nessov L A & Panteleeva T M. 1999. *Gar Atractosteus turanensis* sp. nov. (Lepisosteidae) from the Upper Cretaceous of Kyzylkum Desert. Trudy Zoologicheskogo Instituta RAN, **277**: 104-118
- Nessov L A & Prizemlin B V. 1991. A large advanced flightless marine bird of the order Hesperornithiformes of the Late Senonian of Turgai Strait: the first find of the group in the USSR. Trudy Zoologicheskogo Instituta AN SSSR, **239**: 85-107
- Nessov L A, Sigogneau-Russell D & Russell D E. 1994. A survey of Cretaceous tribosphenic mammals from Middle Asia (Uzbekistan, Kazakhstan and Tajikistan), of their geological setting, age and faunal environment. Palaeovertebrata, **23**: 51-92
- Nessov L A & Udovichenko N I. 1986. [New findings of remains of Cretaceous and Paleogene vertebrates of Middle Asia]. Voprosy Paleontologii, **9**: 129-136
- Nessov L A & Yarkov A A. 1993. [Hesperornithiforms in Russia]. Russkii Ornitologicheskii Zhurnal, **2**(1): 37-54
- Neuman A G & Brinkman D B. 2005. Fishes of the fluvial beds. In: Currie P J & Koppelhus E B eds. Dinosaur Provincial Park: a spectacular ancient ecosystem revealed. Bloomington: Indiana University Press. 167-185
- Nixon K C. 1999. Winclada (Beta) version 0.9.9. Software published by the author, Ithaca, NY. Available online at www.cladistics.org
- Osmólska H, Hua S & Buffetaut E. 1997. *Gobiosuchus kielanae* (Protosuchia) from the Late Cretaceous of Mongolia: anatomy and relationships. Acta Palaeontologica Polonica, **42**(2): 257-289
- Osmólska H, Currie P J & Barsbold R. 2004. Oviraptorosauria. In: Weishampel D B, Dodson P & Osmólska H eds. The dinosaurs (Second edition). Berkeley: University of California Press. 165-183
- Panteleyev A V, Popov E V & Averianov A O. 2004. New record of *Hesperornis rossicus* (Aves, Hesperornithiformes) in the Campanian of Saratov Province, Russia. Paleontological Research, **8**(2): 115-122
- Peng J H, Russell A P & Brinkman D B. 2001. Vertebrate microsite assemblages (exclusive of mammals) from the Foremost and Oldman formations of the Judith River Group (Campanian) of southeastern Alberta: an illustrated guide. Provincial Museum of Alberta, Natural History Occasional Paper, **25**: 1-54
- Pol D & Norell M A. 2004a. A new crocodyliform from Zos Canyon, Mongolia. American Museum Novitates, (3445): 1-36
- Pol D & Norell M A. 2004b. A new gobiosuchid crocodyliform taxon from the Cretaceous of Mongolia. American Museum Novitates, (3458): 1-31
- Pol D, Turner A H & Norell M A. 2009. Morphology of the Late Cretaceous crocodylomorph *Shamosuchus djadochtaensis* and a discussion of neosuchian phylogeny as related to the origin of Eusuchia. Bulletin of the American Museum of Natural History, **324**: 1-103
- Prieto-Márquez A. 2010. Global historical biogeography of hadrosaurid dinosaurs. Zoological Journal of the Linnean Society, **159**(2): 503-525
- Pyatkov K K, Pyanovskaya I A, Bukharin A K & Bykovskii Y K. 1967. Geological structure of Central Kyzylkum. Tashkent: Fan. 1-177
- Raup D M & Crick R E. 1979. Measurement of faunal similarity in paleontology. Journal of Paleontology, **53**(5): 1213-1227
- Rees J & Lindgren J. 2005. Aquatic birds from the Upper Cretaceous (lower Campanian) of Sweden and the biology and distribution of hesperornithiforms. Palaeontology, **48**(6): 1321-1329
- Roček Z. 2008. The Late Cretaceous frog *Gobiates* from Central Asia: its evolutionary status and possible phylogenetic relationships. Cretaceous Research, **29**(4): 577-591
- Roček Z & Nessov L A. 1993. Cretaceous anurans from Central Asia. Palaeontographica A, **226**: 1-54
- Roček Z, Eaton J G, Gardner J D & Přikryl T. 2010. Evolution of anuran assemblages in the Late Cretaceous of Utah, USA. Palaeobiodiversity and Palaeoenvironments, **90**(4): 341-393

- Rougier G W, Wible J R & Novacek M J. 1998. Implications of *Deltatheridium* specimens for early marsupial history. *Nature*, **396**(6710): 459-463
- Rougier G W, Wible J R & Novacek M J. 2004. New specimen of *Deltatheroides cretacicus* (Metatheria, Deltatheroidea) from the Late Cretaceous of Mongolia. *Bulletin of Carnegie Museum of Natural History*, **36**: 245-266
- Russell L S. 1975. Mammalian faunal succession in the Cretaceous System of western North America. In: Caldwell W G E ed. *The Cretaceous System of the Western Interior*. The Geological Association of Canada, Special Paper Number **13**: 137-161
- Sanchiz B. 1998. Saliencia. *Handbuch der Paläoherpetologie*. Teil 4. Munich: Verlag Dr. Friedrich Pfeil. 1-275
- Sankey J T. 2008. Diversity of latest Cretaceous (late Maastriichtian) small theropods and birds: teeth from Lance and Hell Creek formations, USA. Sankey J T & Baszio S eds. *Vertebrate microfossil assemblages. their role in paleoecology and paleobiogeography*. Bloomington: Indiana University Press. 117-134
- Sankey J T, Brinkman D B, Guenther M & Currie P J. 2002. Small theropod and bird teeth from the Late Cretaceous (late Campanian) Judith River Group, Alberta. *Journal of Paleontology*, **76**(4): 751-763
- Schultz S S Jr. 1972. [Geological structure of the Junction Zone of Urals and Tian-Shan]. Moscow: Nedra. 1-208
- Simpson G G. 1960. Notes on the measurement of faunal resemblance. *American Journal of Science*, **258-A**: 300-311
- Shuvalov V F & Trusova E K. 1979. [Late Cretaceous conchostracans of Mongolia]. *Trudy Sovmestnoi Sovetsko-Mongol'skoi Paleontologicheskoi Ekspeditsii*, **8**: 83-93
- Skutschas P P. 2007. New specimens of albanerpetontid amphibians from the Upper Cretaceous of Uzbekistan. *Acta Palaeontologica Polonica*, **52**(4): 819-821
- Skutschas P P. 2009. Re-evaluation of *Mynbulakia* Nesov, 1981 (Lissamphibia: Caudata) and description of a new salamander genus from the Late Cretaceous of Uzbekistan. *Journal of Vertebrate Paleontology*, **29**(3): 659-664
- Smith D & Galton P M. 1990. Osteology of *Archaeornithomimus asiaticus* (Upper Cretaceous, Iren Dabasu Formation, People's Republic of China). *Journal of Vertebrate Paleontology*, **10**(2): 255-265
- Špinar Z V & Tatarinov L P. 1986. A new genus and species of discoglossid frog from the Upper Cretaceous of the Gobi Desert. *Journal of Vertebrate Paleontology*, **6**(2): 113-122
- Storrs G W & Efimov M B. 2000. Mesozoic crocodyliforms of north-central Eurasia. In: Benton M J, Shishkin M A, Unwin D M & Kurochkin E N eds. *The age of dinosaurs in Russia and Mongolia*. Cambridge: Cambridge University Press. 402-419
- Sues H-D & Averianov A O. 2009a. *Turanoceratops tardabilis*—the first ceratopsid dinosaur from Asia. *Naturwissenschaften*, **96**(5): 645-652
- Sues H-D & Averianov A O. 2009b. A new basal hadrosauroid dinosaur from the Late Cretaceous of Uzbekistan and the early radiation of duck-billed dinosaurs. *Proceedings of the Royal Society B*, **276**(1667): 2549-2555
- Sukhanov V B. 2000. Mesozoic turtles of Middle and Central Asia. In: Benton M J, Shishkin M A, Unwin D M & Kurochkin E N eds. *The age of dinosaurs in Russia and Mongolia*. Cambridge: Cambridge University Press. 309-367
- Sukhanov V B, Danilov I G & Syromyatnikova E V. 2008. The description and phylogenetic position of a new nanhsiungchelyid turtle from the Late Cretaceous of Mongolia. *Acta Palaeontologica Polonica*, **53**(4): 601-614
- Swofford D L. 2002. PAUP*. *Phylogenetic analysis using Parsimony (*and other methods)*. Version 4.0. Sunderland, Sinauer Associates
- Syromyatnikova E V. 2011. Turtles of the genus *Ferganemys* Nessov et Khosatzky, 1977 (Adocidae): shell morphology and phylogenetic position. *Proceedings of the Zoological Institute of the Russian Academy of Sciences*, **315**(1): 38-52
- Syromyatnikova E V & Danilov I G. 2009. New material and a revision of turtles of the genus *Adocus* (Adocidae) from the Late Cretaceous of Middle Asia and Kazakhstan. *Proceedings of the Zoological Institute of the Russian Academy of Sciences*, **313**(1): 74-94
- Tokaryk T T, Cumbaa S L & Storer J E. 1997. Early Late Cretaceous birds from Saskatchewan, Canada: the oldest diverse avifauna known from North America. *Journal of Vertebrate Paleontology*, **17**(1): 172-176
- Tong H, Claude J, Suteethorn V, Naksri W & Buffetaut E. 2009. Turtle assemblages of the Khorat Group (Late Jurassic-Early Cretaceous) of NE Thailand and their palaeobiogeographical significance. In: Buffetaut E, Cuny G, Le Loeuff J & Suteethorn V eds. *Late Palaeozoic and Mesozoic Ecosystems in SE Asia*. London: Geological Society of London, Special Publications **315**: 141-152
- Van Itterbeeck J, Horne D J, Bultynck P & Vandenberghe N. 2005. Stratigraphy and palaeoenvironment of the dinosaur-bearing Upper Cretaceous Iren Dabasu Formation, Inner Mongolia, People's Republic of China. *Cretaceous Research*, **26**(4): 699-725
- Vitek N S & Danilov I G. 2010. New material and a reassessment of soft-shelled turtles (Trionychidae) from the Late Cretaceous of Middle Asia and Kazakhstan. *Journal of Vertebrate Paleontology*, **30**(2): 383-393
- Vullo R & Neraudeau D. 2009. Pterosaur remains from the Cenomanian (Late Cretaceous) paralic deposits of Charentes, western France. *Journal of Vertebrate Paleontology*, **29**(1): 277-282
- Watabe M, Tsuihiji T, Suzuki D & Tsogtbaatar K. 2009. The first discovery of pterosaurs from the Upper Cretaceous of Mongolia. *Acta Palaeontologica Polonica*, **54**(2): 231-242
- Weishampel D B, Barrett P M, Coria R A, Le Loeuff J, Xu X, Zhao X J, Sahní A, Gomaní E M & Noto C R. 2004. Dinosaur distribution. In: Weishampel D B, Dodson P & Osmólska H eds. *The dinosauria* (Second edition). Berkeley: Uni-

- versity of California Press. 517-606
- Wellnhofer P & Buffetaut E. 1999. Pterosaur remains from the Cretaceous of Morocco. *Paläontologische Zeitschrift*, **73**(1/2): 133-142
- Wilson L E, Chin K, Cumberbatch S L & Dyke G J. 2011. A high latitude hesperornithiform (Aves) from Devon Island: palaeobiogeography and size distribution of North American hesperornithiforms. *Journal of Systematic Palaeontology*, **9**(1): 9-23
- Wu X C. 2005. Crocodylians. In: P J Currie & E B eds. *Dinosaur provincial park: a spectacular ancient ecosystem revealed*. Koppelman. Bloomington: Indiana University Press. 277-291
- Xu X, Wang D Y, Sullivan C, Hone D W E, Han F, Yan R H & Du F M. 2010a. A basal parvicursorine (Theropoda: Alvarezsauridae) from the Upper Cretaceous of China. *Zootaxa*, **2413**: 1-19
- Xu X, Wang K, Zhao X & Li D. 2010b. First ceratopsid dinosaur from China and its biogeographical implications. *Chinese Science Bulletin*, **55**(16): 1631-1635
- Xu X, Wang K, Zhao X, Sullivan C & Chen S. 2010c. A new leptoceratopsid (Ornithischia: Ceratopsia) from the Upper Cretaceous of Shandong, China and its implications for neoceratopsian evolution. *PLoS ONE*, **5**(11): e13835
- Zanno L E. 2010. A taxonomic and phylogenetic re-evaluation of Therizinosauria (Dinosauria: Maniraptora). *Journal of Systematic Palaeontology*, **8**(4): 503-543