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Oligocene-Miocene Vertebrates from the Valley of Lakes (Central Mongolia): Morphology, phylogenetic and stratigraphic implications

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3. Herpetofauna (Anura, Squamata) and palaeoclimatic implications: preliminary results

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(With 2 tables and 2 text-figures)

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Abstract

Fourteen samples belonging to the biozones A, B, (Early Oligocene), D1 (Early Miocene) and E (Late Miocene, biostratigraphy after HÖCK et al. 1999) produced determinable herpetofaunal remains. The Early Oligocene fauna consists of pelobatid frogs, agamids (*Tinosaurus*), at least three species of lizards (*Lacerta*), anguids (Melanosaurini), so far undeterminable squamates, and an erycine boide snake (*Calamagras*). The Early Miocene yield only scarce and fragmentary material belonging to lacertids. The Late Miocene gives a comparatively rich fauna characterized by "modern" snakes (*Eryx*, colubrines, natricines) and lizards (*Lacerta, Eremias*). All of these Late Miocene taxa also occur today in Mongolia. The Early Oligocene amphibians and reptiles point to a dry, probably arid to semi-arid climate with a short rainy season and open landscapes without permanent water bodies. This stands in sharp contrast to published Late Eocene faunal compositions which indicate humid climate conditions, mild winter temperatures (> 5°C) and the presence of permanent water bodies. Evidently, at the Eocene-Oligocene transition an important climate change took place in Central Asia characterized by a rapid shift toward strong continental climate (aridification, winter cooling). The Late Miocene fauna indicates a slightly more humid climate than during the Early Oligocene, an open environment and the existence of standing water.

Zusammenfassung

Vierzehn Proben der Biozonen A, B (Unter-Oligozän), D1 (Unter-Miozän) und E (Ober-Miozän, Biostratigraphie nach HÖCK et al. 1999) lieferten bestimmbare Herpetofaunen Reste. Die unteroligozäne Fauna setzt sich zusammen aus pelobatiden Fröschen, Agamen (*Tinosaurus*), wenigstens drei Arten von Eidechsen, Schleichen (Melanosaurini), bisher noch unbestimmbaren Squamaten und einer Sandboa (*Calamagras*). Das Unter-Miozän lieferte nur wenige und schlecht erhaltene Reste von Eidechsen. Die obermiozäne Fauna ist wieder reichhaltiger und ist gekennzeichnet durch moderne Schlangen (*Eryx*, Colubrinae, Natricinae) und Eidechsen (*Lacerta, Eremias*). Diese Faunenelemente kommen auch heute in der Mongolei vor. Die oligozänen Amphibien und Reptilien weisen auf ein trockenes, wahrscheinlich arides bis semi-arides Klima mit kurzen Regenzeiten und offenen Landschaften ohne permanente Wasserkörper hin. Dies steht im scharfen Kontrast zu publizierten Faunenzusammensetzungen aus dem Ober-Eozän, welche humide klimatische Verhältnisse mit milden Wintertemperaturen (> 5°C) und die

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Existenz von permanenten Gewässern anzeigen. Offenbar ereignete sich an der Eozän-Oligozän-Grenze ein bedeutender Klimawandel in Zentral-Asien, gekennzeichnet durch einen Übergang zu starker Kontinentalität (Aridifizierung, Abkühlung im Winter). Die obermiozäne Fauna zeigt humidere Klimaverhältnisse im Vergleich zum Unter-Oligozän an, mit weiterhin offenen Habitaten, aber der Existenz permanenter Wasserkörper.

Introduction

Not much is known about Paleocene and Eocene amphibians and reptiles from Mongolia, whereas the Oligocene and Neogene record is practically unknown. The newly discovered Oligocene and Miocene herpetofaunas (joint Austrian-Mongolian Expedition, Höck et al. 1999) admit therefore an important insight into Central Asian herpetofaunal diversity and evolution. This will be crucial not only from a biogeographic point of view, but also for palaeoclimatic studies, because it could be shown that amphibians and reptiles are climatic sensitive organisms (Böhme et al. 2006, Böhme 2003).

At the present state of knowledge the Mongolian Late Paleocene to Middle Eocene herpetofauna contains members of cryptobranchid salamanders, Crocodylia (*Tsaganosuchus*), Chelonia (*Adocus*, *Kansochelys*, *Mongolemys, Macrobaena, Pseudochrysemys, Trionyx*), Iguania (*Arretosaurus*, diversified Isodontosaurinae and Agaminae), Anguimorpha (Necrosauridae, Varanidae) and few archaic scincomorphs (Gao & Dashzeveg 1999, Alifanov 1993, Efimov 1988, Badamgarev & Reshetov 1985, Sukhanov & Narmandakh 1976, Tatarinov 1959).

The Late Eocene faunas are characterized apart from undetermined crocodiles and urodeles by the first pelobatid frogs (*Macropelobates*, *Uldzinia*), Iguania (*Arretosaurus*, Agaminae), Varanidae (*Varanus*), Chelonia (C*hrysemys, Ergilemys, Melanochelys,* Trionychidae), and the first Anguidae (*Placosaurus*) and Lacertidae (*Lacerta*) (Sanchiz 1998, Gubin 1996, Alifanov 1993, Efimov 1988, Yanovskaya et al. 1977, Mlynarski 1968).

In the present paper I will summarize the Early Oligocene to Late Miocene herpetofaunal remains sampled during the field seasons 1995 to 1997 in the Valley of Lakes in Central Mongolia (for geological, topographical, and biochronological details see Höck et al. 1999).

Oligocene to Late Miocene herpetofauna from the Valley of Lakes

Amphibians are known from three localities (Tab. 1) which all belong to the Early Oligocene biozone A. Undeterminable frogs (Anura indet.) are documented from SHG-C/2 and SHG-C/1 by maxillary fragments, and a more instructive maxilla-fragment (posterior third of the bone, Fig. 1/1b, c) and a praemaxilla (Fig. 1/1a) determined as belonging to the Pelobatinae (aff. *Uldzinia*) coming from TAT-D/1. The labial side of the maxilla is sculptured by shallow grooves and the lingual side exhibits a strong dental shelf. This could indicate some affinities to the imperfectly known genus *Uldzinia* (found only at his type locality Ergilin-Dzo, Late Eocene, Mongolia, Gubin 1996). In comparison to the two European pelobatins from the Oligocene *Eopelobates* and *Pelobates* the maxilla under study more closely resembles the former. These remains represent the first Oligocene frog records from Mongolia.

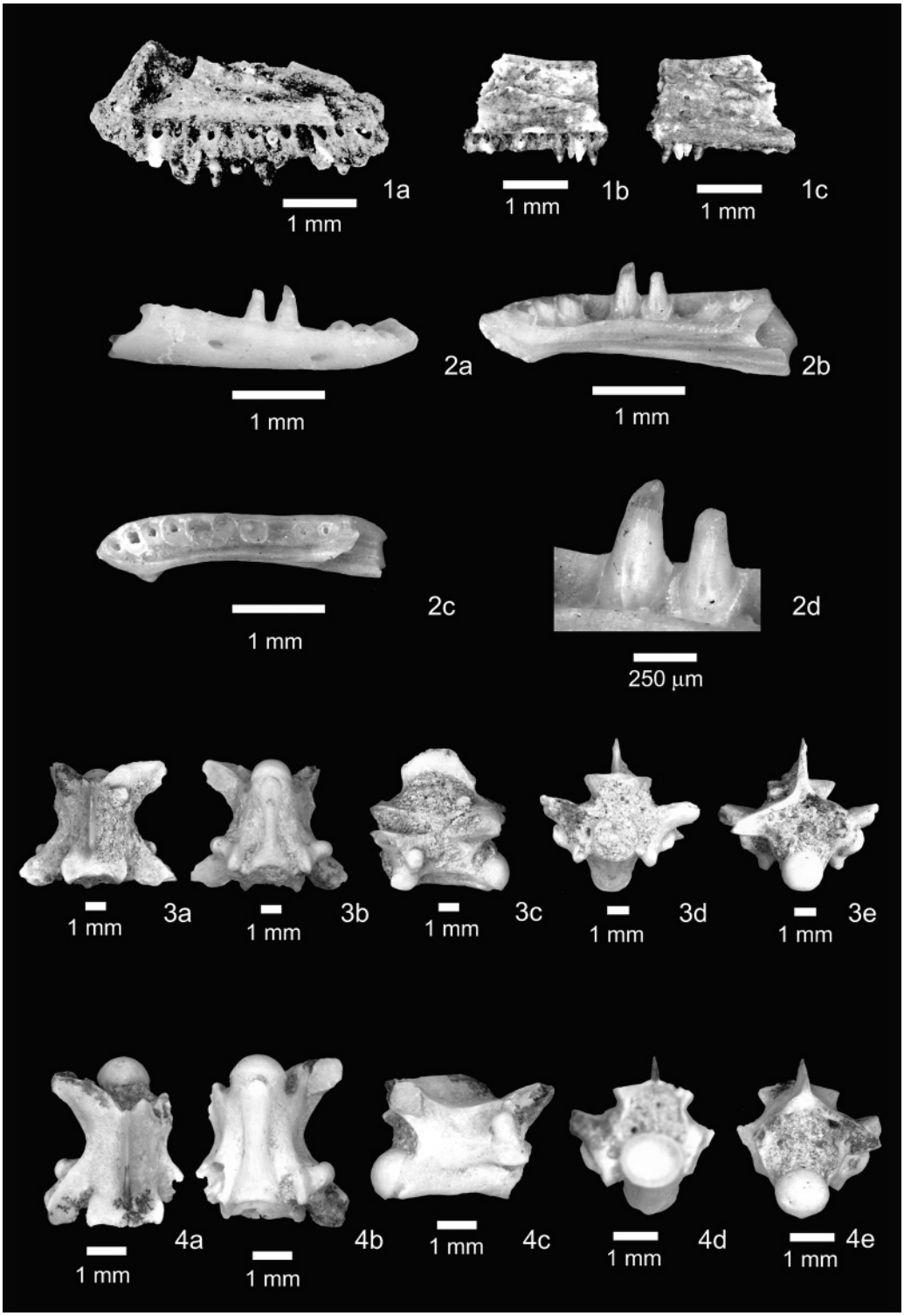
Tab. 1: Distribution of the herpetofauna from 14 fossil horizons and/or fossil sites from the Valley of Lakes: Builstyn Khudang (BUK-A), Hsanda Gol (SHG-A, SHG-C), Ikh Argalatyn Nuruu (IKH-A), Olon Ovoony Deng (ODO-A), Tatal Gol (TAT-D), Taatsiin Gol (TGR-A, TGR-ZO)

biozone	localities	Pelobatidae (aff. *Uldzinia*)	Anura ndet.	Tinosaurus sp.	Acrodonta indet.	Lacerta sp. 1	Lacerta sp. 2	Lacerta sp. 3	Eremias sp.	Lacertidae indet.	Scincomorpha indet.	Melanosaurini indet.	Squamata indet.	Calamagras sp.	Eryx sp. 1	Eryx sp. 2	Large size Colubrinae 1	Large size Colubrinae 2	Natricinae
E	BUK-A/12+14					X			X						X	X	X	X	X
D1	ODO-A/2					X													
	ODO-A/6										X								
B	SHG-A/1			X								X							
	TGL-A/11a					X													
	TGR-ZO/2					X	X	X					X						
	IKH-A/1				X	X													
A	TAT-D/1	X				X	X												
	SHG-C/1		X																
	SHG-C/2		X							X				X					
	TGL-A/2					X	?						X						
	TGR-A/13			X							X								
	TGR-A/14					X													

Squamates are documented by at least four orders: Iguania, Scincomorpha, Anguimorpha and Serpentes. Dental fragments of the agamine (Iguania) genus *Tinosaurus* are coming from the Early Oligocene of TGR-A/13 and SHG-A/1 (biozone A and B respectively). Scincomorph lizards belong to the family Lacertidae which are found in all biozones. Their fragments (dentalia, maxillaria, praemaxillaria) are relatively frequent, but difficult to be determined precisely. Because of their generalized morphology most of the specimens belong to the extant genus *Lacerta* sensu latu. Based on differences in size, up to three species co-occur in some localities (e.g. TGR-ZO/2). In the Late Miocene locality BUK-A/12+14 beside *Lacerta* probably the genus *Eremias* occurs which is based on praemaxilla morphology. Both genera are known from Mongolia today, but at least the Miocene *Lacerta* doesn't belong to the present day species (*L. agilis*, sand lizard).

Anguimorph lizards are found in one locality only (SHG-A/1, biozone B). Seven robustly built and intensively tuberculated osteoderms which possess an oblique ridge on their outer side are determined as belonging to the clade Melanosaurini (cf. DUFFAUD & RAGE 1997: Fig. 1) known from the Paleogene of North America, Asia and Europe. Beside the large sized Colubrines (see below), these glass lizards represent the largest reptiles in the studied faunas, with a tail length probably over 1.5 m.

In addition to these Iguania, Scincomorpha and Anguimorpha a fourth lizard group occurs (Squamata indet.) which could not be included within one of these three orders. These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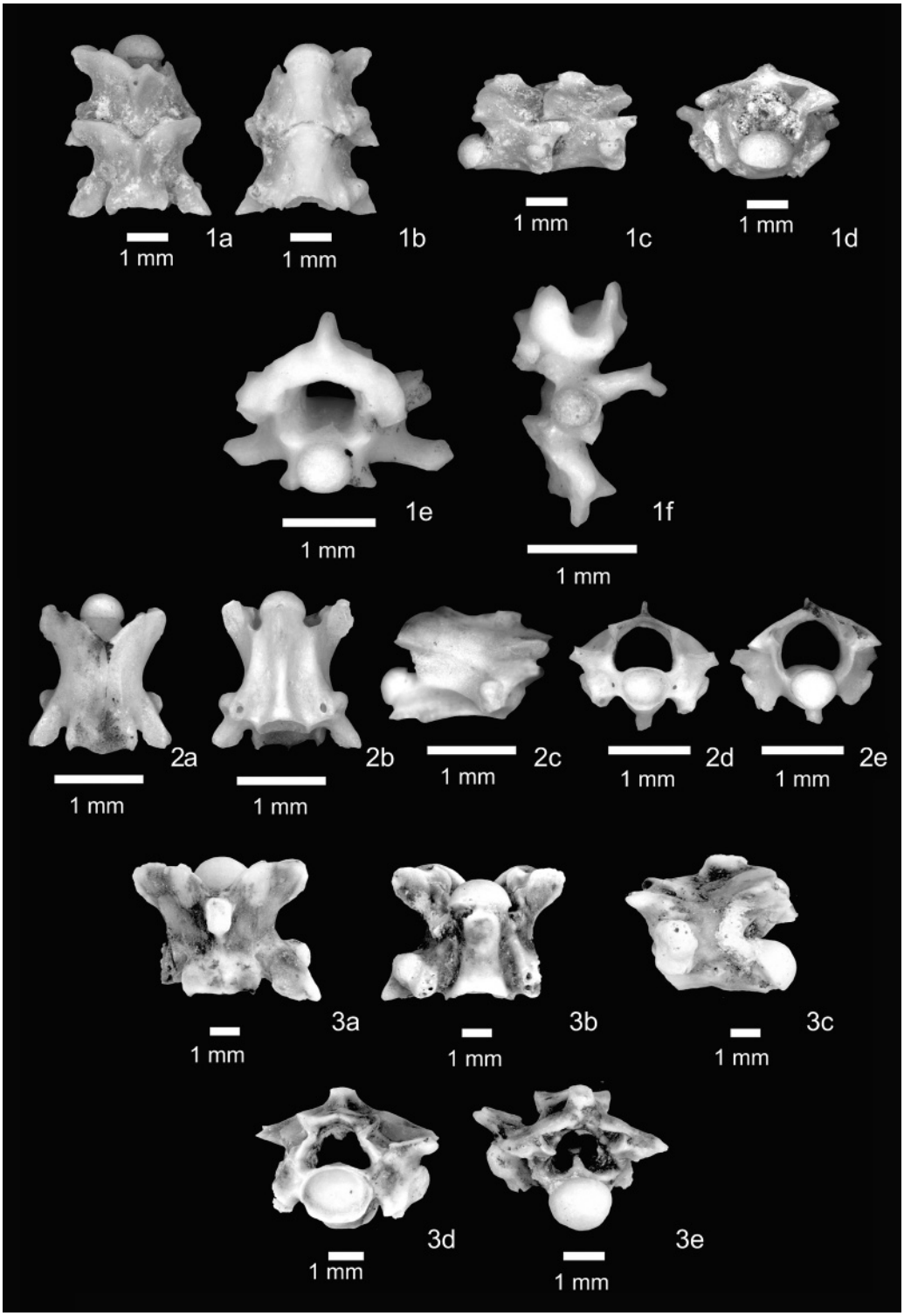
highly unusual dentaries (Fig. 1/2) and maxillaries are found in both Early Oligocene samples TGL-A/2 and TGR-ZO/2 (biozones A and B respectively).

The most diverse squamate order is Serpentes (snakes), documented by at least six species from two localities. From SHG-C/2 (biozone A, Early Oligocene) a single vertebra (Fig. 2/3) indicates the genus *Calamagras* (Boidae, Erycinae) and shows some similarities (broad and flat haemal keel; low, short and thick neural spine) to *C. platyspondyla* from the Late Oligocene/?Early Miocene of North America (HOLMAN 2000), rather than to *C. turkestanicus* from the Early Eocene of Kirghizia (DANILOV & AVERIANOV 1999) which is the only other Asian *Calamagras*. Interestingly this record is not the first erycine boid from the Hsanda Gol Formation. *Crythiosaurus mongoliensis*, an articulated skull from the Grand Canyon north of Tsagaan Noor (e.g. in the vicinity of SHG-C/2), originally described by GILMORE (1943) as an amphisbaenian lizard, actually belongs to an erycine boide snake (ESTES 1983). It could therefore be possible that *Crythiosaurus* GILMORE, 1943 is a junior synonym to *Calamagras* COPE, 1873.

The snake record from the Late Miocene (biozone E) of BUK-A/12+14 contains 33 vertebrae. They belong to three subfamilies (Erycinae, Colubrinae, Natricinae) and probably five species. Erycine boas are documented by several trunk and few anterior and posterior caudal vertebrae (Fig. 2/1). By the lack of a haemal keel and a very low neural spine on the trunk vertebra they closely resemble the genus *Eryx* (especially *E. jaculus*). Minor differences in morphology and size indicate probably two species (one *Eryx*-type, one *Gongylophis*-type), although these differences could also be subjected to intraspecific and allometric variations (SZYNDLAR & SCHLEICH 1994). The genus *Eryx* is documented from the Early and Late Miocene of Europe, the Early Miocene of Saudi Arabia and the Middle Miocene of Kazakhstan and Morocco (SZYNDLAR & SCHLEICH 1994). Today two species live in Mongolia (*E. miliaris, E. tataricus*). The second subfamily is represented by several trunk vertebrae which belong to two species (Fig. 1/3 and 1/4) of the large sized Colubrinae-group (sensu SZYNDLAR 1991). A very high neural spine distinguishes both forms from *Texasophis*, a divers Oligocene and Miocene colubrid genus from Europe and North America recorded recently from the Middle Miocene of Asia (Lake Bajkal region, BÖHME in manus). Extant Mongolian colubrines are represented by four genera (*Elaphe, Hemorrhois, Hierophis, Psammophis*). The third snake subfamily from sample BUK-A/12+14, a natricine Colubridae, is documented by a single vertebra from a juvenile individual (Fig. 2/2). The only living Mongolian natricine is *Natrix natrix*. The fossil vertebra shows some similarities to this species, although it exhibits much shorter praezygapophysal processes.

Text-figure 1: Fig. 1: Pelobatidae (aff. *Uldzinia* GUBIN, 1996), Early Oligocene (biozone A), Tatal Gol (TAT-D1); 1a – right premaxilla in lingual view (Inv. Nr. NHMW2007z0053/0001), 1b+c – right maxilla in lingual (1b) and labial (1c) view (Inv. Nr. NHMW2007z0053/0002). Fig. 2: Squamata indet., Early Oligocene (biozone A), Taatsiin Gol (TGL-A/2); right dentary (Inv. Nr. NHMW2007z0054/0001): 2a – labial view, 2b – lingual view, 2c – dorsal view, 2d – details of the tooth morphology. Fig. 3: Large size Colubrinae sp. 1, Late Miocene (biozone E), Builstyn Khudag (BUK-A/12+14); trunk vertebra (Inv. Nr. NHMW2007z0056/0001): 3a – dorsal view, 3b – ventral view, 3c – lateral view, 3d – anterior view, 3e – posterior view. Fig. 4: Large size Colubrinae sp. 2, Late Miocene (biozone E), Builstyn Khudag (BUK-A/12+14); trunk vertebra (Inv. Nr. NHMW2007z0057/0001): 4a – dorsal view, 4b – ventral view, 4c – lateral view, 4d – anterior view, 4e – posterior view.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Implications for palaeoclimate and environment

In contrast to the Early Miocene samples which yield poor and badly preserved material, the Early Oligocene and the Late Miocene assemblages are relatively rich comprising at least eight, respectively seven different herpetofaunal species (Table 2).

The Early Oligocene is characterized by pelobatid frogs (aff. *Uldzinia*), agamids (*Tinosaurus*), at least three species of lizards (*Lacerta*), anguids (Melanosaurini), so far undeterminable squamates, and an erycine boide snake (*Calamagras*). The extant pelobatid frogs are open country dwellers (some are fossorial) and lived even in (sub-) deserted environments. They show a "xeric breeding pattern", stimulated by external factors like precipitation (see BÖHME 2002 for further details). For their reproduction they don't need permanent water bodies. Many agamids, especially the North African and West and Central Asian taxa inhabit deserted environments, although it is not known if this could be assumed also for *Tinosaurus*. Similar environmental preferences have erycine snakes (sand boas) which live today usually in arid and semiarid habitats (ZUG et al. 2001). Lizards of the genus *Lacerta* show their highest diversity in relatively dry Mediterranean regions. Following GAUTHIER (1982) large sized glass lizard (Melanosaurini) may have been ecologically similar to the Australian lygosomine scincids living in desert, grassland and open shrubland environments (PIANKA 1969). The climatic and ecologic requirements of the extant relatives of the Early Oligocene amphibians and reptiles point to a dry, probably arid to semi-arid climate with a short rainy season and open landscapes without permanent water bodies. This stands in sharp contrast to the Late Eocene faunas (see introduction) which show the presence of crocodiles, salamanders and three genera of aquatic turtles, all indicating humid climate conditions, mild winter temperatures (> 5°C according to crocodiles, MARKWICK 1998) and the presence of permanent water bodies. Evidently, at the Eocene-Oligocene transition an important climate change took place in Central Asia characterized by a rapid shift toward strong continental climate (aridification, winter cooling).

Based on the scarce Early Miocene material no interpretation is possible. The Late Miocene assemblage is characterized by a "modern" snake (*Eryx*, colubrines, natricines) and lizard fauna (*Lacerta, Eremias*). All of these taxa also occur today in Mongolia. At least the presence of natricines (water snakes and allies) would indicate the existence of water bodies. But the semi-fossorial sand boas and the lizards point to a dry and open environment, although probably more humid than during the Early Oligocene.

Text-figure 2: Fig. 1: *Eryx* sp., Late Miocene (biozone E), Builstyn Khudag (BUK-A/12+14); two articulated trunk vertebra of *Eryx* sp. 2 (Inv. Nr. NHMW2007z0058/0001): 1a – dorsal view, 1b – ventral view, 1c – lateral view, 1d – posterior view. *Eryx* sp. 1: 1e+f – anterior (1e, Inv. Nr. NHMW2007z0059/0001) and posterior (1f, Inv. Nr. NHMW2007z0059/0002) caudal vertebra in posterior view. Fig. 2: Natricinae indet., Late Miocene (biozone E), Builstyn Khudag (BUK-A/12+14); trunk vertebra (Inv. Nr. NHMW2007z0060/0001): 2a – dorsal view, 2b – ventral view, 2c – lateral view, 2d – anterior view, 2e – posterior view. Fig. 3: *Calamagras* sp., Early Oligocene (biozone A), Hasanda Gol (SHG-C/2); trunk vertebra (Inv. Nr. NHMW2007z0055/0001): 3a – dorsal view, 3b – ventral view, 3c – lateral view, 3d – anterior view, 3e – posterior view.

Tab. 2: List of herpetofaunal elements collected by the Austrian-Mongolian Expedition in the Valley of Lakes in Central Mongolia.

Biozone	Early Oligocene		Early Miocene	Late Miocene
	A	B	D1	E
ANURA				
Pelobatidae (aff. *Uldzinia*)	X			
Anura indet.	X			
SQUAMATA				
Squamata indet.	X	X		
Iguania				
Agamidae				
Tinosaurus sp.	X	X		
Acrodonta indet.		X		
Scincomorpha				
Lacertidae				
Lacerta sp. 1	X	X	X	X
Lacerta sp. 2	X	X		
Lacerta sp. 3		X		
Eremias sp.				X
Lacertidae indet.	X			
Scincomorpha indet.			X	
Anguimorpha				
Glyptosauridae				
Melanosaurini indet.		X		
Serpentes				
Boidae				
Erycinae				
Calamagras sp.	X			
Eryx sp. 1				X
Eryx sp. 2				X
Colubridae				
Colubrinae				
Large size Colubrinae 1				X
Large size Colubrinae 2				X
Natricinae				
Natricinae indet.				X

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References

ALIFANOV, V. (1993): Some peculiarities of the Cretaceous and Paleogene lizard faunas of the Mongolian People's Republic. – Kaupia, Darmstädter Beiträge zur Naturgeschichte, **3**: 9-14. – Darmstadt.

BADAMGAREV, D. & RESHETOV, V.J. (1985): Paleontology and Stratigraphy of the Paleogen of the Za-Altai Gobi. – The joint Soviet-Mongolian Palaeontological Expedition Transactions, **25**: 103 pp. – Moscow.

BÖHME, M. (2002): Lower Vertebrates (Teleostei, Amphibia, Sauria) from the Karpatian of the Korneuburg Basin – paeoecological, environmental and palaeoclimatological implications. – Beiträge zur Paläontologie, **27**: 339-353. – Wien.

––– (2003): Miocene Climatic Optimum: evidence from Lower Vertebrates of Central Europe. – Palaeogeography, Palaeoclimatology, Palaeoecology, **195**: 389-401. – Amsterdam.

––– , ILG, A., OSSIG, A. & KÜCHENHOFF, H. (2006): A new method to estimate paleoprecipitation using fossil amphibians and reptiles and the Middle and Late Miocene precipitation gradients in Europe. – Geology, **34**/6: 425-428. – Boulder.

EFIMOV M.B. (1988): The fossil crocodiles and champsosaurides of Mongolia and USSR. – Transactions of the joint Soviet-Mongolian palaeontological expedition, **36**: 1-108. – Moscow.

ESTES, R. (1983): Encyclopedia of Paleoherpetology, Part 10A, Sauria terrestria, Amphisbaenia. – 249 pp. – Stuttgart and New York (Gustav Fischer Verlag).

DANILOV, I.G. & AVERIANOV, A.O. (1999): A new species of *Calamagras* COPE 1873 (Serpentes, Boidae, Erycinae) from the Early Eocene of Kirghizia. – Geodiversitas, **21**/1: 85-92. – Paris.

HÖCK, V., DAXNER-HÖCK, G., SCHMID, H.P., BADAMAGAREV, D., FRANK, W., FURTMÜLLER, G., MONTAG, O., BARSBOLD, R., KHAND, Y. & SODOV, J. (1999): Oligocene-Miocene sediments, fossils and basalts from the Valley of Lakes (Central Mongolia) – An integrated study. – Mitteilungen der Österreichischen Geologischen Gesellschaft, **90**: 83-125. – Wien.

DUFFAUD, S. & RAGE, J.-C. (1997): Les remplissages karstiques polyphases (Eocene, Oligocene, Pliocene) de Saint-Maximin (Phosphorites de Gard) et leur apport a la connaissance des faunes Europeennes, notamment pour l'Eocene moyen (MP 13). – In: AGUILAR, J.-P., LEGENDRE, S. & MICHAUX, J. (Eds.) : Actes du Congres BiochroM'97. – Mem. Trav. E.P.H.E., Inst. Montpellier, **21**: 729-735. – Montpellier.

GAO, K. & DASHZEVEG, D. (1999): New lizards from the Middle Eocene Mergen Formation, Mongolian Gobi Desert. – Paläontologische Zeitschrift, **73**/3-4: 327-336. – Stuttgart.

GAUTHIER, J.A. (1982): Fossil xenosaurid and anguid lizards from the early Eocene Wasatch Formation, southeast Wyoming, and a revision of the Anguidea. – Contributions to Geology, University of Wyoming, **21**/1: 7-54. – Laramie.

GILMORE, J.W. (1943): Fossil lizards of Mongolia. – Bulletin of the American Museum of Natural History, **81/** 4: 361-384. – New York.

GUBIN, Y.M. (1996): First find of a pelobatid (Anura) from the Paleogene of Mongolia. – Palaeontologitcheski Zhurnal, **1996**/4: 73-76. – Moscow.

HOLMAN, J.A. (2000): Fossil snakes of North America. – 357 pp. – (Indiana University Press).

MARKWICK, P.J. (1998): Fossil crocodilians as indicators of Late Cretaceous and Cenozoic climates: implications for using palaeontological data in reconstructing palaeoclimate. – Palaeogeography, Palaeoclimatology, Palaeoecology, **137**: 205-271. – Amsterdam.

MLYNARSKI, M.(1968): Notes on tortoises (Testudinidae) from the Tertiary of Mongolia. – Palaeontologica Polonica, **19**: 85-99. – Warshawa.

PIANKA, E.R. (1969): Sympatry of desert lizards (*Ctenotus*) in Western Australia. – Ecology, **50**: 1012-1030. – Ithaca.

SANCHIZ, B. (1998): Encyclopedia of Paleoherpetology, Part 4, Salientia. – 275 pp. – München (Verlag Dr. Friedrich Pfeil).

SUKHANOV, V.B. & NARMANDAKH P. (1976): Paleocene turtles from Mongolia. Paleontology and Biostratigraphy of Mongolia. – The joint Soviet-Mongolian Palaeontological Expedition Transactions, **3**: 107-133. – Moscow.

SZYNDLAR, Z. (1991): A review of Neogene and Quartarnary snakes of Central and Eastern Europe. Part I: Scolecophidia, Boidae, Colubrinae. – Estudios Geologicos, **47**/1-2: 103-126. – Madrid.

––– & SCHLEICH, H.-H. (1994): Two species of the genus *Eryx* (Serpentes; Boidae; Erycinae) from the Spansh Neogene with comments on the past distribution of the genus in Europe. – Amphibia-Reptilia, **15**: 233-248. – Leiden.

TATARINOV L.P. (1959): New turtles of the family Baenidae from the Lower Eocene of Mongolia. – Palaeontologitcheski Zhurnal, 1959/1: 100-113. – Moscow.

YANOVSKAYA, N.M., KUROTCHKIN, E.N. & DEVIATKIN E.V. (1977): The locality Ergilin Dzo - the stratotype for the Lower Oligocene in southeast Mongolia. – The joint Soviet-Mongolian Palaeontological Expedition, Transactions, **4**: 14-33. – Moscow.

ZUG, G.R., VITT, L.J. & CALDWELL, J.P. (2001): Herpetology – An introductory biology of amphibians and reptiles. – 630 pp. – San Diego and London (Academic Press).