Neogene amphibians and reptiles (Caudata, Anura, Gekkota, Lacertilia, Testudines) from south of Western Siberia, Russia and Northeastern Kazakhstan

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Abstract

Background. Recent amphibian and reptile fauna of Western Siberia is the less diverse of the Palaearctic Realm, influenced by unfavourable climate conditions. The origin and emergence of these groups are poorly known. Aside from better-explored European Neogene localities yielding amphibian and reptile remains, the Neogene herpetofauna of Western Asia is understudied. The few available data need critical reviews and new interpretations, taking into account the more recent records of the European herpetofauna. The comparison with European fossil record will provide data on palaeobiogeographic affiliations of the region as well as on the origin and emergence of the present-day fauna of Western Siberia. An overview about the earliest occurrences of certain amphibian lineages is still missing. These studies can be useful for molecular biologists for the calibration of the molecular clocks.

Methods and Results. The amphibian and reptile fauna from over 40 Western Siberian, Russian and Northeastern Kazakh localities ranging from Middle Miocene to Early Pleistocene have been studied. For that, the already published data have been considered, critically reviewed and new interpretations are provided. More than 50 amphibian and reptile taxa have been identified belonging to families Hynobiidae, Cryptobranchidae, Salamandridae, Palaeobatrachidae, Bombinatoridae, Pelobatidae, Hylidae, Bufonidae, Ranidae, Gekkonidae, Lacertidae and Emydidae. Palaeobiogeographic analyses for those groups have been performed and palaeoprecipitation values were estimated for 12 localities, using the bioclimatic analysis of herpetofaunal assemblages.

Conclusions. The Neogene assemblage of Western Siberia is dominated by groups of European affinities as Palaeobatrachidae, *Bombina, Hyla*, *Bufo bufo*, and a small part of the assemblage

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includes Eastern Palaearctic taxa (e.g. *Salamandrella*, *Tylototriton*, *Bufotes viridis*). For several taxa (e.g. *Mioproteus, Hyla, Bombina*, *Rana temporaria*), the Western Siberian occurrences represent their most east Eurasian records. The most diverse faunas are found in the Middle Miocene, whereas the less diverse are registered towards the Early Pleistocene. This tendency could be due to the progressive global cooling of the climate in the Northern Hemisphere. Our results showed higher-amplitude changes of precipitation development in Western Siberia from the Early Miocene to the Pliocene, than earlier assumed.

Introduction

Western Siberia is a geographic region restricted to the territories of Russia and partly northern Kazakhstan. It includes the region between the Ural Mountains in the west, Central Siberian Plateau in the east, and the Kazakh Plain and Altay Mountains, including the Zaisan Lake in the south (Fig. 1). The region comprises the drainage basin of the major Siberian rivers, like the Irtysh river and Ob river, both flowing into the Kara Sea of the Arctic Ocean. Western Siberia is characterised by a highly continental climate, under the influence of the Westerlies. The mean annual precipitation (MAP) is relatively uniform and varies from 400 mm in the North (415 mm at Omsk) to 200 mm in the South (255 mm at Pavlodar). The atmosphere during summer is enriched in water-vapour and due to relatively labile convective heating, torrential rainfalls are frequent. The mean annual range of temperature reaches 4 °C and more (Omsk: cold month temperature – CMT -19 °C, warm month temperature – WMT 20 °C, mean annual temperature – MAT 0.4 °C; Semipalatinsk: CMT -16 °C, WMT 22 °C, MAT 3.1 °C; Lake Zaisan: CMT up to -27 °C, WMT 23 °C; after *Müller & Hennings*, 2000). The area is covered by the tundra ('cold steppe'),

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the taiga (coniferous forests), which is replaced by open landscapes in the north (tundra) and in the south (steppe). The region with studied Neogene outcrops belongs to the transitional zone between dry and more humid temperate biomes, where taiga, forest-steppe and steppe are distributed (*Ravkin* et al., 2008).

Due to the strong continental climate, the Recent herpetofauna in the territory of Western Siberia is comparatively poorly diverse. According to different authors, it is represented by six to ten amphibian and seven reptile species (Table 1). It is assumed that the present distribution of amphibians and reptiles in Western Siberia was strongly influenced by Quaternary climatic fluctuation (*Ravkin, Bogomolova & Chesnokova*, 2010). According to Borkin (1999), the Recent amphibian fauna of Western Siberia belongs to the Siberian region of amphibian distribution in the Palaearctic Realm. According to different authors (e.g. *Kuzmin*, 1995; *Amphibiaweb*, 2016), the region is inhabited by few amphibians, two salamanders and four to nine anurans, belonging to five genera and five families (Table 1). This is the poorest regional fauna of the Palaearctic Realm, without any endemic species. Only *Salamandrella keyserlingii* and *Rana amurensis* are characteristic of the territory, but they are widely distributed and are also found in smaller areas in the neighbouring regions (*Borkin*, 1999). The Western Siberian reptile fauna includes few species: *Natrix natrix*, *Elaphe dione*, *Vipera berus*, *Vipera renardi*, *Gloydius halys*, *Zootoca vivipara*, *Lacerta agilis* and *Eremias arguta* (*Ananjeva* et al., 2006; *Ravkin, Bogomolova & Chesnokova*, 2010).

Geology and stratigraphy

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In Western Siberia, the Neogene sediments have a wide distribution. Since many decades ago, through systematic palaeontological studies and researching in Neogene and Quaternary sediments of Western Siberia, rich molluskan and small and large mammal fossil faunas were recovered (e.g. *Zykin*, 1979; *Zykin & Zazhigin*, 2008; *Zykin*, 2012). Based on the studies of the small mammals, the Neogene stratigraphy of the area is complemented with bio-chronologic data. Continental sedimentation in the western part of the Siberian Plain began in the Oligocene, after regression of the Turgai Strait in the Late Eocene, and continued until the Quaternary (e.g. *Chkhikvadze*, 1984, 1989; *Tleuberdina* et al., 1993; *Malakhov*, 2005). The sedimentary basin is bordered on the west by the Ural Mountains, in the south by the Central Kazakh Steppe and Altai-Sayan Mountains, and in the east by the western margin of the Siberian Plateau, supplying clastic material into the basin. Some authors include into this territory also the Zaisan Basin, located at the west of the Altai-Sayan Mountains (*Borisov*, 1963). The Neogene sediments are represented by lacustrine, fluvial, alluvial and other continental depositions, overlying marine Eocene sediments. The Neogene and Early Quaternary sediments have their maximal thickness of 300 m in the Omsk Basin. Neogene strata crop out mainly in the interfluves of the rivers Irtysh and Ishim (*Gnibitenko*, 2006; *Zykin*, 2012). All these sediments are terrestrial (fluvial and alluvial facies) and produce a rich vertebrate fauna (*Zykin*, 2012). The vertebrate-bearing Neogene sediments are found in several areas along the Irtysh River and its tributaries – Petropavlovsk-Ishim (e.g. Petropavlovsk 1, Biteke 1A), Omsk (e.g. Novaya Stanitsa 1, Cherlak), Pavlodar (e.g. Pavlodar, Baikadam), and Novosibirsk areas (e.g. Kamen-na-Obi) (Fig. 1). Detailed geological descriptions of the stratigraphic sections and fossil localities are summarised in *Zykin* (1979); *Zykin & Zazhigin* (2004); *Gnibitenko* (2006); *Zykin* (2012).

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The stratigraphic subdivision is based mainly on the Russian concept of svitas. A svita has lithologic, biochronologic and genetic (sedimentologic) significance and has no precise equivalent in Western stratigraphic theory and terminology (*Lucas* et al., 2012). The stratigraphy of Neogene sediments in Western Siberia is supported by magnetostratigraphic investigation (e.g. *Gnibitenko*, 2006; *Gnibidenko* et al., 2011). The recovered polarity signals are combined with biochronologic data and correlated to the GPTS (*Fejfar* et al., 1997; *Vangengeim, Pevzner & Tesakov*, 2005; *Zykin, Zykina & Zazhigin*, 2007). The biozonation is based on fast-evolving lineages of small mammals, mainly jerboas (Dipodidae), hamsters (Cricetidae) and voles (Arvicolidae). Thanks to these bio-magnetostratigraphic data the mean temporal resolution of the late Neogene faunal record from the Ob-Irtysh Interfluve is about 200 kyrs (Fig. 2, Table S1, Data S2). The main part of the vertebrate localities are referred to certain svitas (e.g. Kalkaman, Pavlodar, Irtysh Svitas), however, the stratigraphic assignment of three localities Olkhovka 1A, 1B, 1C to svitas is not available (Fig. 2, Table S1). No fossils are available from the early Late Miocene deposits.

State-of-art in palaeoherpetological studies in Western Siberia

The record of fossil amphibians and reptiles of Western Siberia, including the Zaisan Basin record, remains largely unknown. There are very few works devoted to the studies of the Western Siberian late Paleogene and Neogene herpetofaunal assemblages (e.g. *Chkhikvadze*, 1984, 1989; *Tleuberdina* et al., 1993; *Malakhov*, 2005). The vast majority of data on fossil amphibians and reptiles are given as short notes or mentioned in faunal lists (e.g. *Bendukidze & Chkhikvadze*, 1976; *Chkhikvadze*, 1985; *Malakhov*, 2005). In the present contribution, apart

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from the study of the new material, we also analysed the available specimens mentioned in those works.

The earliest report on Neogene fossil amphibians is from *Iskakova* (1969). There, she described amphibian faunas from two Priirtyshian localities, Gusiniy Perelet and Karashigar. The locality Gusiniy Perelet is a famous Late Miocene vertebrate locality, situated on the riverbank of the Irtysh River within Pavlodar town. The sedimentary sequence contains layers of different ages from the late Late Miocene until late Early Pliocene. Three localities (=horizons) Pavlodar 1A, 1B, 3B, grouped into several svitas, can be distinguished in Gusiniy Perelet vertebrate locality and its fossil content comes from the lower horizon – Pavlodar 1A. *Iskakova* (1969) described a fossil amphibian fauna from this layer.

The age of the Karashigar locality is unclear, *Tleuberdina et al.* (1989) indicated its age as Late Oligocene, while *Lychev* (1990) places it in the Middle Miocene, Kalkaman Svita (the list of the small mammal fauna; see Data S2). However, the amphibian taxa mentioned to be present in these localities by *Iskakova* (1969) (*Bombina* cf. *bombina*, *Pelobates* cf. *fuscus*, *Bufo* cf. *viridis*, *Bufo* cf. *bufo*, *Rana* cf. *ridibunda*, *Rana* cf. *temporaria*) have been identified mainly based on the vertebrae (cervical, dorsal and sacral) morphology, which is not diagnostic in frogs at that taxonomic level. *Chkhikvadze* (1984) restudied the material from Pavlodar 1A (= loc. Gusiniy Perelet) and identified *Bufo* cf. *raddei*, *Bufo* sp., *Pelophylax* cf. *ridibundus*, *Eremias* sp., and *Coluber* sp. However, we did not study the material mentioned in that work and could not verify his taxonomic identifications. The sample from the same locality (Pavlodar 1A) studied in the present work (Table S1), did not reveal any element listed in the earlier studies.

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Chkhikvadze (1984) summarised all known fossil amphibians and reptiles from the former USSR, including those from the Western Siberia. For many of them, accurate descriptions are not yet available. The Middle Miocene Kalkaman locality (*Tleuberdina*, 1993), now known as Malyi Kalkaman 1 (*Zykin*, 2012), provided a diverse herpetofauna. This fauna has been partially restudied and amended by us, including newly collected material. During the last decade, a new attempt to study the herpetofauna from the Western Siberian localities has been done (*Malakhov*, 2003, 2004, 2005, 2009). In these works, undescribed material from several Neogene localities of Kazakhstan was summarised, revised and studied, providing a critical overview. In spite of the advances of the last years, the Neogene herpetofauna from Western Asia is largely unknown, and available material continues being insufficiently studied. Thus, the main goal of the present study is the description and the taxonomic study of the new amphibian and reptile fossil material from the collections of V. Zazhigin, as well as to provide a faunistic analysis and palaeobiogeographic and environmental interpretations. In addition, we summarise the available literature data and include them in our results. To avoid the confusion with the locality names used by different authors in the Russian literature, here we provide all known names for the studied fossil localities.

Materials & Methods

The material of the present study has been collected by one of us (VZ) during his longtime excavations in different Western Siberian localities from the 1960's to 2008 using the screen-washing technique. The fossiliferous layers outcrop along the riverbanks of the Irtysh, Ishim and

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Ob Rivers. The material is deposited in the Institute of Geology, Russian Academy of Sciences under the collection numbers:

GIN 950/2001 (Baikadam), GIN 1107/1001 (Malyi Kalkaman 1), GIN 1107/2001 (Malyi Kalkaman 2), GIN 1106/1001 (Shet Irgyz 1) GIN 952/1001 (Petropavlovsk 1), GIN 1109/1001 (Znamenka), GIN 640/5001 (Pavlodar 1A), GIN 951/1001 (Selety 1A), GIN 951/2001 (Kedey), GIN 948/2001 (Novaya Stanitsa 1A), GIN 1115/1001 (Borki 1A), GIN 1110/2001 (Cherlak), GIN 945/2001 (Beteke 1A), GIN 640/6001 (Pavlodar 1B), GIN 1130/1001 (Lezhanka 2A), GIN 1130/2001 (Lezhanka 2B), GIN 1111/1001 (Olkhovka 1A), GIN 1111/2001 (Olkhovka 1B), GIN 1111/3001 (Olkhovka 1C), GIN 1118/3001 (Peshniovo 3), GIN 1131/2001 (Isakovka 2), GIN 1131/1001 (Isakovka 1A), GIN 1131/3001 (Isakovka 1B), GIN 1117/1001 (Kamyshlovo), GIN 945/2001 (Beteke 1B), GIN 945/3001 (Beteke 1C), GIN 1112/1001 (Andreievka – Speranskoe), GIN 1108/2001 (Pavlodar 2B), GIN 1112/2001 (Andreievka 1), GIN 1129/2001 (Livenka), GIN 1129/1001 (Lezhanka 1), GIN 1108/3001 (Pavlodar 3A), GIN 950/3001 (Lebiazhie 1A), GIN 950/4001 (Lebiazhie 1B), GIN 950/5001 (Podpusk 1), GIN 945/60001 (Beteke 2), GIN 946/2001 (Kamen-na-Obi), GIN 945/8001 (Beteke 4), GIN 664/2001 (Razdole).

Various groups of amphibians and reptiles are represented in the available material. Part of them – snakes and anguine lizards, has been published in separate papers (e.g. *Vasilyan, Böhme & Klembara*, 2016). Further, materials collected from four fossil sites in Kazakhstan were studied in the present work: Akyspe (also known as Agyspe), Aral Horizon, leg. by Bendukidze in 1977; Kentyubek, Turgai Basin; Ryzhaya II (Ryzhaya Sopka), Zaisan Svita, Zaisan Basin, leg. in 1970;

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Ayakoz (known also as Ayaguz), Zaisan Basin, leg. in 1970-1971; Petropavlovsk 1/2[1], leg. 1972 (Table S1). In addition, few data from the literature (after critical revision) has been included to amend the herpetofaunal assemblages of some localities as well as to reassign and revise the stratigraphic position of these localities using biostratigraphic information of small and large mammal faunas (see full list in the Datas S2, S 3).

The photographs of the fossil material were taken by a digital microscope LEICA DVM5000 (Tübingen) and inspect scanning electron microscope Inspect S (Madrid). Figures and tables were produced by using Adobe Photoshop and Illustrator programs. The osteological nomenclature for salamander remains is given following *Vasilyan* et al. (2013), for frogs after *Sanchíz* (1998a) and for the lizard nomenclature we referred to lepidosaurian terminology of *Evans* (2008). Additionally, the standardrised osteological nomenclature of *Daza, Aurich & Bauer* (2011) and *Daza & Bauer* (2010) was used for Gekkota.

Based on the herpetofaunal assemblages the palaeoprecipitation values for the fossil localities were estimated using the method of bioclimatic analysis of the ecophysiologic groups of amphibian and reptile taxa (*Böhme* et al., 2006). For the localities 'poor' in amphibian and reptile taxa, the range-through approach (*Barry* et al., 2002) is used, by which the faunas of two or more localities with age differences less than 100 kyr and/or belong to a single stratigraphic unit – svita, are considered as only one. Those taxa added additionally to the herpetofaunal assemblage by range-through approach are indicated by grey colour in Table 4.

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[1] In Petropavlovsk town two fossil sites (Petropavlovsk 1 (MN12) and Petropavlovsk 2 (MN14)) having different ages are known, see *Zykin* (2012). Since the enclosed collection label to the material indicates only 'locality Petropavlovsk, leg. 1972' any stratigraphic allocation of the fossils to one of those layers is impossible.

Institutional/collection abbreviations.

GPIT: Paläontologische Sammlung der Universität Tübingen, Tübingen, Germany; **HC**: collection of Marcela Hodrova (Prague University), now stored in GPIT; **MNCN:** Museo Nacional de Ciencias Naturales, Madrid, Spain; **NMNHK:** National Museum of Natural History, Kiev, Ukraine; **PIN:** Palaeontological Institute, Russian Academy of Sciences, Moscow, Russia; **GNM**: National Museum of Georgia, Tbilisi, Georgia; **GIN:** Geologic Institute, National Academy of Russia, Moscow, Russia.

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Anatomical abbreviations.

ao: antrum olfactorium; **alo**: antrum pro lobo olfactorio; **dl**: dental lamina; **ds**: dental shelf; **hl**: horizontal lamella; **is**: incisura semielliptical; **ff**: frontoparietal facet; **fcpr**: facial process of maxilla; **fMx5**: foramina for mandibular division of the fifth cranial (trigeminal) nerve; **hfr**: haemal foramen; **hl**: horizontal lamella; **lf**: lacrimal facet; **lg**: longitudinal groove; **lh**: lamina horizontalis; **lp**: lateral processes; **ls**: lamina supraorbitalis; **mc**: Meckelian canal; **na**: neural arch; **nc**: neural canal; **nf**: nasal facet; **onf**: orbitonasal foramina; **olf**: olfactory foramina; **pf**: parasphenoid facet; **pfc**: palatine facet; **ph**: paries horizontalis; **prz**: prezygapophysis; **psz**: postzygapophysis; **pv**: paries verticalis; **pxp**: premaxillary process; **pyp**: pterygapophysis; **sac**: opening of superior alveolar canal; **sg**: symphyseal groove; **sf**: splenial facet; **tpr**: transverse process.

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RESULTS

Systematic palaeontology

Class **Amphibia** *Gray*, 1825

Order **Caudata** *Scopoli*, 1777

Family **Hynobiidae** *Cope*, 1859

Genus ***Salamandrella*** *Dybowski*, 1870

Salamandrella sp.

(Figs. 3D-3G)

Localities and material examined. Selety 1A, GIN 951/1001-AM01 – -AM03, 3 trunk and GIN 951/1001-AM04, 1 caudal vertebra; GIN 951/1001-AM05, 1 ?proximal?distal end of bone (humerus?); Novaya Stanitsa 1A, GIN 948/2001-AM01 – -AM11, 11 dorsal vertebrae; Lezhanka 2A, GIN 1130/1001-AM01 – -AM26, 26 trunk and GIN 1130/1001-AM27 – -AM28, 2 caudal vertebrae; Cherlak, GIN 1110/2001-AM01 – -AM12, 12 dorsal vertebrae; Lezhanka 2B, GIN 1130/2001-AM01, 1 dorsal vertebra, GIN 1130/2001-AM02, 1 bone extremity; Olkhovka 1B, GIN 1111/2001-AM01, 1 dorsal vertebra; Iskakovka 2A, GIN 1131/2001-AM01, 1 dorsal vertebra; Andreievka – Speransko, GIN 1112/1001-AM01, 1 dorsal vertebra; Lezhanka 1, GIN 1129/1001-AM01 – -AM02, 2 dorsal and GIN 1129/1001-AM02, 1 caudal vertebrae; Beteke 1C, GIN 945/3001-AM01 – -AM02, 2 dorsal vertebrae.

Description and comments. The vertebrae have an elongated to nearly slender form. The vertebral centrum is amphicoelous. The basapophyses at the vertebral centrum are either absent or are present in the form of a small protuberance at the laterodorsal corners of the anterior portion of the vertebral centrum. A pair of subcentral foramina is situated at the basis

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of the transverse processes. In lateral view, the neural arch is tall and relatively broad in dorsal view. The posterior edge of the pterygapophysis is bifurcated. Sometimes the neural spine is present, but generally, the dorsal surface of the neural arch is flat. The pre- and postzygapophyses have an elongated oval shape. In anterior view, the neural canal has an outline of a regular pentagon. The transverse process is unicapitate. The anterior and posterior alar processes are absent. The vertebrae can be assigned to the family Hynobiidae based on the small size and their amphicoelous centrum with circular articular surfaces; lacking basapophyses or being weakly pronounced; the neural spine lacks the notch on the posterior margin of neural arch; fused rib-bearers as well as intervertebrally exiting spinal nerve in both trunk and caudal vertebrae (e.g. *Edwards*, 1976; *Venczel*, 1999a, 1999b). Further, features characteristic for the genus *Salamandrella*: absence of the subcentral foramen; concave anterior margin of the neural arch which reaches the middle part of the prezygapophyseal articular facets (*Venczel*, 1999b; *Syromyatkova*, 2014), can be observed on the vertebrae (Fig.???). The detailed description of hynobiid material from the Western Siberian localities and comparison with Recent and fossil hynobiids will be provided in a separate paper.

Family **Cryptobranchidae** *Fitzinger*, 1826

Cryptobranchidae indet.

(Figs. 3A-3C)

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Localities and material examined. Pavlodar 1A (=Gusini Perelet), 1 fragmentary right dentary and 2 fragments of jaw bones, for details about the stratigraphic allocation see the section 'Cryptobranchidae', unnr. PIN specimen.

Description and comments. Among the fragments, a posterodorsal portion of a large right dentary, 27 mm in length, is present. In lingual view, the pars dentalis is composed entirely of dental lamina, the subdental lamina is present, but reduced. The pars dentalis possesses 30 pedicels of pleurodont teeth. The subdental shelf inclines slightly ventrally. The lamina horizontalis is prominent. The corpus dentalis above the Meckelian groove has a concave surface; ventrally this surface possesses a ridge, running parallel to the lamina horzontalis. The cross section of the dentary shows a relatively low portion of cancellous bone and a dominance of compact bone. The sizes of the bone, the form and structure of the pars dentalis and the cross section of the bone are characteristic of giant salamanders (*Vasilyan* et al., 2013).

Family **Proteidae** *Gray*, 1825

Genus ***Mioproteus*** *Estes & Darevsky*, 1977

Mioproteus sp.

(Figs. 3H-3S)

Localities and material examined. Ryzhaya II (known also Ryzhaya Sopka), GNM unnr. specimen, 2 dorsal vertebrae; Malyi Kalkaman 2, GIN 1107/2001-AM01, 1 right premaxilla; Borki 1A, GIN 1115/1001-AM01, 1 dorsal vertebra; Ayakoz, GNM unnr. specimen, 1 dorsal vertebra;

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Akespe, unnr. HC specimens, 3 vertebrae; Petropavlovsk 1/2, GNM unnr. specimen, 22 vertebrae.

Description. The preserved left premaxilla is fragmentary (Fig. 3P-3Q), the posterior process is broken off. In ventral view, the bone has a rough surface. The pars dentalis of the premaxilla is located at the anterior side of the bone. The crowns of pleurodont teeth are missing, only their pedicellar portions are preserved. In dorsal view, the bone surface is slightly rough. At the middle part of the bone, the lamelliform anterolateral ridge of the posterior process is high?. The amphicoelous vertebrae are flat and wide. The centrum is dumb-belled in shape and narrows to the middle region. The basapophyses, if present, are small and weakly developed. Two subcentral foramina are present at the central part of the vertebral centrum. In lateral view, the vertebra is low; the anterior and posterior zygapophyseal crests are pointed, forming the dorsal border of the deep depressions anteriorly and posteriorly to the transverse process. The middle part of the neural arch is lower than its cranial and caudal margins. The neural arch is forked posteriorly (Fig. 3I) (not visible at Fig. 3M). The neural spine extends as far as the preserved anterior margins of the neural arch, whereas posteriorly, it terminates before the posterior margin of the neural arch. The preserved right prezygapophyseal and postzygapophyseal articular facets are ellipsoid.

Comparison and comments. A direct comparison with *Mioproteus* specimens reported previously is not possible due the extremely scarce description of the skull elements attributed to this taxon (e.g. *Estes & Darevsky*, 1977; *Miklas*, 2002). Hence, we used the unpublished material of *Mioproteus* sp. from the locality Grytsiv (Ukraine, earliest Late Miocene) (Fig. 3R-3S) for the taxonomic identification of the fossil premaxilla from Malyi Kalkaman 2 (Fig. 3P-3Q). Our

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comparison shows no differences in the premaxilla morphology between Kazakhian and Ukrainian *Mioproteus* sp. The vertebrae from the localities Borki 1A and Ayakoz can be easily assigned to the genus *Mioproteus* based on following characters: (1) robust vertebra with an amphicoelous centrum; (2) cranial margin of the neural arch is tall; (3) presence of the basapophyses; (4) distinct wide depression at the anterior base of the transverse process; (5) intervertebrally exiting spinal nerves and (6) forked neural spine (*Edwards*, 1976; *Estes & Darevsky*, 1977; *Ivanov*, 2008).

Family **Salamandridae** *Goldfuss*, 1820

Subfamily **Pleurodelinae** *Tschudi*, 1838

Genus ***Chelotriton*** *Pomel*, 1853

Chelotriton sp.

(Figs. 3T-3Y)

Localities and material examined. Malyi Kalkaman 1, GNM unnr. specimen, 1 dorsal vertebra; Ayakoz, GNM unnr. specimen, 1 dorsal vertebra.

Description. The single fragmentary dorsal vertebra of *Chelotriton* from Malyi Kalkaman 1 has been scanty described (*Tleuberdina* et al., 1993, pp. 133-134). The centrum of the vertebra is dorsally curved. The posterior third region and the cotyle is broken. The condyle is dorsoventrally slightly compressed and oval in shape. The ventral surface of the centrum bears a pair of the foramina subcentrale in its middle part. The ventral bases of both transverse processes are pierced by a foramen (ventral foramen for spinal nerve?).

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The neural spine is tall and long, nearly as long as the vertebral centrum. The dorsal surface of the neural spine has the form of an elongated isosceles triangle and it is covered by a distinct pustular sculpture. The anterior margin of the neural spine is concave in outline. The posterior half of the spine is wider than the anterior one. In anterior view, the neural arch, as well as the neural canal, has a triangular form. The roof of the neural canal, laterally on both sides of the spine, is flat.

The pre- and postzygapophyses are damaged. The anterior portion of the left postzygapophysis is present, it shows a horizontal surface. The anterior bases of both prezygapophyses at the contact with the centrum possess small subprezygapophyseal foramina. Behind the left prezygapophysis the accessory alar process exhibits a marked step (Fig. ???), projects posteroventrally and connects caudally with the anterior alar process. Most probably, the contact point of the accessory and anterior alar processes corresponds to the base of the parapophysis. Both transverse processes are broken, but the bases are preserved. Apparently, two rounded upper and lower prominences, seen in left lateral view, correspond to the dia- and parapophysis. The parapophysis is located anterior and below the level of the diapophysis, thus, the transverse process becomes a bent projection. The arterial canal is running behind the base of the transverse process. Anteriorly its dorsal and ventral walls are built by the accessory and anterior alar processes.

The vertebra from the locality Ayakoz (Fig. 3T-3X) is fragmentary, its neural arch and left transverse process are lost. The centrum is compact, short and wide. It possesses an elliptical central foramen. The diapophysis of the preserved right transverse process is broken, but it can be assumed that the dia- and parapophysis were separated from each other. The accessory alar

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process runs from the praezygapophysis to the dorsal edge of the diapophysis. The posterior and anterior alar processes are running from the cotyle and condyle straight along the transverse process to the parapophysis. This morphology is characteristic of the first dorsal vertebrae.

Comparison and comments. Earlier this vertebra was described by Tleuberdina et al. (1993). Here it has been assigned to the genus *Chelotriton* by the presence of triangular and well-sculptured plate on the top of the neurapophysis. This character is not a unique feature of *Chelotriton*. A triangular and well-sculptured plate on the neurapophysis is known also in other salamanders, e.g. Recent species of *Tylototriton* and *Echinotriton*, and in *Cynops pyrrhogaster*, *Lissotriton boscai* (unnr. GPIT specimen), *Paramesotriton* (MNCN 23557, 13645), as well as the fossil taxa *Archaeotriton* (*Böhme*, 1998), aff. *Tylototriton* sp. (loc. Baikadam, this paper), *Carpathotriton* (*Venczel*, 2008). The vertebra from the Malyi Kalkaman 1 resembles species of *Chelotriton*, *Paramesotriton*, *Tylototriton*, *Echinotriton*, *Cynops pyrrhogaster*, and *Carpathotriton* by the presence of a subprezygapophyseal foramen. However, the vertebra can be justified as *Chelotriton* sp. and distinguished from other salamanders by its higher length (vs. *Echinotriton*, *Cynops* and *Carpathotriton*); a longer neural spine with rugose sculptured, triangular dorsal surface (vs. aff. *Tylototriton* sp., loc. Baikadam, this paper); a well-pronounced accessory alar process (vs. *Tylototriton*).

The fragmentary vertebra from the locality Ayakoz can be assigned to this group too, because of the shape of massive rib-bearers and large dimensions (*Ivanov*, 2008). It shows the identical morphology of vertebra to *Chelotriton* sp., type II described from Mokrá-Western Quarry, 2/2003 Reptile Joint (Early Miocene, Czech Republic) (*Ivanov*, 2008).

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The abundant European Cenozoic record of the genus *Chelotriton* showed that vertebral morphology is insufficient for taxonomic identification as *Chelotriton* (*Böhme*, 2008). This genus has an unknown higher diversity, which can be uncovered by the study of complete skeletons of those species. Hence, we assign the vertebrae from studied localities as aff. *Chelotriton* sp.

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Genus ***Tylototriton*** Anderson, 1871 (*Anderson*, 1871)
aff. ***Tylototriton*** sp.

(Figs. 4A-4K)

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Locality and material examined. Baikadam, GIN 950/2001-AM01, -A14–-A17 5 dorsal vertebrae; Ayakoz, GNM unnr. specimen, 2 dorsal vertebrae.

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Description. All preserved vertebrae are opistocoelous. The condyle and cotyle are compressed dorsoventrally. The vertebrae are slender, slightly narrow and high. The neural canal is round, but in anterior view, the ventral margin of the neural canal is flat (the same occurs with the dorsal wall of vertebral centrum). In lateral view, the centrum is curved dorsally. The neural spine was most probably high but does not reach the level of the pustular region. The neural spine begins behind the cranial margin of the neural arch. The latter is tilted dorsally and does not extend beyond the posterior edge of the postzygapophysis. The dorsal plate of the neural spine is short, poorly developed, and covered with rugosities. It has the form of an isosceles triangle. Due to the concave shape of the posterior margin of the caudal border, we suggest that most probably, the neural spine was bifurcated. The length of the neural spine without the

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sculptured structure is the same in all preserved vertebrae and corresponds nearly to the half of the entire vertebral length.

The pre- and postzygapophyses are horizontal and almost at the same level. The pre- and postzygapophyseal articular facets are oval in shape. Small subprezygapophyseal foramina are present at the level of the connection between the anterior bases of both prezygapophyses with the vertebral centrum. The posterolaterally directed transverse process is horizontally flattened and displays a bicapitate articulation surfaces with the rip. The diapophysis and parapophysis are separated. The former is smaller than the latter. A low and moderately deep notch is developed at the posterior edge of the neural arch. The transverse process has an anterior (accessory alar process) and a posterior laminar edges (the posterior alar process and dorsal lamina). The straight, posteroventrally directed accessory alar process connects the prezygapophysis caudally with the base of the parapophysis. The dorsal lamina starts from the diapophysis and extends to the postzygapophyses, whereas the lamelliform posterior alar process starts at the parapophysis and terminates directly before the cotyle. Subparallel to the accessory alar process, a thin anterior alar process runs along the cranial half of the centrum. Behind and in front of the transverse process two – anterior shallow and posterior deep- 'cavities' are present. These 'cavities' are connected by a (arterial ?) canal, running through the transverse process. In ventral view, the vertebral centrum does not possess a ventral keel. In the middle portion, the centrum is flattened and nearly plane. Its surface is rough and pierced by numerous foramina. Two large subcentral foramina are located at the posterior corner between the centrum and transverse process.

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Comparison and comments. The vertebrae resemble the morphology of pleurodeline salamanders *Echinotriton*, *Tylototriton*, *Cynops*, *Chelotriton*, *Paramesotriton* and *Tylototriton* and *Carpathotriton* in characteristics such as: (1) presence of rugosities on the neural arch; (2) prezygapophysis and parapophysis connected with the accessory alar process, beside *Carpathotriton*, *Cynops* and cf. *Tylototriton* sp. from Möhren 13 (*Böhme*, 2010: p. 11, fig. 6f), where this process connects prezygapophysis with diapophysis; (3) moderately developed posterior 'cavity' behind the transverse process; (4) presence of subprezygapophyseal foramen (for collection references see subsection 'Comparison' of *Chelotriton* sp. in this paper). In general morphology, the vertebrae resemble mainly the genus *Tylototriton* and they differ from the compared genera in having: (1) a low, elongate, narrow and lesser flattened vertebrae; (2) a weakly developed pustular structure of the neural arch (similar character like in *Paramesotriton*); (3) a low and long neural spine without the sculptured structure; (4) a dorsoventrally compressed cotyle and condyle; (5) a deep posterior 'cavity' behind the transverse process and extended dorsal lamina and posterior alar process; (6) a low and shallow posterior notch of the neural arch; (7) it differs from specimens of the genus *Cynops* in having accessory alar processes reaching the parapophysis; in *Cynops* it reaches the diapophysis. The Siberian *Tylototriton* differs from the European Oligocene cf. *Tylototriton* (see *Böhme*, 2010: p. 11, fig. 6f) by having a ventrally deflected accessory alar process which terminates ventrally to the parapophysis; a shorter and lower neural spine as well as a shorter dorsal plate of the neural spine.

Taking into account the mentioned differences, we suggest that the described vertebrae should be assigned to a new pleurodeline salamander genus, that show affinities with the genus

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Tylototriton. However, we do not consider reasonable to describe a new form unless cranial material of this salamander is available.

Order **Anura** *Fischer von Waldheim*, 1813

Family **Palaeobatrachidae** (*Cope*, 1865)

Palaeobatrachidae sp. indet.

(Fig. 5A-5D)

Locality and material examined. Novaya Stanitsa 1A, GIN 948/2001-AM12, 1 sphenethmoid.

Description. A very robust sphenethmoid lacking the posterior region. The two anterior cavities corresponding to the antrum olfactorium are anteroposteriorly shallow, the posterior cavity – antrum pro lobo olfactorio, is deep and narrow (Fig. ???). The olfactory foramen is larger than the orbitonasal one. The processus rostralis is elongated and projects anteriorly. Anteriorly, on the dorsal face of the bone, two sharply marked crescentic depressions correspond to the contacts with the nasal bones (nasal facet). In dorsal view, the frontoparietal facet (contacting with the frontoparietal) shows a slightly striated surface. The lateral processes protrude laterally. The lamina supraorbitalis is well developed. The most anterior part of the incisura semielliptical is preserved on the specimen. The remaining part of this structure demonstrates that it approaches cranially to the anterior border of the bone. The ventral face of the sphenethmoid possesses a narrow and long depression corresponding to the contact area with the cultriform process of the parasphenoid (parasphenoid facet).

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Comparison and comments. The bone has strong similarities to that of palaeobatrachids in having: (1) a long sphenethmoid with a frontoparietal fenestra corresponding to more than a half of the bone length; (2) in ventral view, the articulation area of the parasphenoid delimited by two parallel ridges; (3) a very short septum nasi and lateral process (*Vergnaud-Grazzini & Młynarski*, 1969; *Sanchíz & Młynarski*, 1979). The palaeobatrachid from Novaya Stanitsa 1A shows all these characters besides the short septum nasi, which is long in the fossil bone. We presume that the frontoparietal fenestra was long more than a half of the sphenethmoid length since the overall length of the frontoparietal and nasal facets have similar proportion like in other palaeobatrachids. Furthermore, according to *Venczel, Codrea & Fărcaş* (2012) the sphenethmoidal ossification composes the anterior margin of frontoparietal fontanelle in palaeobatrachid frogs (*Palaeobatrachus* + *Albionbatrachus*), which can be also observed in the studied specimen.

Family **Bombinatoridae** *Gray*, 1825

Genus ***Bombina*** *Oken*, 1816

Bombina sp. / ***Bombina*** cf. ***bombina*** (*Linnaeus*, 1761)

(Figs. 6A-6F)

Localities and material examined. Malyi Kalkaman 2, GIN 1107/2001-AM02, 1 ilium; Selety 1A, GIN 1107/2001-AM06, 1 ilium; Cherlak, GIN 1107/2001-AM06, 1 ilium.

Description. The bone description is based on the ilium from Selety 1A, since the specimens from the localities Malyi Kalkaman 2 and Cherkal are strongly damaged. In lateral view, the iliac

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shaft is almost straight and lacks the dorsal crest. The tuber superior is a weakly pronounced tubercle. In dorsal view, a spiral groove is observable, which continues on the medial surface of the shaft. The acetabulum is round and strongly extended. The junction between the iliac shaft and corpus ossi is slightly constricted and the ventral base of the corpus ossi possesses a preacetabular fossa. The ventral ridge of the acetabulum is high. In lateral and posterior views, the pars descendens is reduced and wide, whereas the pars ascendens is high but narrow. In ventral view, the pars descendens is broad and nearly flat. In medial view, the acetabular area is bordered by shallow ridges. Between them, a triangular and medially prominent interiliac tubercle, is present.

Comparison and comments. The lack of the vexillum, a weakly developed tuber superior is characteristic for the genus *Bombina* (*Böhme*, 1977). The ilium differs from *Bombina orientalis* by a weakly developed tuber superior. The ilium from Selety 1A distinguishes from *Bombina variegata* and resembles *Bombina bombina* in having: (1) a developed pars descendens; (2) a posteroventral ridge of the pars descendens projecting ventrally rather than posteriorly (*Böhme*, 1977); (3) a developed preacetabular fossa (*Sanchíz & Młynarski*, 1979). Therefore we assign tentatively the bone to *Bombina bombina* due to the absence of well-preserved material of the fire-bellied toads from Selety 1A,. The specific assignment of the ilia from Malyi Kalkaman 2 is impossible due to their fragmentary preservation, thus we describe them as *Bombina* sp.

The specimen from the loc. Cherlak (Fig. 6D-6F) is strongly damaged, only some character are observable, allowing its identification within Bombinatoridae, such as (1) a large pars descendens at its anterior part but reduced dorsally; (2) the tuber superior is present but larger than that of the Maly Kalkaman 2 and Selety 1A (withing the family larger tuber superior are

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Con formato: Sin subrayado, Color de subrayado: Automático, Diseño: Claro present in the *Barbatula* (*Folie* et al., 2013)); (3) although the ventral wall of the acetabulum is not preserved, the remaining part of its base allows to assume that it was markedly pronounced. Due to the incomplete preservation, the important characters for taxonomic identification, e.g. interiliac tubercle and junctura ilioischiadica, cannot be observed. Thus, the ilium from Cherlak can be tentatively referred to the family Bombinatoridae.

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Family **Pelobatidae** *Bonaparte*, 1850

Genus ***Pelobates*** *Wagler*, 1830

Pelobates sp.

(Fig. 6G-6I)

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Localities and material examined. Selety 1A, GIN 1110/2001-AM13, 1 right ilium.

Description. The corpus ossi and distal portion of the iliac shaft are present. The tips of the pars descendes and pars ascendes are broken. The bone surface is smooth; there is no tuber superior. An oblique posterolaterally-anteromedially directed spiral groove extends on the dorsal surface. Laterally, the high and long pars ascendens possesses a supraacetabular fossa. The junction between the iliac shaft and corpus ossi is not constricted. The subacetabular groove is shallow and broad. The acetabulum has nearly triangular form, with a well-marked rim. In medial view, the corpus ilii possesses an interiliac facet with a rugose surface. It is composed by a large lower and smal upper portions. Between these portions a well-developed interiliac tubercle is visible. The lower portion is ventroposteriorly oblique, whereas the upper

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one is flat, less rugose and has a concave surface. The rugose surface of the facet indicates an extensive contact between two ilia. The acetabular dorsal tuber is higher than the ventral one.

Comparison and comments. The ilium can be assigned to the family Pelobatidae based on the absence of a dorsal crest and dorsal tubercle and the presence of an oblique spiral groove on the dorsal surface (*Roček* et al., 2014). The bone has the following characters of the genus *Pelobates*: (1) a high and long pars ascendes; (2) a well-developed spiral groove (*Böhme*, 2010); (3) lack of the dorsal crest of the iliac shaft (*Folie* et al., 2013); (4) a rugose surface of the interiliac facet (*Rage & Hossini*, 2000). However, further identification of the ilium is impossible, as it does not show relevant differences at the specific level.

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Family **Hylidae** *Rafinesque*, 1815

Genus ***Hyla*** *Laurenti*, 1768

Hyla savignyi *Audouin*, 1827

Código de campo cambiado

Hyla gr. ***H. savignyi***

(Figs. 6J-6O)

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Localities and material examined. Shet-Irgyz 1, GIN 1106/1001-AM01, 1 left ilium; Novaya Stanitsa 1A, GIN 948/2001-AM13, 1 scapula and GIN 948/2001-AM14, 1 sacral vertebra; Lezhanka 2A, GIN 1130/1001-AM29 – -AM32, 4 ilia and GIN 1130/1001-AM33 – -AM36, 4 scapulae; Cherlak, GIN 1130/1001-AM14 – -AM15, 2 ilia; Olkhovka 1B, GIN 1111/2001-AM02, 1 fragmentary ilium; Pavlodar 2B, GIN 1108/2001-AM01 – -AM03, 3 ilia.

Description. The scapula, a triradiate element of the pectoral girdle, is comparatively long. The bone surface is relatively smooth; it is pierced by several foramina. The corpus scapulae, the middle part of the bone, is slender and long. The pars suprascapularis is preserved fragmentary and most probably was not high. In dorsal view, the elongate pars acromialis is narrow and subequal in length. The shorter and flattened processus glenoidalis is slightly broad. The processus glenoidalis and pars acromialis are separated by relatively deep sinus interglenoidalis. The margo posterior at the corner of the processus gleinoidalis and corpus scapula possesses an oval to elongated oval fossa supragleinoidalis. The tear shaped glenoid fossa reaches the posterior corner of the processus glenoidalis. The crista supraglenoidalis is slightly pronounced. The ilia from all localities resemble the same morphology – the tuber superior is prominent dorsally and slightly laterally. The tuber superior is located at the anterior corner of the acetabulum. The preserved iliac shaft is nearly cylindrical and mediolaterally slightly compressed. It is devoid of crista dorsalis. The supraacetabular part of the ilium is smaller than the preacetabular. The ventroposterior margin of the iliac shaft is connected with the pars descendes by an expanded preacetabular zone – building a broad and thin lamina. The acetabulum has a nearly triangular form. The acetabular rim is prominent at its high ventroanterior edge. The posterodorsal corner of the acetabulum ascends and builds a small and prominent acetabular tuber. In medial view, the bone surface is smooth, sometimes with a shallow depression in the middle part of the corpus ossi. In distal view, the junctura ilioischiadica is slender; the acetabulum is high and the interiliac facet displays a well-pronounced ventromedial expansion. The acetabular dorsal tuber is higher than the ventral one.

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Comparison and comments. The Siberian fossil tree frog differs from already described fossil and some recent species of the genus *Hyla*. The following recent material is available for comparison: *Hyla savignyi*, Armenia (four individuals, unnr. GPIT specimen), *Hyla orientalis*, Armenia (two individuals, unnr. GPIT specimen) and *Hyla arborea*, Germany ? (one individual, unnr. GPIT specimen). The Siberian forms can be distinguished from *Hyla* sp. (Rudabánya, Hungary, middle Late Miocene (*Roček*, 2005); Bois Roche Cave, France, early Late Pleistocene (*Blain & Villa*, 2006)), *Hyla arborae* (loc. TD8, Spain, early Middle Pleistocene (*Blain*, 2009)), *Hyla* cf. *arborea* (Mátraszőlős 2, Hungary, middle Middle Miocene (*Venczel*, 2004)); *Hyla* gr. *H. arborea* (Capo Mannu D1 Local Fauna, Italy, Late Pliocene (*Delfino, Bailon & Pitruzzella*, 2011)), and recent *Hyla japonica* (*Nokariya*, 1983) in having: (a) a fossa supragleinoidalis; (b) a slenderer and lower corpus scapula and pars suprascapularis; (c) a shorter and broader processus glenoidalis. Apart from these differences, the Siberian fossil tree frogs resemble *Hyla* sp. from Bois Roche Cave, France (*Blain & Villa*, 2006) and *H. arborea* (one individual, unnr. GPIT specimen) in possessing a low and broad processus glenoidalis. The Recent *H. savignyi* is the only tree frog showing a fossa supragleinoidalis like one present in the studied remains. The Recent *H. savignyi* possesses also some similarity to fossil tree frog in having: (1) a slender junction ilioischiadica; (2) the same position of the tuber superior; (3) comparable acetabular tubers and (4) a similar slightly curved pars ascendens. However, there are also differences between these two forms – the fossil tree frog has: (1) a dorsally and slightly laterally prominent tuber superior; (2) a deeper and larger fossa supragleinoidalis; (3) a ventromedial expansion of the interiliac facet; whereas *H. savignyi* has: (1) a dorsally and laterally significantly prominent tuber superior; (2) a shallow and small fossa supragleinoidalis; (3) the interiliac facet devoid of

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Con formato: Sin subrayado, Color de subrayado: Automático ventromedial expansion. Among other fossil tree frogs, the Western Siberian *Hyla* sp. has the lowest and broadest processus glenoidalis. Another fossil tree frog *Hyla* sp. reported from loc. Kuznetsovka, Russian Platform (0.5-0.65 Ma) (*Ratnikov*, 2002: fig. 2), displays a similar morphology of the ilium as in the Siberian fossil concerning the orientation of the tuber superior and in the form of the junctura ilioischiadica. Because the indicated differences to both Recent and fossil forms, as well as similarities to *H. savignyi*, we assume that fossil tree frogs from Western Siberian and Russian Platform, probably represent a new form related to the group of *Hyla savignyi*.

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Family **Bufonidae** *Gray*, 1825

Genus ***Bufo*** *Laurenti*, 1768

Bufo bufo (*Linnaeus*, 1758)

(Figs. 6P-6W)

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Localities and material examined. Novaya Stanitsa 1A, GIN 948/2001-AM15, 1 left and GIN 948/2001-AM16 – -17, 2 right ilia, GIN 948/2001-AM18 – -19, 2 dorsal vertebrae; Borki 1A, GIN 1115/1001-AM02, 1 sacral vertebra, GIN 1115/1001-AM03, 1 left ilium; Olkhovka 1B, GIN 1111/2001-AM02, 1 left, GIN 1111/2001-AM03 – -AM04, 2 right ilia and GIN 1111/2001-AM05, 1 dorsal vertebra; Olkhovka 1C, GIN 1111/3001-AM01, 1 left scapula, GIN 1111/3001-AM02, 1 dorsal vertebra and GIN 1111/3001-AM03, 1 urostyle; Lezhanka 2A, GIN 1130/1001-AM37, 1 left ilia, GIN 1130/1001-AM38, 1 left scapula, GIN 1130/1001-AM39, 1 sacral and GIN 1130/1001-AM40, 1 dorsal vertebrae; Isakovka 1B, GIN 1131/3001-AM01, 1 left ilium; Isakovka

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1A: GIN 1131/1001-AM01, -AM05, 2 right ilia; Peshniovo 3, GIN 1118/3001-AN01, 1 sacral vertebra; Lezhanka 1, GIN 1129/1001-AM04, 1 dorsal vertebra; Andreievka 1, GIN 1112/2001-AM01 1 right scapula.

Description and comments. The ilia are large and have a robust corpus ossi. The spiral groove is present; it is board and very shallow. The tuber superior is broad and low and covered with irregular tubercles. It is situated above the acetabulum. The smooth and concave pars descendens is more developed than the pars ascendens. The ventral edge of the pars descendens is thin and lamelliform. The preacetabular fossa is absent. In posterior view, the anterolateral edge of the acetabular is strongly curved; the junctura ilioischiadica shows a higher acetabular ventral tuber than the dorsal tuber; the ventral half of the corpus ossi projects ventromedially.

The scapula is a robust bone; it is longer than high. The material is represented by all size groups. The angular fossa is absent, a shallow groove on the ventral side of the pars acromialis is present and well pronounced in larger individuals. The pars acromialis and corpus scapula have nearly the same height, the pars suprascapularis increases in height laterally. The pars suprascapularis and corpus scapulae (anteriorly) have smooth surfaces. The base of the lateral edge of the fossa glenoidalis is elevated but does not project laterally. The crista supraglenoidalis is well developed in larger individuals. The anterior margin is concave. The base of the pars acromalis is high and thin. In ventral view, there is a shallow and expanded depression. The anteriomadial margin of the pars acromalis possesses a low tubercle. The transition from the corpus scapula to the pars acromialis is nearly straight; the wall is thin.

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In several localities, isolated large-sized frog vertebrae and urostyle (Figs. 6H, 6I) are present in association with diagnostic elements (ilia and scapula) (e.g. loc. Olkhovka 1C) or isolated (e.g. loc. Pehsniovo 3). They are individuals of the same size that can be assigned to the large *Bufo bufo*. The morphological traits described above (e.g. lack of angular fossa on the scapula and preacetabular fossa on ilium, general outline, form and size of the scapula and ilium) as well as the bone dimensions are found in the common toad *Bufo bufo* (*Blain, Gibert & Ferràndez-Cañadell*, 2010).

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Genus ***Bufotes*** *Rafinesque*, 1815

Bufotes viridis *Laurenti*, 1768

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(Figs. 6X, 6Y, 6Z)

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Localities and material examined. Baikadam, GIN 950/2001-AM02 – -AM04, 3 left and GIN 950/2001-AM05 – -AM09, 5 right ilia; Malyi Kalkaman 1, GIN 1107/1001-AM02 and -AM03, 1 left and 1 right scapulae; Malyi Kalkaman 2, GIN 1107/2001-AM03, 1 right scapula; Znamenka, GIN 1109/1001-AM01 and -AM02, 1 left and 1 right scapulae, GIN 1109/1001-AM03 – -AM07, 5 left and GIN 1109/1001-AM08 – -AM11, 4 right ilia; Pavlodar 1A, GIN 640/5001-AM01 – -AM30, 30 left and GIN 640/5001-AM31 – -AM62, 32 right ilia, GIN 640/5001-AM63 – -AM78, 15 left and GIN 640/5001-AM79 – -AM90, 11 right scapulae; Cherlak, GIN 1110/2001-AM16, 1 right ilium; Selety 1A, GIN 951/1001-AM08 – -AM10, 3 left and GIN 951/1001-AM11 – -AM14, 4 right ilia; Isakovka 1A, GIN 1131/1001-AM02 – -AM04, 3 left ilia; Kedey, GIN 951/2001-AM01 and – -

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AM02, 1 left and 1 right ilia; Lebiazhie 1A, GIN 950/3001-AM01, 1 left scapula, GIN 950/3001-AM01 2 left ilia; Lebiazhie 1B, GIN 950/4001-AM01, -AM02, 2 right ilia.

Description and comments. The iliac shaft is slightly compressed lateromedially and bears a weakly pronounced depression along the middle part. The spiral groove between the corpus ossi and iliac shaft is weakly developed. The tuber superior is low and possesses a uni- or bilabiate protuberance in its central part. The angular fossa is well pronounced. In posterior view, the acetabular central tuber is higher than the dorsal tuber. The anteroventral edge of the acetabular rim is straight. The pars descendens projects sharply ventrally. No 'calamita' ridge can be observed. The remains show typical features for *Bufotes viridis*: form and shape of tuber superior and acetabulum (*Böhme*, 1977; *Blain, Gibert & Ferràndez-Cañadell*, 2010). However, due to the absence of well-preserved material, we prefer a tentatively assignment of the remains to the *Bufotes viridis* group.

Bufo sp.

Localities and material examined. Cherlak, GIN 1110/2001-AM17, 1 left scapula; Olkhovka 1A, GIN 1111/1001-AM01, -AM02, 2 left ilia; Pavlodar 2B, GIN 1108/2001-AM04 – -AM06, 3 left ilia.

Description and comments. Strongly damaged ilia showing typical morphology of the genus *Bufo* as the iliac shaft without the dorsal crest and a spiral groove between shaft and corpus illi (*Böhme*, 1977). There is a preacetabular fossa in the caudoventral corner of the acetabulum. The tuber superior is eroded. In medial view, the pars descendens is ventromedially directed.

Family **Ranidae** *Batsch, A. J. G. K.*, 1796

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Genus ***Pelophylax*** *Fitzinger*, 1843

Pelophylax sp.

(Figs. 6AA-6AD)

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Localities and material examined. Malyi Kalkaman 1, GIN 1107/1001-AM04, 1 left ilium; Malyi Kalkaman 2, GIN 1107/2001-AM04, 1 right and GIN 1107/2001-AM05, -AM06, 2 left ilia; Petropavlovsk 1, GIN 952/1001-AM01, 1 left ilium; Olkhovka 1C, GIN 1111/3001-AM04, 1 right ilium; Kamyshovo, GIN 1107/1001-AM01, 1 right scapula; Lezhanka 1, GIN 1129/1001-AM05, 1 left and GIN 1129/1001-AM06, 1 right ilia, GIN 1129/1001-AM07, 1 left scapula; Andreevka 1, GIN 1112/2001-AM02, 1 right and GIN 1112/2001-AM03, 1 left ilia; Livenka, GIN 1129/2001-AM01, 1 right ilium.

Description and comments. The ilia have a strong, oval, nearly vertically oriented and ventrally well-defined high tuber superior. The dorsal crest is high; anteriorly it is often broken. The tuber superior is high and slightly S-shaped than the crest; a well-developed supraacetabular fossa is present. Posterior to the tuber, the dorsal margin of the bone is bent ventrally towards the acetabulum. In posterior view, the tuber superior is curved ventromedially. The junctura ilioschiadica is damaged but based on the preserved structures we speculate that it was tall. The scapula is an elongate and low bone. In ventral view, a weakly developed crista supraglenoidalis is observable. It runs subparallel to the margo posterior and reaches the middle part of the pars suprascapulars. The characters listed above, like the form and orientation of both bones, tuber superior, and crista supraglenoidalis, allow attribution of the fossils to the genus of the green (water) frogs *Pelophylax* (*Böhme*, 1977; *Sanchíz, Schleich & Esteban*, 1993;

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Bailon, 1999; *Blain, Bailon & Agustí*, 2007). Any further identification due to the fragmentary preservation of the material is impossible.

Genus ***Rana*** Linnaeus, 1758 (*Linnaeus*, 1758)

Rana sp. / ***Rana temporaria*** Nilsson, 1842 (*Nilsson*, 1842)

(Figs. 6AE-6AH)

Localities and material examined. Ayakoz, unnr. HC specimens, numerous ilia, Baikadam, GIN 950/2001-AM10, 1 left, GIN 950/2001-AM11 – -AM13, and 3 right ilia; Malyi Kalkaman 1, GIN 1107/1001-AM05 – -AM09, 5 left ilia, GIN 1107/1001-AM10, 1 right ilia, GIN 1107/1001-AM01, -AM11, 2 right scapula; Malyi Kalkaman 2, GIN 1107/2001-AM07, 1 right ilium, GIN 1107/2001-AM08 – -AM13, 6 left ilia; Olkhovka 1C, GIN 1111/3001-AM05, 1 right ilium; Lezhanka 1, GIN 1129/1001-AM08, 1 left ilium;Kentyubek, unnr. HC specimens, 2 left ilia.

Description. The ilia have a reduced, compact, anteriorly directed, and low tuber superior. Its lateral surface is rough. The dorsal crest is low. The pars descendens is more developed than the pars ascendens. In posterior view, the junctura ilioschiadica, in comparison to the ilium of *Pelophylax* sp., is low. The tuber superior projects dorsolaterally, the pars descendens medially. The middle portion of two scapulae, without the proximal parts of the pars acromialis and suprascapularis are preserved. In dorsal view, a crista supraglenoidalis is observable at the processus glenoidalis, which continues until the pars suprascapularis along the longitudinal axis of the bone. It is very prominent and forms a lamelliform convex ridge. The base of the processus glenoidalis is high and straight.

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Comments. The ilia and scapulae morphology strongly resembles that of the brown frogs genus *Rana* (Böhme, 1977). Due to the fragmentary preservation of the bone material, any precise taxonomic identification of the frogs from nearly all localities is impossible. The comparison with Recent species (e.g. *Rana temporaria* (unnr. GPIT specimen), *Rana dalamtina* (unnr. GPIT specimen; *Bailon*, 1999), *Rana graeca* (unnr. GPIT specimen), *Rana arvalis* (unnr. GPIT specimen), *Rana dybowskii* (MNCN 40459), *Rana amurensis* (unnr. GPIT specimen) etc.) revealed more similarities with the European and Western Asiatic species rather than to Eastern Asiatic brown frogs.

Only the locality Malyi Kalkaman 1 provides adequate material for specific identification. The ilia and scapulae from there resemble the Recent species *Rana temporaria*, which has the widest distribution among the brown frogs in Eurasia. The fossil bones of brown frogs from other Western Siberian localities are described here as *Rana* sp. Due to the poor preservation of the ilia from Kentyubek, it can be only identified at the family level.

Class **Reptilia** *Laurenti*, 1768

Order **Squamata** *Oppel*, 1811

Suborder **Gekkota** *Cuvier*, 1817

Family **Gekkonidae** *Gray*, 1825

Genus ***Alsophylax*** *Fitzinger*, 1843

Alsophylax sp.

(Fig. 7)

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Locality and material examined. Cherlak, GIN 1110/2001-RE01 – -RE10, 10 right dentaries, GIN 1110/2001-RE11 – -RE25, 14 left dentaries, GIN 1110/2001-RE26 – -RE39, 13 left maxillae, GIN 1110/2001-RE40 – -RE44, 5 right maxillae, GIN 1110/2001-RE45, 1 anterior trunk vertebra, GIN 1110/2001-RE46, 1 femur; Mynsualmas-MSA 3: 1 right maxilla, unnr. GPIT specimen.

Description.

Tooth morphology. The teeth are slender, unicuspid, and not narrowly arranged. All maxillaries and dentary teeth are strait, except the most anterior ones on the dentary, which are anteriorly light oblique. The central teeth on dental lamina of both maxilla and dentary are larger than the anterior and posterior ones (Figs. 7C, 7G). Rarely, the cusps of maxilla teeth are posteriorly oriented. The most complete dentary bone contains at least 17 (in total 20?) teeth, counted by both teeth and their alveoles (Fig. 7B-7D).

Dentaries. The dentary is a slender and elongate bone. In the symphyseal region, the bone is slightly curved medially. The pars ventralis is enlarged, due to which the bone increases in height posteriorly. The dentary is characterised by a completely closed Meckelian canal, which runs along about two-third of the bone length (Fig. 7B). The symphyseal articulation surface is reduced. It does not build a pronounced articulation surface. The ventral surface of the symphysis bears a longitudinal, posteriorly deepening symphyseal groove, visible both in lingual and ventral views (Figs. 7B-7D). The Meckelian canal is open posteriorly at about the 15-16th teeth position. The splenial facet on the dentary – the anterior margin of Meckelian opening, shows a light concave and elongated surface (Figs. 7B-7E). In lateral view, the bone is smooth, and the only complete dentary possesses five foramina, arranged in a longitudinal row (Fig. 7A). The size of the foramina slightly increases in anteroposterior direction, also changing in form

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from more rounded outline into oval appearance. The position of the last mental foramen is arranged lingually in front of the posterior opening of the Meckelian canal. The cavity of the Meckelian canal is divided by a distinct horizontal lamella into two – upper and lower subcanals (Fig. 7E). The horizontal lamella runs parallel to the lamina horizontalis and can be observed posteriorly behind the opening of the Meckelian canal. The upper subcanal opens on the labial surface of the bone by mental foramina. The symphyseal groove corresponds to the anterior opening of the lower subcanal. In lingual view, the lamina horizontalis is situated in a low position. Its margin is rounded but not prominent. A shallow and anteriorly extending dental shelf divides the lamina horizontalis from the dental lamina (Fig. 7C). Posteriorly, the bone is nearly L-shaped in transverse section. The pars horizontalis is always destroyed in the preserved bone. The caudal portion of the paries verticalis shows bifurcation (Fig. 7E), which corresponds to the coronoid insertion.

Maxilla. The preserved posterior part of the maxillary possesses a relatively low lacrimal facet of the facial process of the maxilla (pars nasalis sensu *Estes* (1969)), while the later is always not preserved. The internal wall of the maxilla bears a small distinct longitudinal groove posteriorly, running parallel to the lamina horizontalis (Figs. 7F-7H). The groove begins at the posterior basis of the lacrimal facet and continuous until the preserved posterior tip of the bone. At its middle part (at the 3rd or 4th last teeth), where the lacrimal facet terminates, the groove narrows. The lamina horizontalis is clearly visible, it expands laterally just under the tip of the lacrimal facet (? = at its midsection) and builds a palatine facet (Figs. 7F-7H). It becomes distinctly narrower posteriorly but does not diminish fully at the posterior end of the bone. The jugal process of the maxilla is bifurcated at its distal end (Fig. 7H). The maxillary lappet is damaged, but its base is

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preserved. The internal wall surface of the maxilla contains few rugosities. Here an anteroposteriorly directed, more or less well-pronounced, median ridge, is observed. In labial view, above the dental row, several foramina occur. Some of them are arranged in a longitudinal 'short' line that corresponds to the foramina for the mandibular division of the fifth cranial (trigeminal) nerve. This line runs parallel to the lamina horizontalis. The last foramen of the row pierces the maxilla at the base of the lacrimal facet under its tip. The bases of the facial process and maxillary lappet lay a relatively large superior alveolar canal (sac, Figs. 7J and 7L) for the maxillary nerve and accompanying blood vessel. The remaining foramina at the maxilla are disposed irregularly on the bone surface. The premaxillary process is present, but it is highly damaged. The anterior basis of the lacrimal facet, is pierced by a foramen.

Vertebra. A single cervical vertebra of gecko shows an elongate amphicoelous centrum (Fig. 7N-7P). The cotyles are approximately circular. In anterior view, the vertebra has semicircular outline. In lateral view, it is flattened anteroposteriorly and concave from both sides. The transverse processes are high, extremely short and vertically aligned. The distal end of the process is round. The haemal foramina are present at the lower base of the transverse processes. The prezygapophyses are small and slightly prominent. The neural arch is plane and triangular in outline. It possesses a slender and low neural crest. The postzygapophyses are small and nearly invisible. They are situated on the ventrolateral edges of the pterygapophysis.

Comparison and comments. The amphicoelous condition of the vertebra along to; maxillae and dentaries bearing numerous pleurodont, isodont, densely packed, cylindrical, and slender monocuspid teeth, the presence of a medially extended dental shelf of the maxilla and the lingually closed Meckelian canal, allows the identification of the material as a member of the

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family Gekkonidae (*Hoffstetter & Gasc*, 1969; *Daza, Alifanov & Bauer*, 2012). The gekkonid remains from Cherlak display a low teeth number on the dentary (up to 20) and rounded tooth apex (making the teeth digitiform), which are diagnostic characters for the genus *Alsophylax* (*Nikitina & Ananjeva*, 2009). Within gekkonids low teeth number (up to 20) is known also in *Mediodactylus russowi*, *Phelsuma laticauda*, and *Ph. serraticauda* (*Nikitina*, 2009). The Siberian fossil geckos can be distinguished from *Mediodactylus* by peculiarities of the maxilla (presence of a lingual longitudinal groove, a reduced row of foramina of the trigeminal nerve) and dentary with a distinct and longer horizontal lamella, plus reduced symphyseal groove. The Recent genus *Phelsuma* can be excluded from consideration since these geckos are restricted to the islands of the southwest part of the Indian Ocean and belong to another zoogeographic zone. The fossil geckos resemble the Recent species *Alsophylax pipiens* (see in *Estes* (1969); tab. 2C) in the presence of the prefrontal process, short row of foramina of the trigeminal nerve, which terminates below the prefrontal process. Due to the lack of an available comparative osteological material of the Recent *Alsophylax* species, further comparison is impossible. Fossil geckos were present in the Early Miocene of Kazakhstan from the locality Mynsualmas-MSA 3 (unnr. GPIT specimen) (*Böhme & Ilg*, 2003). The re-study of the material reveals that the posterior fragment of a right maxilla shows a morphology similar to *Alsophylax* sp. from Cherlak in the presence of a lingual longitudinal groove and the absence of foramina at the posterior portion of the bone and a round tooth apex. However, it is different regarding its larger size (Fig. 7Q). Taking this into account, we tentatively consider the Mynsualmas record as cf. *Alsophylax* sp. Probably, this fossil represents a larger *Alsophylax* species than the registered in the Western Siberia.

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Suborder **Lacertilia** Owen, 1842 sensu *Estes, Queiroz & Gauthier*, 1988

Family **Lacertidae** *Fitzinger*, 1826

Genus ***Lacerta*** *Linnaeus*, 1758

Remarks. Generic assignment of fossil lacertid remains is extremely difficult. This group is anatomically generalised (*Lacera* sensu lato) and shows very few characteristic features (bone and teeth morphology) for detailed taxonomic assignments (*Böhme*, 2010; *Böhme & Vasilyan*, 2014).

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Lacerta s.l. sp. 1.

(Fig. 8A)

Material. Baikadam, GIN 650/2001-RE07 – -RE09, (3?) left dentaries, GIN 650/2001-RE10, 1 postsacral vertebra; Pavlodar 1A, GIN 640/5001-RE01 – -RE15, 15 left dentaries, GIN 640/5001-RE16 – -RE26, 10 right dentaries.

Description. The bones bear pleurodont bicuspid teeth. The most completely preserved dentary possesses at least 20 teeth. The pars dentalis is tall. Its height corresponds to the two-third of the teeth length. The Meckelian groove is open ventrolingually. It starts from the ventral side of the symphysis and increases in height posteriorly. The lamina horizontalis is slightly curved. Its anterior portion is high and broad and reaches its maximal height in the middle part corresponding to the 10th tooth position. Behind this point, the lamina horizontalis articulates

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Comments. See in *Lacerta* s.l. sp. 2.

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Lacerta s.l. sp. 2.

(Fig. 8B)

Material. Pavlodar 1A, GIN 640/5001-RE27 – -RE33, 7 left dentaries, GIN 640/5001-RE34 – -RE39, 6 right dentaries; Cherlak, GIN 1110/2001-RE47, 1 left maxilla, GIN 1110/2001-RE48, -RE49, 2 right maxillae, GIN 1110/2001-RE50, 1 left dentary, GIN 1110/2001-RE51, 1 right dentary.

Description. The dentaries possess 19 bicuspid teeth. The pars dentalis is high. Its height corresponds to the two-third of the teeth length. The lamina horizontalis is curved and has nearly the same height along its entire length. Only at the 9-10th tooth positions, where the splenial articulates with the lamina horizontalis, the lamina horizontalis decreases slightly in height. The articulation facet exposes lingually only in its most posterior portion. The crista

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dentalis is short but is longer than the ventral margin of the lamina horizontalis. The Meckelian groove is low and open ventrolingually. In labial view, up to seven small foramina are present.

Comments. *Lacerta* s.l. sp. 2 differs from *Lacerta* s.l. sp. 1 in having more curved lamina horizontalis, showing nearly the same height along its length, higher and broader anterior portion of the lamina horizontalis, a shorter cirsta dentalis and a lower Meckelian groove.

Lacerta **s.l. sp.**

Material. Malyi Kalkaman 2, GIN 1107/2001-RE01, 1 dorsal vertebra; Olkhovka 1A, GIN 1111/1001-RE01 and –RE02, 1 anterior and 1 posterior dorsal vertebrae; Cherlak, GIN 1110/2001-RE52 – -RE58, 7 dorsal vertebrae, Pavlodar 1A, GIN 640/5001-RE40, 1 premaxilla, GIN 640/5001-RE41, numerous fragments of dentaries and maxillae; Pavlodar 1B, GIN 640/6001-RE01, -RE02, 2 left dentaries, GIN 640/6001-RE03, -RE04, 2 right dentaries; Olkhovka 1B, GIN 1111/2001-RE01, 1 right dentary; Pavlodar 3A, GIN 1108/3001-RE01, 1 right maxilla; Beteke 2, GIN 945/6001-RE01, 1 left dentary; Beteke 4, GIN 945/8001-RE01, 1 left dentary.

Description and comments. The preserved maxillaries and dentaries possess pleurodont bicuspid teeth. The Meckelian groove is lingually open. The labial surface of maxillaries shows no ornamentation. In labial view, the foramina for mandibular division of the fifth cranial (trigeminal) nerve are observable. They are situated along a longitudinal line, parallel to the ventral margin of the bone. The opening of the superior alveolar canal is large. In lingual view, a shallow but broad groove is present at the anterior portion of the frontal process. The large foramen of the fifth cranial (trigeminal) nerve opens at the ventral surface of the lamina

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Eliminado: a shallow but broad groove is present horizonalis. A single premaxilla from Pavlodar 1A, GIN 640/5001-RE40 has a tapering nasal process with a row of seven pleurodont and monocuspid teeth.

The bone material is extremely fragmentary, and any comparison between different localities is impossible. The fossil remains (maxillae and premaxilla) from Pavlodar 1A do not show any taxonomical differences, so we are not able to group them neither to *Lacerta* s.l. sp. 1 nor *Lacerta* s.l. sp. 2. Besides the jaw material, vertebrae from the dorsal region are available in the localities Maly Kalkaman 2, Olkhovka 1A and Cherlak. They are all not possible to identify below the family level.

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Genus ***Eremias*** *Fitzinger*, 1843

Eremias sp.

(Fig. 8C-8D)

Material. Pavlodar 2B, GIN 1108/2001-RE01, -RE02, 1 frontal and 1 dorsal vertebra.

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Description. A preserved frontal has a sandglass shape, the most anterior and posterior portions are broken. In lateral view, the bone is slightly curved. The posterior portion of the dorsal surface is rough. The crista cranii at the narrowest portion of the bone are round and slightly elevated. Anteriorly, they increase in height and build the lateral walls of the cranial vault. The anteroventral surface of the bone has two drop-shaped grooves. The posteroventral surface is plain and slightly lower than the anterocentral surface. The prefrontal facets are developed but do not show any lateral extension. The bone margin connecting both facets is concave. In dorsal view, the nasal facets, situated at the anterolateral corners, are narrow, deep, and elongated.

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In lateral view, a single preserved vertebra has a rectangular shape. The neural arch is moderately convex. At the transition of the neural arch and prezygapophysis, a narrow and deep groove is present. The neural spine is reduced and builds posteriorly a rounded process, projecting over the posterior margin of the arch. The centrum is compressed anteroposteriorly and possesses two shallow subcentral grooves, with a subcentral foramina in each. The condyle is small and round, situated in the middle part of the posterior margin of the centrum.

Comments. Among the Eurasian lacertids, fused dorsally sculptured frontals are known in *Acanthodactylus*, *Eremias*, *Ophisops* (*Evans*, 2008). Our own observation in Recent species of those genera (*Eremias strauchi*, *Eremias pleskei*, *Eremias arguta*, *Eremias multicellata*, *Ophisops elegans*, *Acanthodactylus erythrurus*) allows to assign frontals to the genus *Eremias* and to separate it from: (1) *Ophisops* by a robust frontal, better pronounced grooves at the anteroventral bone surface, lack of the lateral extension of the prefrontal facet; (2) *Acanthodactylus* by a flat posteroventral surface of the bone and a less curved outline in lateral view. The preserved single vertebra resembles strongly morphology found in *Eremias* (*Rage*, 1976).

Order **Testudines** *Linnaeus*, 1758

Suborder **Cryptodira** *Cope*, 1868

Family **Emydidae** (*Rafinesque*, 1815)

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Lacertidae sp. indet.¶
Material. Malyi Kalkaman 2, GIN 1107/2001-RE01, 1 trunk vertebra; Olkhovka 1A, GIN 1111/1001-RE01 and –RE02, 1 anterior and 1 posterior trunk vertebrae; Cherlak, GIN 1110/2001-RE52 –-RE58, 7 trunk vertebrae.

Genus ***Eymdoidea** Gray*, 1870[3]

Emydoidea sp.

(Figs. 8E-8G)

Material. Novaya Stanitsa 1A, GIN 948/2001-RE01, 1 posteriorly incomplete right hypoplastron, GIN 948/2001-RE02, 1 left femur.

Description and comments. The caudal part of the left hypoplastron, having 54.3 mm in width is preserved (Fig. 8E). Probably it belongs to a middle size individual with a total length of the carapace about 30 cm. In ventral view, the femoral/abdominal sulcus is nearly straight and curves anteriorly only near the lateral edge of the bone and terminates at the base of the inguinal buttress. The bone is comparatively thin medially from the bridge (4 mm) to behind the bridge (7.2 mm). The lateral edge of the bone projects slightly posterolaterally. The outline of the femoral/abdominal sulcus and the profile of the lateral edge are similar to those of the emydid genus *Emydoidea* (both fossil and Recent) (*Chkhikvadze*, 1983, figs. 26 and 27, p. 138; *Holman*, 1995).

An almost complete left femur is available from the same locality where the hypoplastron fragment was found. The bone is slender and bent (Fig. 8F-8G), it is 50.6 mm in length. It could have belonged to an individual of about 30 cm of the carapace length. The femur lacks its proximal portion (i.e. femoral head, major and minor trochanters). In ventral view, the fossa delimited by the trochanters is observable below the femoral head. The dimension of the bone is characteristic of aquatic testudinoids. Taking this into account, as well as the comparable

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[3] We follow taxonomy suggested by *Fritz, Schmidt & Ernst*, 2011 recognizing *Emydoidea* as a distinct genus from *Emys*.

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reconstructed total body-sizes of both elements (ca. 30 cm), we consider the remains belonging to the genus *Emydoidea*.

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Material. Shet-Irgyz 1, GIN 1106/1001-RE01, 1 neuralia; Petropavlovsk 1, GIN 952/1001-RE01, several fragments of carapax; Borki 1B, GIN 1115/2001-RE01, 1 fragment of carapax.

Comments. The preserved remains are not informative for any other taxonomic interpretation.

DISCUSSION

Neogene evolution of amphibian and reptile assemblages in the Western Siberia

In general, amphibian and reptile faunas from the Neogene of Asia are very little known, contrasting with the well studiedEuropean record. This is mainly caused on the one hand by less explored Neogene deposits from the Asian Continent, which are not extensively studied, and on the other hand, the amphibian and reptile remained entirely unstudied until recent times, although the intense study of small mammals by many scholars. The Western Siberian localities provide an exceptional opportunity to fill the lack of information and to explore both unknown diversity of the Asian herpetofaunal assemblages and the palaeobiogeographic affinities of the Western Siberian Neogene herpetofauna with European faunas. Unluckily, the yielded fossil material is not rich in amphibian and reptile remains. In average, only four taxa are available from each locality. Hence, our faunistic, palaeogeographic and palaeoclimatic interpretations are very tentative and should be carefully taken. The unbiased comparison and analysis of our data are also hindered by the scarce record of the Asian Neogene fossil faunas.

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For the comparison with the European record we used already published data on amphibian and reptile groups (families, genus, species etc.) summarised in the fosFARbase database (*Böhme & Ilg*, 2003). These data are given in the Table S5. As 'Europe' record, we consider all known fossil records from Western, Central and Eastern Europe as well as from Anatolia (Fig. 9). Analysing the Neogene amphibian and reptiles records from Europe and Asia, we provide useful data applicable for fossil calibration of molecular clock of the phylogenetic trees.

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Hynobiidae

The Asiatic salamanders (*Salamandrella* sp.) have the most abundant and frequent record among studied Western Siberian localities. They appear there in the middle Late Miocene (loc. Selety 1A) and are present until the early Early Pleistocene. Although the herpetofaunal assemblages of the older localities are rich and represented by numerous taxa, they do not contain any hynobiid remain, showing that there is no sampling bias in their record and they are not present in earlier localities.

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Newly the oldest record of the genus (*Salamandrella* sp.) has been described from the late (?) Early Miocene of Eastern Siberia (Lake Baikal) (*Syromyatkova*, 2014) and a new species of *Salamandrella* is indicated to be present in the Late Miocene locality Ertemte 2, China (*Vasilyan* et al., 2013). Further, the fossil Asiatic salamander *Ranodon* cf. *sibiricus* is recovered from the Early Pleistocene of Southern Kazakhstan (*Averianov & Tjutkova*, 1995), and *Salamandrella* sp. is reported from few Middle Pleistocene age localities of European Russia (*Ratnikov*, 2010).

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In Central Europe, hynobiids (genus *Parahynobius*) appear at the terminal Middle Miocene and are registered until the Early Pleistocene (*Venczel*, 1999a, 1999b; *Venczel & Hír*, 2013).

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According to our unpublished data, the hynobiids are present also in three Ukrainian localities – Grytsiv (11.1 Ma) (*Kirscher* et al., 2016), earliest Late Miocene, Cherevichnoe lower level, middle Late Miocene and Kotlovina lower level, late Pliocene. The Ukrainian occurrences coincide both with Central European and Western Siberian records of hynobiids, which most probably were time characterised by favourable conditions for their distribution. Taking into account their oldest records, most probably their origin was in the early Miocene of Eastern Asia. A detailed study on the Cenozoic record of fossil Hynobiidae including the Western Siberian material will be presented in a separate paper.

Cryptobranchidae

The cryptobranchid remains are known from two localities in town Pavlodar and three localities in the Zaisan Basin. The stratigraphic positions of the Pavlodar localities are not clear. The only giant salamander record studied by us is stored at the Palaeontological Institute of Moscow, Russia. The collection label provides following information: 'collected by Gaiduchenko, in 1970, from locality Gusiniy Perelet, at the contact of the Aral clays with overlying sands, about 200-300 meters south far from the locality 'Gusini Perelet' [=Pavlodar 1A]'. The only explanation of the stratigraphic allocation of the giant salamander remains is that they originated from the basal horizon of the Pavlodar Svita, overlaying the 'Aral clays' (= limnic clays of the Kalkaman Svita). *Gaiduchenko* (1984) and *Gaiduchenko & Chkhikvadze* (1985) mention a giant salamander (Cryptobranchidae indet.) from a locality named Detskaya Zheleznaja Doroga (engl. Children Railway) (Fig. 2, Table S1, Data S3) – a sand pit located 10 km south-east from the 'Gusini Perelet' [=Pavlodar 1A]. The age of the fossiliferous horizon may be near the Miocene-Pliocene

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boundary (mostly based on geology, age and accompanying fauna; see Data S2). This record represents the most northern (52.3° N) occurrence of the giant salamanders in the Northern Hemisphere known so far. Unfortunately, the material was not available for our study.

Giant salamander remains are reported also from three Burdigalian localities – Tri Bogatyrya, Vympel, Poltinik of the Zaisan Basin (Fig. 1, Table S1) (*Chkhikvadze*, 1984; *Böhme, Vasilyan & Winklhofer*, 2012). The remains are assigned by *Chkhikvadze* (1984) to a species *Andrias karelcapeki*. The taxonomic validity of the species still requires revision, which is necessary for any further interpretations.

Proteidae

The oldest record of the genus is described from the locality Akespe, Aral Formation, north coast of the Aral Sea, Kazakhstan (cf. *Mioproteus*,) (*Malakhov*, 2003), Late Oligocene (*Bendukidze, Bruijn & Van den Hoek Ostende, Lars W.*, 2009). Here we add a new earliest Miocene (Aquitanian) Asian occurrence from the locality Ayakoz, Kazakhstan (Fig. 3D, Table S1). In the Middle Miocene, they occur in several localities in southern Russia and northern Kazakhstan (Table S1). According to our results, they survive until latest Miocene/earliest Pliocene (?) (locality Petropavlovsk 1/2). The oldest stratigraphic record of *Mioproteus* (*Mioproteus caucasicus*) in Europe is described from the late Ottnangian (late Early Miocene about 17 Ma) (*Reichenbacher* et al., 2013) at Illerkirchberg and Bodman of the North Alpine Foreland Basin (*Reichenbacher* et al., 2004). The fossil proteids are known in Europe until Pleistocene (*Böhme & Ilg*, 2003). *Malakhov* (2003), due to the lack of complete fossil skeletons and unclear taxonomic assignments of the fossil records, preferred to refer all known specimen

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Salamandridae

As already known, *Chelotriton* is a busket taxon (*Böhme*, 2008), and need further taxonomic study. It is one of fossil amphibians having abundant and wide distribution in the late Paleogene and Neogene localities of Europe. From Asia the genus was known previously only from the late Middle Miocene locality Malyi Kalkaman 1 (*Tleuberdina*, 1993). Our study shows this genus was present here at least since the Aquitanian (Aykoz, Kazakhstan, Early Miocene) (Table S1), making their Asiatic record older than known.

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Two localities (Ayakoz and Baikadam) from Western Siberia revealed aff. *Tylototriton*. The vertebrae show significant similarities with the Recent East Asiatic genus *Tylototriton*. In *Böhme*

& *Ilg* (2003) and *Böhme* (2010), the genus *Tylototriton* (cf. *Tylototriton* sp. and *Tylototriton* sp. nov.) has been reported from several Early Oligocene localities of southern Germany. Two Siberian records represent the first fossil occurrence of the genus in Asia, which is, however, quite younger than the European. These two Western Siberian and European records can be clearly separated from each other by the morphology of the trunk vertebrae. Most probably, the Siberian salamanders represent new forms, strongly related to the East Asian terrestrial salamander *Tylototriton*. The Aquitanian age locality Ayakoz documents for the first time the sympatric occurrence of two fossil terrestrial salamander genera *Chelotriton* and *Tylototriton*.

Palaeobatrachidae

The palaeobratrachids are considered as a European family, with probable occurrence in the terminal Cretaceous of North America (*Wuttke* et al., 2012). During the Paleogene, they are known from Western and Central Europe. It should be taken into account also the fact that the Paleogene of Turkey, as well as Paleogene and Early – Middle Miocene of Eastern Europe is very scarcely known. In the Miocene, they expanded their distribution to Eastern Europe and also reached Anatolia, where they existed since the latest Oligocene and remained during the entire Early Miocene. During the Middle Miocene, they are present in Europe over an area from Germany to Ukraine (*Wuttke* et al., 2012). The Late Miocene is characterised by a four-million-year-long (ca. 5.6-9.78 Ma) gap in the palaeobatrachid record of Europe (Fig. 9). During this gap, no palaeobatrachid is known from Western to Eastern Europe even in rich localities with diverse herpteofauna (e.g. Staniantsi, Bulgaria; Morskaya 2, Russia) (see *Böhme & Ilg*, 2003), even in those localities, which are characterised by favourable environmental conditions for their life.

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After this gap, they occur near the Mio– Pliocene transition in studied localities from Italy (Ciabot Cagna), (*Cavallo* et al., 1993) and Hungary (Osztramos 1C) (*Venczel*, 2001)). They disappeared after Early Pleistocene from Western (Tegelen, Holland, *Villa* et al., 2016) and Central Europe (Betfia IX/B, Romania, *Venczel*, 2000) and are present until middle Pleistocene exclusively in Eastern Europe (Poland – European Russia) (*Wuttke* et al., 2012). Their most east distribution never reached the east of Ural Mountains, the Late Pleistocene locality Apastovo in Russia (*Wuttke* et al., 2012), where they occur, is about 600 km west from the Ural Mountains.

The Western Siberian record does not only represent the first and only out-of-Europe occurrence of the family, but, surprisingly, it falls into the Late Miocene palaeobatrachid gap of the European record. It is possible that palaeobatrachids occupied Western Eurasia again at the Mio-Pliocene boundary from the East.

Bombinatoridae

The primitive family of aquatic toads Bombinatoridae includes two recent genera *Bombina* and *Barbourula*. The family is known since the Maastrichtian, Late Cretaceous of Romania, genus *Hatzegobatrachus* (*Venczel* et al., 2016) and Early Eocene of India, genus *Eobarbourula* (*Folie* et al., 2013). The Recent distribution of *Bombina* is confined to the continental Europe and East Asia, representing the western and eastern genetic clades of the genus respectively. In Europe, two species *Bombina bombina* and *Bombina variegata* are known. *B. bombina* has the widest distribution and is found in Central to Eastern Europe, whereas *B. variegata* – in Central, south-eastern and western part of the Eastern Europe (*Pabijan* et al., 2013). The fire-bellied toad *Bombina* fossil record is patchy and limited to the European continental Neogene. According to

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Sanchíz & Schleich (1986), the oldest fossil occurrences of the genus (*Bombina* sp.) are known from the localities Weißenburg 6, earliest Aquitanian and Stubersheim 3, early Burdigalian of Germany (*Sanchiz & Schleich*, 1986; *Böhme & Ilg*, 2003). The personal observations of one of us (MB) did not confirm the Weißenburg 6 record of *Bombina*. Thus we consider in the present study Stubersheim 3 as the earliest occurrence of the genus.

Later they appeared in the Middle Miocene of Central Europe (*Bombina* sp., Opole 2, Poland) (*Młynarski* et al., 1982). At the middle Tortonian, the fire-bellied toads are present in three localities including also the first fossil occurrences of the Recent European species – *Bombina* sp. from Rudabánya, Hungary (9.9-10.30 Ma) (*Roček*, 2005), *Bombina* cf. *bombina* from Kohfidisch, Austria (8.55-8.95 Ma) (*Tempfer*, 2005), and *Bombina* cf. *variegata* from Suchomasty, Czech Republic (8.8-9.2 Ma) (*Hodrová*, 1987). During the Pliocene, they are represented mainly by the species *Bombina bombina* in the Central European six localities (*Böhme & Ilg*, 2003). The Pleistocene record is the richest with over 15 localities ranging from Central to Eastern Europe, here both Recent European species *B. variegata* and *B. bombina* are documented (*Böhme & Ilg*, 2003) (Fig. 9, Table S5).

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In Western Siberia, they are known from three localities: Malyi Kalkaman 2, Selety 1A, and Cherlak. The oldest record is known from the late Serravalian (Middle Miocene), in the latest Tortonian the fossil form of the Recent *B. bombina* is present (*B.* cf. *bombina*) (Fig. 9). The last record of the genus dates by the late Messinian (late Late Miocene). It is interesting to note that the Western Siberian record of the genus does not coincide with their European occurrences, here they are present during those periods when in Europe *Bombina* is missing. According to our analysis, it is clear that the ancestor of the '*B. bombina* – *B. variegata*' clade was present in

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Europe at least from the later part of the Early Miocene, and later in the Middle Miocene, they expanded into Western Asia, reaching the east from the Ural Mountains. The Western Siberian fossil *Bombina* can be clearly separated osteologically from *Bombina orientalis*, a member of the East Asian clade of the genus. Taking into account their recent distribution and the fossil record, the split of European and Asian *Bombina* clades seems most probable in Asia during the Paleogene.

Pelobatidae

The family of European spadefoot toads Pelobatidae includes only one extant genus with four species distributed in north-western Africa, Europe, in small areas placed at the east from the Ural Mountains in Russia and in the north of Kazakhstan (*Kuzmin*, 1995). The family shows Laurasian affinities and is known from the Late Cretaceous of North America. From the Early Eocene they are present in Europe by the fossil genus *Eopelobates* (Middle Eocene – late Pliocene), as well as by fossil forms of the Recent genus *Pelobates* (Middle Oligocene – Recent) (*Roček* et al., 2014). The Asian record of Pelobatidae is very scanty and includes forms from the Eo– Oligocene of Kazakhstan (*Chkhikvadze*, 1985) and Eocene of India (*Folie* et al., 2013). Recently, *Roček* et al. (2014) excluded the genus *Uldzinia* (Oligocene, Mongolia) (*Gubin*, 1995) from the family Pelobatidae. The Kazakh fossil record of the family (*Chkhikvadze*, 1985, 1998) includes numerous remains of Pelobatidae indet. are from: (1) the localities of the Zaisan Basin from the Upper Aksyr Svita[4], early Priabonian; rare finds in the Kusto Svita and basal horizon of

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[4] localities: Zertsalo [Sunduk Section], lager Biryukova [Kiin-Kerish Section], lower faunistic level of Plesh [Kusto-Kyzylkain Section], probably also Tabtym [Sarykamysh Section]

Buran Svita[5], late Priabonian and earliest Rupelian; abundant occurrence in the Buran Svita[6], early Rupelian and (2) large-sized spadefoot toads from the Kyzyl-Kak locality of the Turgay Basin, Central Kazakhstan, Late Oligocene (*Chkhikvadze*, 1998). Any revision of this rich pelobatid record from the Zaisan Basin was not possible due to the lack of descriptions and illustrations of the material as well as to the difficult access to the specimens,. Nevertheless, taking into account the Paleogene fossil records, we infer that the spadefoot toads might disperse from Europe to Western Asia during the Late Eocene – Early Oligocene. Whether *Pelobates* sp. from the Selety 1A (late Tortonian, Miocene) is a European or Asian migrant cannot be clearly asserted.

Hylidae

The family of tree frogs (Hylidae) has a wide distribution in Eurasia and is represented by the monophyletic genus *Hyla*. The most recent phylogenetic study of the genus *Hyla* by *Li* et al. (2015) recognised two closely related clades (West Palaearctic *arborea*-group and East Palaearctic *chinensis*-group) in Eurasia, as well as a small East Palaearctic *japonica*-group related to the North American clade of *Hyla*. The revision of Western Eurasian *Hyla* phylogeny based on molecular genetic studies revealed a high diversity in the area containing about eight (?nine) (*Li* et al., 2015) or ten (*Gvoždík* et al., 2010) species. Among them two clades: (1) *H. savignyi* in the East (Levant and the area of Turkey, Iran, Armenia, Georgia) and (2) *H. arborea* (Western,

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[5] localities: main level of Plesh, Tuzkabak, Cherepakhovoe Pole [Tayzhuzgen Section], Raskop [Aksyr Section], Tyubiteika, sopki ‘Rybnaya’ and Kontrolnaya [Juvan-Kara Section]

[6] localities: Maylibay, Tologay [Tayzhuzgen Section], Podorozhnik [Jaman-Kara Section]

Central Europe and Balkan) + *H. orientalis* (Southeastern Europe, Georgia, Armenia, Iran) have wide distributions in the East and West respectively (*Stöck* et al., 2008a; *Gvoždík* et al., 2010). In Europe, the oldest record of the genus is known from the late Early Miocene of Central Europe Oberdorf O4, in Austria (*Sanchíz*, 1998b). After about three million year interruption/gap, it continues in the late Langhian with the first fossil appearance of the Recent species *Hyla arborea* (*H.* cf. *arborea*, Mátraszőlős 2, Hungary) (*Venczel*, 2004). The record is almost consistent in the entire Neogene and Quaternary of Europe (Fig. 9). In Western Siberia, the genus shows a quite abundant record with the oldest and first occurrences of *H. savignyi* (*H.* cf. *savignyi*) from five localities along the late Late Miocene and early Early Pliocene. Apart from this, *H. savignyi* occurs also in the Middle Miocene of southern Russia (see 'Comparison and Discussion' in *Hyla* gr. *H. savignyi*), representing the oldest fossil record of the species.

Based on the fossil record of the tree frogs, we conclude that two large Western Eurasian clades split in Europe during the Middle Miocene. Our data showed older ages for the first fossil occurrences of these clades than the previously estimated molecular data in two recent studies (*Gvoždík* et al., 2010; *Li* et al., 2015). Thus, *Gvoždík* et al. (2010)[7] suggested the split of *H. orientalis/arborea* and *H. savignyi* at 11.1 Ma (early Late Miocene, early Tortonian), which is about three million years younger than the first fossil occurrence of *H.* cf. *arborea* (Table S5). Whereas, *Li* et al. (2015), without calibrating the molecular clock by the oldest European fossil *Hyla* (*Hyla* sp., loc. Oberdorf O4, Austria), estimated this split at 20-12 Ma, in a time interval in which the oldest fossil tree frogs related to the Recent *H. arborea* occur. In both of the cases,

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[7] The divergence dates of split events were estimated by a relaxed molecular clock approach, based on the mitochondrial data set, where the calibration with fossil record is missing.

the interpretation of the molecular phylogeny of the group can be improved by calibrating the tree with the fossil record introduced in this study.

Considering our data and the results presented in *Li* et al. (2015), we suggest the following distribution pattern for the West Palaearctic *arborea*-group: entering Eurasia from the East via Beringian from North America, in the Paleogene. The ancestors of the group reached Europe in the early Miocene over no more existing north geographic barrier between Europe and Asia (the Turgai Strait) and diversify apparently, in the Western Siberian. The Late Miocene and Early Pliocene records represent the most eastern expansion of the European genera, when the climatic conditions were still favourable for their distribution; it is conceivable for us that the *H. savignyi* may have potentially uncovered fossil occurrences in the Miocene of Eastern Europe and/or from the Caucasus at the south.

Bufonidae

Two groups of toads are found in the studied Western Siberian localities; the common (*Bufo bufo*) and the green toads (*Bufotes* cf. *viridis*) (Figs. 7F-7K, Table S1). The toads of both groups are the most frequent elements, with abundant occurrences among frogs of fossil localities.

Common toads. *Bufo bufo* is the Recent species with the widest distribution (Central, Southern, Eastern Europe and Western and Eastern Asia) among other members of the common toads *Bufo bufo* species group. The group includes three further species with limited distribution *Bufo spinosus* (northern Africa, Western Europe), *Bufo eichwaldi* (south coast of the Caspian Sea), and *Bufo verrucosissimus* (east of the Black Sea) (*Arntzen* et al., 2013). These species are known also as the western group of the genus, having their near relatives – the eastern group *Bufo*

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gargarizans species group- in the Eastern Asia. The Western Siberian fossil record of this group is restricted to the late Late Miocene to the early Early Pliocene, which in comparison to the European record, is very poor. The oldest toad remains assigned to the group are from the Middle Miocene of Slovakia: *Bufo bufo* from the loc. Devinská Nová Ves – Zapfe's fissure, 13.7-14 Ma (*Hodrova*, 1980; *Böhme*, 2003) and *Bufo* cf. *bufo* from the loc. Devinská Nová Ves – Bonanza 13.5-13.7 Ma (*Hodrová*, 1988). Then, since 9.2 Ma, Late Miocene (loc. Suchomasty, Czech Republic) (*Hodrová*, 1987), they are present in Central Europe and extend their distribution across Europe. At ca. 4.7 Ma, remains of the common toad showing characters of the Recent *B. spinosus* appeared in Spain, loc. Celadas 6 (*Böhme & Ilg*, 2003). The oldest fossil remains referred to *B. verrucosissimus* were recovered from the Late Pliocene (3.0-3.8 Ma) locality Apastovo, in Russia (*Ratnikov*, 2001). The Western Siberian record suggests at least a late Miocene dispersal of *Bufo bufo* to the East, reaching the present distribution area of the species. Considering the genomic data of *Recuero* et al. (2012), these 'migrants' should represent the common ancestor of the *B. bufo* + *B. verrucosissimus* clade, expanding to the East into Asia and to the south into Eastern Europe. Most probably in these areas, they were present permanently until present times. Lack of their fossil record in the Late Pliocene and Quaternary sites can be explained by sampling bias. Although those two species do not occur sympatrically nowadays, in two Middle Pleistocene localities (Koziy Ovrag and Yablonovets from Russia; see more in Table S5) they are present together.

Two recent molecular studies (*Garcia-Porta* et al., 2012; *Recuero* et al., 2012; pp. 71-86) suggested models of palaeobiogeographic history and timing of major cladogenetic events in the *Bufo bufo* species group; e.g. origin in South-western Asia, subsequent migration into

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Europe via Anatolia. In fact, the works did not consider entire fossil record, including the oldest record of the groups from the Middle Miocene of Slovakia (*Hodrova*, 1980) nor those of the species group for both calibration of the molecular clock and palaeogeographic considerations. Thus, updating and improvement of the distribution models, are necessary. Moreover, finds on the fossil forms of the south-eastern species *B. eichwaldi* will help to reveal the place of origin and distribution routes of the ancestors of the group. Although just the molecular clock, and not the entire fossil record of the group has been used for the calibration, the results on mtDNA sequence seem to provide reliable data on diversification rates within the *Bufo bufo* species group, which can be proved by first appearances of the fossils related to each Recent species.

Green toads. The widely distributed *Bufotes viridis* species group (or *Bufotes viridis* sensu lato) extends its distribution range across Central Europe to Central Asia, as well as entire northern Africa and Mediterranean area with numerous islands. The species complex is highly diverse and includes over ten recognised species, e.g. *Bufotes balearicus* (southern Mediterranean and Apennine Peninsula, Corsica, Sardinia, Balearic Islands), *Bufotes boulengeri* (northern Africa), *Bufotes siculus* (Sicily), *Bufotes viridis* (Central and Eastern Europe), *Bufotes variabilis* (Balkans, Anatolia, Caucasus) etc., found in broad range of environments (*Stöck* et al., 2006; *Stöck* et al., 2008b). Among them, no osteological characters valuable for the taxonomic identification are established (*Blain, Gibert & Ferràndez-Cañadell*, 2010). Hence. no precise specific assignment of any fossil material is possible. As *Blain, Gibert & Ferràndez-Cañadell* (2010) recently showed (1.1-1.3 Ma, Early Pleistocene), the green toads were also present in the Iberian Peninsula and became extinct due to climatic changes and/or competition, as suggested.

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In the studied Western Siberian localities, the fossil remains related to *Bufotes viridis* are the most frequently occurring element in the Western Siberian herpetofauna. This species is almost permanently present from the Middle Miocene to Early Pleistocene. They are found in the late Middle Miocene localities, and with gaps, they are present in the late Late Miocene to Early Pleistocene localities (Table S1). In the youngest localities (Olkhovka 1A, Lebiazhie 1A, Lebiazhie 1B), they are found as a sole taxon. Further fossils assigned to the family Bufonidae (Bufonidae indet.) were already reported from the loc. Kentyubek, Turgay Basin, Middle Miocene (*Bendukidze & Chkhikvadze*, 1976) and two localities in the Zaisan Basin – the loc. Zmei Gorynych, Akzhar Svita, Early Miocene (*Chkhikvadze*, 1985) and the early Rupelian age fossil sites (see section 'Pelobatidae') of the Buran Svita (*Chkhikvadze*, 1998). *Malakhov* (2005) described the stratigraphically oldest fossil green toad *Bufotes* aff. *viridis* from the early Early Miocene (20.4-22.5 Ma, Aquitanian) locality Ayakoz, north-eastern Kazakhstan (Fig. 1, Table S1). *B.* aff. *viridis* from loc. Ayakoz is older than the *Bufotes* aff. *viridis* from loc. Keseköy, Early Miocene (18-20 Ma), north-western Turkey (*Claessens, Leon P. A. M.*, 1997) and all oldest European fossil green toad occurrences are from the Early Miocene: loc. Vieux-Collonges (14-17 Ma) (*Bailon & Hossini*, 1990), France, locs. Petersbuch 2 and 7 (17.5-18 Ma), Germany (*Böhme & Ilg*, 2003) and probably, loc. Córcoles (17-18 Ma), Spain (*Sanchíz*, 1998a). Once they entered into Europe, they became a regular element of the European Neogene and Quaternary herpetofaunal assemblages (Fig. 9). Besides *Bufotes* (aff.) *viridis*, the European record of green toads includes another species *Bufotes priscus* from four localities of latest Early Miocene to earliest Late Miocene age (see Table S5). Taken together the *B. viridis* Neogene records and the bufonid records from the Eurasian Paleogene, we suggest that the group arriving the Old World

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in the Paleocene (*Rage*, 2003), entered Central Asia in the Early Oligocene and diversified there.

Although we were not able to study the Paleogene bufonid record from Kazakhstan, taking into consideration the palaeogeography of common and green frogs, an assignment of the Kazakh Early Oligocene record to the green toad seems most probable. Apparently, the Early Oligocene forms were ancestral for the *Bufotes viridis* lineage, which evolved in Central Asia in the Early Miocene. This assumption is also supported by molecular data suggesting that: (1) green toad clade diversificated in Asia during the Oligocene/early Miocene and (2) a high genomic and specific diversity is found within the Central Asian green toads (*Stöck* et al., 2006). Present in the Central Asian fossil record from the Early Miocene; they dispersed consequently via Anatolia in the early Burdigalian into Europe during the middle Burdigalian. Apparently, the European Neogene record should not necessarily represent one 'linage' or one dispersal event of the *B. viridis* group from Asia. Most probably, several migration events took place during the Miocene. The descendants of these events were replaced later, as indicated by the genetic data at the Mio-Pliocene transition, by the ancestors of the Recent species *B. viridis*, *B. Variabilis*, etc. (*Stöck* et al., 2006). As perspective work for further studies would be: (1) verification of dispersal events in the European fossil record, with help of richer and much abundant fossil material from stratigraphically well-dated localities; (2) exploring the Miocene record of Anatolian and South-eastern Europe, as well as the Paleogene record of Asia. Another challenging project will be establishing of osteological characters important for systematic identification among the members of the *Bufotes viridis* species group.

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The family of true frogs Ranidae are present in the Western Siberian record by both green (*Pelophylax* sp.) and brown (*Rana* sp.) frogs. The green frogs appear more frequently in the record than the brown frogs. Both frog genera are common amphibians in the Recent herpetofauna of the area. Besides this record, further true frog finds (e.g. Ranidae indet.) are reported from early Rupelian age fossil sites (see section ‘Pelobatidae’) of the Buran Svita, Zaisan Basin. we are not able to revise their taxonomic validity due to lack of figured fossils and the inaccessibility of the material .

Green frogs. The genus *Rana* includes 21 Recent species of aquatic frogs having a wide distribution ranging from northern Africa, Europe to Eastern Asia. Two genetically distinct clades Western Palaearctic and the Far East are recognised within the green frogs genus *Pelophylax* (*Lymberakis* et al., 2007). The oldest green frog record from the Western Siberian (*Pelophylax* sp.) is dated as late Middle Miocene, coinciding stratigraphically with the Eastern Siberian record of the group (Middle Miocene, ca. 13 Ma, Tagay Section, Baikal Lake) (*Daxner-Höck* et al., 2013). In the studied localities, this group is present until the late Early Pliocene with long (during Late Miocene) and short gaps (during Early Pliocene). Due to the fragmentary preservation of the studied bones as well as the lack of other informative elements of the skeleton (e.g. frontoparietals), any assignment to the Recent green frog species is impossible. Even considering the present distribution of the two green frog clades, an affiliation of the Western Siberian fossil record to the Western Palaearctic clade is most probable.

Even though the green frog record described in this work is not rich, it enlarges significantly the scarce and poorly known fossil history of the genus. Moreover, both Middle Miocene records from Western and Eastern Siberia represent the oldest records of the green frogs in the Asian

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Continent. Although an Asiatic origin of the green frogs has been already assumed by several authors e.g. *Sanchíz, Schleich & Esteban* (1993), *Lymberakis* et al. (2007), the earliest frog remains referred to the *P. ridibundus* species group occurred in the early Oligocene of Europe (loc. Möhren 13, Germany) (*Sanchíz, Schleich & Esteban*, 1993). Its affiliation to a living species is impossible. In Europe, the fossil record of *Pelophylax* is continuous and goes through the Oligocene and entire Neogene (Table S5). Nevertheless, until well-documented Paleogene record of the group is not available from Asia, any interpretations would not be confident. The only scenario, which can be possible taking into account the fossil record and genomic data, is that the Western Palaearctic green frogs split from the sister Far East clade in the Eocene; diversify in the territory of Europe and/or Western Asia in Oligocene; dispersed back to the East in the middle Miocene, reaching the territory of the Western Siberia.

Brown frogs. The genus *Rana* (subgenus Rana sensu *Veith, Kosuch & Vences*, 2003) comprises more than 15 species distributed over Eurasia. Similar to green frogs, among brown frog species two lineages are known for the Western and Eastern Palaearctic (*Veith, Kosuch & Vences*, 2003). Based on the osteological characters, the studied Western Siberian brown frog remains can be related to the Western Asiatic lineage of the genus *Rana*, more precisely to the *Rana temporaria* species group (sensu *Veith, Kosuch & Vences*, 2003). Among the late Paleogene and Early Miocene fossil frogs (*Böhme & Ilg*, 2003), which generic identification is unclear (*Rana* vel *Pelophylax*), only the frog remains from Dietrichsberg, Germany, Early Miocene (*Böhme*, 2001) have been definitely referred to the brown frog *Rana* cf. *temporaria*, representing the oldest record of the group known so far. As already suggested by *Böhme* (2001) brown frogs migrated to Europe from the possible centre of origin in Western or Central Asia during the second half of

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the Early Miocene. The brown frog finds from the Aquitanian age locality Ayakoz in Kazakhstan, which is stratigraphically older than the Dietrichsberg frogs, confirms this hypothesis. Further argument for the Asiatic origin of the brown frogs is their present-day biogeography and diversity, as well as the presence of a distinct Eastern Palaearctic lineage in Eastern Asia and the Asian distribution of many European species. Most likely, the dispersal route of brown frogs is similar with that of the green toad (*Bufotes* cf. *viridis*) and underwent into Europe, via Anatolia, during the Early Miocene.

It is interesting to note that the earliest brown frog from the studied Western Siberian localities (Malyi Kalkaman 2, ca. 12 Ma) shows osteological similarities with the Recent species *Rana temporaria*, representing herewith the oldest fossil record of the species in the east. The molecular studies (*Veith, Kosuch & Vences*, 2003; *Lymberakis* et al., 2007) on both green and brown frogs tried to reconstruct the phylogenetic relationships, suggesting models of biogeographic history as well as to date the splits between different genera, clades, species etc. They provided contradictory results, e.g. split of *Rana* and *Pelophylax* was at 9.32 Ma (*Veith, Kosuch & Vences*, 2003), whereas *Lymberakis* et al. (2007) indicated the split of the Western Palaearctic and Far East lineages of *Pelophylax* significantly earlier - already at 15 Ma. Here neither geologic events nor fossil records have been used consistently for the calibration of the molecular clock. Thus, the timing for the splits recalibrating with the new fossil finds, given in the present study, will provide more reliable results on phylogenetic reconstructions.

For the better understanding of relationships between these groups, as well as for revealing the origin and palaeobiogeographic history of them, it will be interesting to revises the Paleocene frogs (Ranidae indet.) reported from the early Rupelian fossil sites (see section ‘Pelobatidae’) of

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the Buran Svita, Zaisan Basin (*Chkhikvadze*, 1998). This was not possible to implement in the present work, due to the lack of figures of the fossils and the inaccessibility of the material.

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Gekkonidae

The family Gekkonidae is present in the Western Siberian fossil record by a genus of the straight-fingered or even-fingered geckos *Alsophylax*. They occur only in the locality Cherlak, dated as terminal Miocene ca. 5.9 Ma. *Alsophylax* sp. is the most abundant element in the herpetofaunal assemblage of the Cherlak locality, about 70% of the identifiable bone material belongs to this taxon. The genus *Alsophylax* is distributed mainly in Central Asia, partly occurring also in Mongolia and China. They prefer habitats in arid and warm landscapes (*Ananjeva* et al., 2006). The appearance of these dry and warm adapted geckos in Western Siberia, which is four degrees north of their present occurrence, suggests a shift of the arid environment from the south to the north at the end of the Late Miocene (see below). It is interesting to note that from seven gecko genera, e.g. *Eublephareus*, *Mediadactylus*, *Terratoscincus* (*Ananjeva* et al., 2006) inhabiting Central Asia, only *Alsophylax*, having the most north distribution, occurs in the fossil record. Apparently, this genus is ecologically more plastic in comparison to other genera, not only for the present, but also in the past.

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Lacertidae

Lacertid remains are the most frequent fossil bones among lizards occurring in Western Siberian localities. They are very rare in the Middle Miocene faunas, but occur more frequently in the Late Miocene, Pliocene and Pleistocene localities. In a middle Late Miocene locality Pavlodar 1A (ca. 7.25 Ma) two taxa (*Lacerta* s.l. sp. 1 and sp. 2) occur sympatrically. In the Pliocene, *Eremias* sp. appears in the Western Siberian record. This genus is widely distributed in the Central Asian steppes, inhabiting dry and warm habitats (*Ananjeva* et al., 2006).

Emydidae

Emydoidea sp. is the only turtle identified from the studied fossil sites. The present-day distribution of the monotypic genus *Emydoidea* is restricted to the water bodies of the north-eastern territory of the USA. In Eurasia, the fossil forms of this aquatic genus are known since the Middle Miocene of Central Kazakhstan (*Emydoidea tasbaka*, loc. Kentyubek, Turgay Basin) (*Chkhikvadze*, 1989). In the Late Miocene, they have been reported from Eastern Europe (loc. Krivoy Rog, *Emydoidea tarashchuki* and loc. Pantishara (8.7-9.2 Ma), Georgia*)* (*Chkhikvadze*, 1980; *Chkhikvadze*, 2003). The Siberian record indicates their occurrence in Asia also during the Late Miocene, which is located interestingly much north than their Middle Miocene record from Kazakhstan. According to *Chkhikvadze* (2003), they can be present also in the Pliocene of Eastern Europe. We avoid interpreting palaeobiogeography, stratigraphic distribution, etc. of this genus, since the available published material (e.g. *Chkhikvadze*, 1983, 1989), together with other extinct testudinoid taxa from Kazakhstan and Eastern Europe, is poorly described and illustrated and needs thorough redescription and revision. Nevertheless, we try to use the available published data on both freshwater turtles and terrestrial tortoises to interpret the record at the family level (Table 2). We summarised in the Table 2 the turtle record from three well-explored regions in the studying area – Zaisan and Turgay Basins and Western Siberia. Through the entire Early Miocene in the Zaisan Basin, the turtle fauna is dominated by aquatic

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forms, from eight taxa only two are tortoises (*Protestudo* spp.). During the Middle Miocene, aquatic forms are still dominant here, whereas the terrestrial family Testudinidae replaced completely aquatic turtles (Emydidae, Triochynidae) in the terminal Middle Miocene and became the only family present in the younger (Late Miocene) deposits. Similar to the Zaisan Basin, the aquatic forms represent the Middle Miocene turtle fauna in two adjacent regions in the west – Turgay Basin and in the north – Western Siberia. Subsequently, in the early Late Miocene, a testudinid appears in Western Siberia and is replaced by an emydid in the late Late Miocene and a chelydrid at the Mio-Pliocene transition. The absence of tortoises since the late Late Miocene in Western Siberia and the Plio-Pleistocene of the Zaisan Basin can be explained by less favourable, probably colder (MAT <15˚C, cold month temperature CMT <8˚C) climate. In Western Siberia, the last chelonids present (since the late Late Miocene) are the emydid and chelydrid aquatic turtles. They indicate not necessarily only a humid (standing water-bodies) but most probably also cooler climate (for emydids: MAT>8˚C, CM>-1.4 ˚C) since in general, aquatic turtles can tolerate much colder conditions (water acts as thermal buffer) in comparison to tortoises, and consequently are able to populate higher poleward latitudes.

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Palaeobiogeographic considerations

Taken together the comparison between European and Asian fossil records, the spatial and temporal patterns in the fossil record including the first and last fossil occurrences, as well as the available genomic data of the recent relatives of the fossil groups present in the studied material, certain palaeogeographic distribution patterns can be followed and newly interpreted.

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Our analysis suggests a (Western) Asiatic origin for Hynobiidae, Proteidae, aff. *Tylototriton*, *Bufotes viridis* species group and brown frogs *Rana*. The green toads and brown frogs dispersed coincidentally in the earliest Miocene, and at least for the *Bufotes viridis* group, Anatolia was involved. Anatolia also played an important role in the distribution of the *Bufo bufo* species group, however, any age estimation of the event is not available. A salamander, showing affinities to the clade of the Recent East Asian genera *Tylototriton* + *Echinotriton*, is present in Western Siberia, most probably it represents, similar to the early Oligocene form (aff. *Tylototriton*) from Europe, a sister group of the Recent clade. To resolve affiliations of these fossils further Paleogene material from both continents, Asia and Europe, are necessary. Based on the data available from both European and Asiatic records today, for at least seven amphibian groups (family Palaeobatrachidae, genera *Chelotriton*, *Pelobates*, *Bombina* (i.e. *Bombina* (cf.) *bombina*), *Hyla* (i.e. *Hyla* cf. *savignyi*), *Pelophylax* ?, *Bufo bufo* species group) an eastward dispersal from Europe into Western Asia can be observed over a period of time ranging from the Middle to Late Miocene. Besides the amphibians, some Western Siberian reptiles like glass lizards and snakes from the Middle Miocene, show European affinities, resembling the Central European faunas (*Vasilyan, Böhme & Klembara*, 2016).

The amphibian genera *Bombina*, *Hyla*, *Bufo*, *Rana* and *Pelophylax* resemble a comparable palaeobiogeographic pattern: the molecular genetic data showed the presence of two clearly separable western and eastern clades (species groups) in each of these genera. In all cases, it was possible to attribute morphologically the Western Siberian fossil amphibians to the western clades or species of the clades. It is interesting to note that even though the first fossil occurrences of these genera have different stratigraphic ages, they are found exclusively in

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Europe (see Fig. 9, Table S5). To explain this common pattern, we hypothesise that the western and eastern clades split already in the Paleogene, most probably in the western or central parts of Asia, and subsequently dispersed into Europe.

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The Western Siberian fossil *Mioproteus*, *Chelotriton*, *Bombina*, Paleobatidae, *Hyla*, *Bufo bufo* and *Rana temporaria* represent the most east records of those groups found in the Eurasian fossil record. In comparison to their present-day geography, the Western Eurasiatic species of the genera *Bombina* and *Hyla* show wider distribution ranges during the Middle – Late Miocene and Late Miocene – Early Pliocene correspondingly. The palaeogeographic affinity of the latest Tortonian pelobatid (locality Selety 1A) is yet unclear. Considering the geographic location of the fossil site, its relation to the Recent genus *Pelobates* seems most possible.

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In Chkhikvadze (1985), two lizards *Varanus* sp. and Agamidae indet. have been reported from three Miocene localities of the Zaisan Basin. Although the taxonomic assignment of the remains could not be verified in this study, we adopt the identifications for biogeographic and palaeoenvironmental interpretations. These lizards are currently widely distributed in Central Asia. *Varanus* as a thermophilous reptile is restricted to the southern part of the region and its presence in the early Late Miocene of the Zaisan Basin can characterise the climate of the Sarybulak Svita (early late Miocene) by a mean annual temperature (MAP) of not less than 14.8 °C (*Böhme*, 2003).

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In summary, Western Siberia (Central Asia) can be hypothesised as a centre of evolution and dispersal for several temperate Neogene herpetofaunal taxa, e.g. the genera *Salamandrella* and *Mioproteus*, the green toad *Bufotes viridis* species group and brown frog *Rana*. The Neogene herpetofauna of Western Siberia and adjacent areas has significant similarities with the

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European amphibian and reptile assemblages. The Western Palaearctic elements entered gradually the Siberian territory from Europe across Middle Miocene to Early Pliocene, strongly shaping the herpetofauna of Western Siberia. It partially retained the faunal elements of an Asiatic origin (e.g. Hynobiidae, Proteidae, *Alsophylax*). The faunal diversity of the fossil record after the Early Pliocene collapses significantly. Only few amphibians and reptiles, e.g. *Salamandrella*, *Bufotes*, *Lacerta*, and *Vipera* are present in the Pliocene fossil record being able to survive in less favourable environments to form the main part of the Western Siberian present-day herpetofauna.

The palaeobiogeographic analysis of the recent amphibian faunas of Western Asia (*Savage; Garcia-Porta* et al., 2012) hypothesises a progressive aridification of Central Asia linked with the global cooling trends during the Miocene, forcing amphibians to shift their distribution to the south.

Palaeoclimatic implications

The Neogene climate evolution of Western Siberia has been previously reconstructed based on palynofloras, showing a progressive change of environmental conditions – climate and vegetation, during the Miocene (*Arkhipov* et al., 2005). Along Early to Late Miocene, a warm and humid climate has been replaced by a warm temperate in the Middle Miocene and boreal-warm temperate climates in the Late Miocene respectively. In the latest Miocene, a sharp turn into semiarid and arid climates took place. The Pliocene climate is prevailed by frequent changes between semiarid forest-steppe/steppe and arid desert environments, whereas from the Late Pliocene it changes into subarctic (*Arkhipov* et al., 2005; fig. 46, p. 76)

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At a lower temporal resolution the testudinoid fossil records from the Zaisan and Turgay Basins and Western Siberia confirm a general trend towards aridity in the Neogene (Data S4). Based on the environmental requirement (aquatic or terrestrial) of the testudinoids from the Zaisan Basin, we infer that the climate changed from humid to dry. So, the Early and Middle Miocene was mostly humid (dominance of aquatic families), whereas the presence of exclusively terrestrial forms – tortoises from the latest Middle Miocene to Late Miocene indicates dry and open habitats in the Zaisan Basin. Unfortunately, any quantification of the palaeoprecipitation values based on these limited taxa is impossible to make and well-documented herpetofaunal assemblages are necessary from those deposits for further environmental reconstructions.

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For a better palaeoclimatic understanding we estimated palaeoprecipitation values for 12 data points. These localities provided six and more amphibian and reptile taxa, applicable for the bioclimatic analysis (*Böhme* et al., 2006). Even so, our data do not be enable to reconstruct in high temporal coverage, the climate development over the Middle Miocene to earliest Pleistocene in Western Siberia. Thus, climate development only for several short intervals can be reconstructed and discussed. Nevertheless, our estimations rather show a dynamic climate development in the Neogene of Western Siberia, with large amplitudes ranging from 158 to over 1.500 mm per year (Table S1, Fig, 10) than that estimated using palynological data (*Arkhipov* et al., 2005). Apart from the fluctuating character of humidity, in general, the mean annual precipitation (MAP) was significantly above the present day values (reaching 550 % of the present-day values) (Fig. 10). Only two localities are characterised by drier climates, the late Serravallian (ca. 12.1 Ma) and the late Messinian (5.9 Ma), having present-day or below present-day levels.

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Reliability of precipitation estimates

The accuracy of precipitation estimates based on bioclimatic analysis of herpetofauna depends primarily on taxon counts and the assumption of low (stochastic) taphonomic bias (*Böhme* et al., 2006). For Western Siberia, we document some cases were a rich aquatic herpetofauna, e.g. composed by freshwater turtles, giant salamanders, proteids, etc. was present, but small terrestrial forms (e.g. lizards, anguids, etc.) were absent, indicating a possible non-stochastic taphonomic bias (exclusion of elements of certain habitats). These localities will result in a bias in humidity estimates toward the wet end. Examples are the localities Kentyubek and Novaya Stanitsa 1A, where the numeric results exceed well MAP of 1.600 mm, the upper limit to which the eco-physiologic index – humidity relation is calibrated (see details in *Böhme* et al. 2006). In these cases, we restrict our estimates to a limit of 1.500 mm.

Aquitanian

For the Aquitanian age locality Ayakoz we estimated a MAP value of 945 mm, representing more than three times higher rainfall in comparison to the recent times. *Arkhipov* et al. (2005) using the palynologic data, estimated a humid climate with MAP 800 mm for the Abrosimov Svita (Aquitanian age) in Western Siberia. Besides this, Bruch and Zhilin (2007) based on the data on fossil macroflora, estimated similar values of precipitation (935 to 1232 mm) for about 30 Aquitanian age localities, distributed from Western to Eastern Kazakhstan. Thus, our reconstruction fits well to the known precipitation picture of the region.

Akzhar Svita

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For the late Early Miocene (Burdigalian), an elevated humidity in Western Siberia can be suggested based on the presence of the giant salamander in three localities of the Zaisan Basin (Tri Bogatyrya, Vympel, Poltinik). As already suggested, their occurrence indicates a high rainfall for those time periods (MAP > 900 mm), as well as an increased basinal relief enabling distribution and reproduction of this group in the lowland settings (*Böhme, Vasilyan &* *Winklhofer*, 2012). This time period of the Akzhar Svita also corresponds to the folding and uplift of the Altai Mountains (*Zykin*, 2012; p. 394), due to which establishment of the higher basinal relief was possible.

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Late Serravallian

In contrast to the already known climate development suggested by Arkhipov *et al.* (2005), our data point to strong humidity fluctuations during the late Middle Miocene (late Serravallian), between MAP values of 282, 884 and 1.096 mm (Fig. 10). The only botanical data of this time (Bescheul macroflora) point to a warm-temperate and humid (MAP ~700 mm) climate (*Arkhipov* et al., 2005), which best compares to our Malyi Kalkaman 2 results (MAP 884 mm).

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Novastanitsa Svita

Although the herpetofaunal assemblage for the early Messinian locality Novaya Stanitsa 1A is not complete, a very high mean annual precipitation value of at least 1.500 mm can be estimated. The value shows significantly more humid than Tortonian-Messinian boundary and late Messinian (see below). Our data are contrary to the palynologic results, which gave lower estimates (400-450 mm; Arkhipov *et al.* 2005).

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Rytov Svita

The Cherlak locality (5.9 Ma, Rytov Suite) is characterised by a rather dry climate (MAP 255 mm), similar to the present humidity level (Fig. 10). Our data for a warm and dry climate are confirmed by the presence of: (1) gekkonid *Alsophylax*; (2) mollusk fauna containing thermophilous species; (3) the small mammal fauna, represented mainly by pikas, hamsters and jerboas, characteristic for open and dry habitats (*Zykin*, 2012); (4) ostriches (*Struthiolithus* sp.) and camels (*Paracamelus* sp.) in this svita (*Shpanskiy*, 2008). Arkhipov et al. (2005) summarised the available palynological and vegetation data of the svita and reported the presence of poor (due to oxidised) spectra containing xerophyte plants (Asteraceae, Chenopodiacea), characterising desert and steppe environments. Interestingly, his results proposed a northward shift of dry steppe and desert environments by 4° (to the latitude of 56°) concurring with our data by showing the presence of the steppe-dwelling gekkonid *Alsophylax* sp. (see the section 'Gekkonidae').

Miocene-Pliocene transition (Detskaya Zhelzna Daroga)

Even though the precise taxonomic identification of the Western Siberian and Zaisan cryptobranchids, is unclear at the generic or species level, if their occurrence indicates a high rainfall > 900 mm MAP (*Böhme, Vasilyan & Winklhofer*, 2012) during the Burdigalian in the Zaisan Basin and the Miocene-Pliocene transition in Western Siberia. Besides Cryptobranchidae indet. from the locality Detskaya Zheleznaja Doroga, the co-occurrence of the aquatic chelonids *Chelydropsis kuznetsovi* and ?*Sakya* sp. (*Gaiduchenko*, 1984; *Gaiduchenko & Chkhikvadze*, 1985) confirms high precipitation at the Miocene-Pliocene boundary in Western Siberia.

Earliest Pliocene (Olkhovka 1A-1C)

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Our earliest Pliocene humidity data are estimated based on the fauna from the localities Olkhovka 1A, 1B and 1C, for which no correlation data to regional svitas is available (see ‘Geology and Stratigraphy section’). Nevertheless, the results indicate still significant precipitation (MAP 575 mm), well above the present-day values in this region. A good correspondence exists to the similar aged Speranovskaya palynoflora (*Volkova*, 1984), indicating warm forests and forest-steppes with MAP estimates between 500-550 mm (*Arkhipov* et al., 2005).

Conclusions

In summary, over 50 salamander, frog, lizard, snake and turtle taxa have been indicated to more than 40 Western Siberian localities ranging from the Middle Miocene to Pleistocene (Table S1). The late Middle Miocene localities have the most diverse faunas including all the main groups of the herpetofauna. According to our analysis, the fauna contains taxa showing an Asian (Eastern Palaearctic) origin such as Hynobiidae, Proteidae, *Bufotes viridis* species group and *Rana*, *Varanus*, and Agamidae. The main part of the herpetofaunal assemblage, including Palaeobatrachidae, Paleobatidae, the genera *Chelotriton*, *Bombina* (i.e. *Bombina* (cf.) *bombina*), *Hyla* (i.e. *Hyla* (cf.) *savignyi*), *Pelophylax* ?, *Bufo bufo* species group, *Ophisaurus* sp. (*Vasilyan, Böhme & Klembara*, 2016), has European (Western Palaearctic) affinities. The Western Siberian records of *Mioproteus*, *Chelotriton*, *Bombina*, Paleobatidae, *Hyla*, *Bufo bufo* and *Rana temporaria* represent the most east occurrences of these groups in Eurasia. The earliest Miocene dispersal of the green toad *Bufotes viridis* species group from Asia via Anatolia into Europe can be inferred. We suggest the same distribution pattern for brown frogs *Rana* too. In

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this scope, it will be important to perform future detailed studies about the Neogene record of the amphibian and reptile faunas in Anatolia and analyse them in a palaeobiogeographic context.

According to our study, the precipitation development in Western Siberia shows high-amplitude changes during the studied intervals. Aside from the certain time periods (late Seravalian, late Messinian), the palaeorainfall in Western Siberia was significantly above the present-day values. The best results on precipitation estimates with reliable age constrain that we were able to reconstruct is the time period from 6.6 to ~4.5 Ma. They show a humid climate during the early Messinian; a dry climate during the late Messinian; a very humid climate during the Miocene-Pliocene transition and a humid climate during the earliest Pliocene (Data S4, Fig. 10). The decreasing tendency of the herpetofaunal diversity towards the end of the Neogene and Quaternary could be referred to the progressive global cooling and forced ice-sheet development in the Northern Hemisphere.

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REFERENCES

Amphibiaweb. 2016. <http://amphibiaweb.org>: Information on amphibian biology and conservation (accessed 1 July 2016).

Ananjeva NB, Orlov NL, Khalikov RG, Darevsky I, Ryaboc SA, Barabanov AV. 2006. *The Reptiles of Northern Eurasia: Taxonomic Diversity, Distribution, Conservation Status*. Sofia: Pensoft.

Anderson J. 1871. Description of a new genus of newts from western Yunan. *Proceedings of the Zoological Society of London* **1871**:423–425.

Arkhipov SA, Volkova VS, Zolnikov ID, Zykina VS, Krukover AA, Kul'kova LA. 2005. West Siberia. *Geological Society of America Special Papers* **382**:67–88.

Arntzen JW, Recuero E, Canestrelli D, Martínez-Solano I. 2013. How complex is the *Bufo bufo* species group? *Molecular Phylogenetics and Evolution* **69 (3)**:1203–1208.

Audouin JV. 1827. Explication sommaire des planches de Reptiles (supplément) ... offrant un exposé des caracteres naturelles des genres, avec la distinction des especes: Description de l'Égypte, ou Recueil des Observations et des Recherches qui ont été faites en Égypte pendant l'Expedition de l'Armée Française, publie par les Ordres de sa Majesté l'Empereur Napoléon le Grand. *Histoire Naturelle* **1 (4)**:161–184.

Averianov AO, Tjutkova L. 1995. *Ranodon* cf. *sibiricus* (Amphibia, Caudata) from the Upper Pliocene of Southern Kazakhstan: The first fossil record of the family Hynobiidae. *Paläontologische Zeitschrift* **69 (1)**:257–264.

Bailon S. 1999. *Différenciation ostéologique des Anoures (Amphibia, Anura) de France*. Antibes: Centre de Recherches Archéologiques du CNRS.

Bailon S, Hossini S. 1990. Les plus anciens Bufonidae (Amphibia, Anura) d'Europe: les espèces du Miocène français. *Annales de Paléontologie* **76**:121–132.

Barry JC, Morgan ME, Flynn LJ, Pilbeam D, Behrensmeyer AK, Raza SM, Khan IA, Badgley C, Hicks J, Kelley J. 2002. Faunal and environmental change in the late Miocene Siwaliks of northern Pakistan. *Paleobiology* **28 (sp3)**:1–71.

Batsch, A. J. G. K. 1796. *Umriß der gesammten Naturgeschichte: ein Auszug aus den frühern Handbüchern des Verfassers für seine Vorfesungen*. Jena, Leipzig: Christian Ernst Gabler.

Bendukidze OG, Bruijn H de, **Van den Hoek Ostende, Lars W. 2009.** A revision of Late Oligocene associations of small mammals from the Aral Formation (Kazakhstan) in the National Museum of Georgia, Tbilissi. *Palaeodiversity* **2**:343–377.

Bendukidze OG, Chkhikvadze VM. 1976. Preliminary results of study on fossil amphibians, reptiles and birds from Turgay and Ustyurt. *Bulletin of the Moscow Society of Naturalists, Geological Series* **51 (5)**:156.

Con formato: Francés (Francia)

Con formato: Francés (Francia)

Con formato: Alemán (Alemania)

Blain H-A. 2009. Contribution de la paléoherpétofaune (Amphibia & Squamata) à la connaissance de l'évolution du climat et du paysage du Pliocène supèrieur au Pléistocène moyen d'Espagne. *Treballs del Museu de Geologia de Barcelona* **16**:39–170.

Blain H-A, Bailon S, Agustí J. 2007. Anurans and squamate reptiles from the latest early Pleistocene of Almenara-Casablanca-3 (Castellón, East of Spain). Systematic, climatic and environmental considerations. *Geodiversitas* **29 (2)**:269–295.

Blain H-A, Gibert L, Ferràndez-Cañadell C. 2010. First report of a green toad (*Bufo viridis* sensu lato) in the Early Pleistocene of Spain: Palaeobiogeographical and palaeoecological implications. *Comptes Rendus Palevol* **9 (8)**:487–497.

Blain H-A, Villa P. 2006. Amphibians and squamate reptiles from the early Upper Pleistocene of Bois Roche Cave (Charente, southwestern France). *Acta zoologica cracoviensia* **49A (1-2)**:1–32.

Böhme G. 1977. Zur Bestimmung quartärer Anuren Europas an Hand von Skelettelementen. *Wissenschaftliche Zeitschrift der Humboldt-Universität zu Berlin, Mathematisch-Naturwissenschaftliche Reihe* **26 (3)**:283–299.

Böhme M. 1998. *Archeotriton basalticus* (v. Mayer, 1859) (Urodela, Salamandridae) aus dem Unteroligozän von Hammerunterwiesenthal (Freistaat Sachsen). *Abhandlungen des staatlichen Museums für Mineralogie und Geologie zu Dresden* **43/44**:265–280.

Böhme M. 2001. The oldest representative of a brown frog (Ranidae) from the Early Miocene of Germany. *Acta Palaeontologica Polonica* **46 (1)**:119–124.

Böhme M. 2003. The Miocene Climatic Optimum: evidence from ectothermic vertebrates of Central Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology* **195 (3–4)**:389–401.

Böhme M. 2008. Ectothermic vertebrates (Teleostei, Allocaudata, Urodela, Anura, Testudines, Choristodera, Crocodylia, Squamata) from the Upper Oligocene of Oberleichtersbach (Northern Bavaria, Germany). *Courier Forschungsinstitut Senckenberg* **260**:161–183.

Böhme M. 2010. Ectothermic vertebrates (Actinopterygii, Allocaudata, Urodela, Anura, Crocodylia, Squamata) from the Miocene of Sandelzhausen (Germany, Bavaria) and their implications for environment reconstruction and palaeoclimate. *Paläontologische Zeitschrift* **84 (1)**:3–41.

Böhme M, Ilg A. 2003. fosFARbase. Available at www.wahre-staerke.com (accessed 1 December 2015).

Böhme M, Ilg A, Ossig A, Küchenhoff H. 2006. 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.

Böhme M, Vasilyan D. 2014. Ectothermic vertebrates from the late Middle Miocene of Gratkorn (Austria, Styria). *Palaeobiodiversity and Palaeoenvironments* **94 (1)**:21–40.

Böhme M, Vasilyan D, Winklhofer M. 2012. Habitat tracking, range dynamics and palaeoclimatic significance of Eurasian giant salamanders (Cryptobranchidae) — indications for elevated Central Asian humidity during Cenozoic global warm periods. *Palaeogeography, Palaeoclimatology, Palaeoecology* **342–343**:64–72.

Bonaparte CL. 1850. *Conspectus systematum. Mastozoölogiae. Ornithologiae. Herpetologiae et Amphibiologiae. Ichthyologiae*. Lugduni Batavorum: E. J. Brill.

Borisov BA. 1963. Stratigraphy of upper Cretaceous and Paleogene-Neogene of Zaisan basin. *Transactions of Pansoviet scientific-research geological institute* **New Series, 94**:11–75.

Con formato: Francés (Francia)

Con formato: Inglés (Estados Unidos)

Con formato: Alemán (Alemania)

Borkin LJ. 1999. Distribution of Amphibians in North Africa, Europe, Western Asia, and the Former Soviet Union. In: Duellman WE, ed. *Patterns of Distribution of Amphibians.* Baltimore and London: The Johns Hopkins University Press, 329–420.

Bruch AA, Zhilin SG. 2007. Early miocene climate of Central Eurasia — Evidence from Aquitanian floras of Kazakhstan. *Palaeogeography, Palaeoclimatology, Palaeoecology* **248 (1-2)**:32–48.

Cavallo O, Sen S, Rage J-C, Gaudant J. 1993. Vertébrés messiniens du dàcies à congèries de Ciabòta Cagna, Corneliano d'Alba (Piémont, Italie). *Rivista Piemontese di Storia Naturale* **14**:3–22.

Chkhikvadze VM. 1980. Systematic position of the Neogene freshwater turtle of Moldavia, Ukraine and some Central European Countries. *Bulletin of the Academy of Sciences of Georgian SSR* **99 (3)**:721–724.

Chkhikvadze VM. 1983. *The fossil turtles of Caucasus and Northern Black Sea region*. Tbilisi: Metsniereba.

Chkhikvadze VM. 1984. Survey of the fossil urodelan and anuran amphibians from the USSR. *Izvestia Akademii Nauk Gruzinska SSR, Seria Biologitcheskaya* **10 (1)**:5–13.

Chkhikvadze VM. 1985. Preliminary results of studies on tertiary amphibians and squamate reptiles of the Zaisan Basin. In: Darevsky I, ed.: Nauka, 234–235.

Chkhikvadze VM. 1989. *Neogene turtles of USSR*. Tbilisi: Metsniereba.

Chkhikvadze VM. 1998. Eocene - Oligocene herpetofauna of USSR. In: Krasheninnikov VA, Akhmetiev MA, eds. *Late Eocene - Early Oligocene geological and biotic events. On the territory of the former Soviet Union*, II. Moscow: Geos, 61–66.

Chkhikvadze VM. 2003. Perspectives of paleontological studies of Late Neogene vertebrate localities in the valley of River Iori, Eastern Georgia and Western Azerbaijan. In: Abdaladze O, ed. *Transactions of scientific works: Conservation arid and semiarid ecosystems in Transcaucasia.* Tbilisi: NAGRES, 63–67.

Claessens, Leon P. A. M. 1997. On the herpteofauna of some Neogene Eastern Mediterranean localities and the occurence of *Palaeobatrachus* and *Bufo* (Amphibia, Anura) in the Lower Miocene of Turkey. *Journal of Vertebrate Paleontology* **17 (Suppl. 3)**:39.

Cope ED. 1859. On the primary division of the Salamandirdae, with description of two new species. *Proceedings of the Academy of Natural Sciences of Philadelphia* **11**:122–128.

Cope ED. 1865. Sketch of the primary groups of Batrachia Salientia. *Natural history review* **5**:97–120.

Cope ED. 1868. On the origin of genera. *Proceedings of the Academy of Natural Sciences of Philadelphia* **20**:242–300.

Cuvier G. 1817. Le Règne Animal distribué d'après son organisation pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Les reptiles, les poissons, les mollusques et les annélides **2**:1–532.

Danilov IG, Cherepanov GO, Vitek NS. 2013. Chelonological studies of l. I. Khosatzky with his annotated bibliography on turtles. *Proceedings of the Zoological Institute RAS* **317 (4)**:382–425.

Daxner-Höck G, Badamgarav D, Erbaeva MA, Göhlich UB. 2013. Miocene Mammal Biostratigraphiy of Central Mongolia (Valley of Lakes): New Results. In: Wang X, J FL, Fortelius M, eds. *Fossil mammals of Asia: Neogene biostratigraphy and chronology.* New York: Columbia University Press, 477–507.

Con formato: Francés (Francia)

Con formato: Alemán (Alemania)

Con formato: Francés (Francia)

Daza JD, Alifanov VR, Bauer AM. 2012. A redescription and phylogenetic reinterpretation of the fossil lizard *Hoburogekko suchanovi* Alifanov, 1989 (Squamata, Gekkota), from the Early Cretaceous of Mongolia. *Journal of Vertebrate Paleontology* **32 (6)**:1303–1312.

Daza JD, Aurich J, Bauer AM. 2011. Anatomy of an enigma: an osteological investigation of the Namibian festive gecko (*Narudasia festiva*: Gekkonidae: Gekkota). *Acta Zoologica* **93 (4)**:465–486.

Daza JD, Bauer AM. 2010. The Circumorbital Bones of the Gekkota (Reptilia: Squamata). *The Anatomical Record: Advances in Integrative Anatomy and Evolutionary Biology* **293 (3)**:402–413.

Delfino M, Bailon S, Pitruzzella G. 2011. The Late Pliocene amphibians and reptiles from "Capo Mannu D1 Local Fauna" (Mandriola, Sardinia, Italy). *Geodiversitas* **33 (2)**:357–382.

Dybowski B. 1870. Beitrag zur Kenntniss der Wassermolche Sibiriens. *Verhandlungen des Zoologisch-Botanischen Vereins in Wien* **20**:237–242.

Edwards JL. 1976. Spinal nerves and their bearing on salamander phylogeny. *Journal of Morphology* **148 (3)**:305–327.

Estes R. 1969. Die Fauna der miozänen Spaltenfüllung von Neudorf an der March (ČSSR) Reptilia (Lacertilia). *Österreichische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse Abteilung I, Sitzungsberichte* **178**:77–82.

Estes R, Darevsky I. 1977. Fossil amphibians from the Miocene of North Caucasus, USSR. *Journal of Palaeontological Society of India* **20**:164–169.

Estes R, Queiroz K de, **Gauthier J. 1988.** Phylogenetic relationships within Squamata. In: Estes R, Pregill G, eds. *Phylogenetic relationships of the lizard families.* Stanford, California: Stanford University Press, 119–281.

Evans SE. 2008. The skull of lizards and tuatara. In: Gans C, ed. *The skull of Lepidosauria*, Volume 20, Morphology H. Ithaca: Society for the Study of Amphibians and Reptiles, 1–347.

Fejfar O, Heinrich W-D, Pevzner MA, Vangengeim EA. 1997. Late Cenozoic sequences of mammalian sites in Eurasia: an updated correlation. *Palaeogeography, Palaeoclimatology, Palaeoecology* **133 (3–4)**:259–288.

Fischer von Waldheim G. 1813. *Zoognosia. Tabulis Synopticis Illustrata, in Usum Prælectionum Academiæ Imperialis Medico-Chirurgicæ Mosquensis Edita*. Moscow: Typis Nicolai Sergeidis Vsevolozsky.

Fitzinger L. 1826. *Neue Classification der Reptilien nach ihrer natürlichen Verwandtschaft*. Wien: J. G. Heubner.

Fitzinger L. 1843. *Systema Reptilium. Fasciculus Primus*. Wien: Braumüller et Seidel.

Folie A, Rana RS, Rose KD, Sahni A, Kumar K, Singh L, Smith T. 2013. Early Eocene frogs from Vastan Lignite Mine, Gujarat, India. *Acta Palaeontologica Polonica* **58 (3)**:511–524.

Fritz U, Schmidt C, Ernst CH. 2011. Competing generic concepts for Blanding's, Pacific and European pond turtles (*Emydoidea*, *Actinemys* and *Emys*)—Which is best. *Zootaxa* **2971**:41–53.

Gaiduchenko LL. 1984. On stratigraphy of Neogene sediments of the southmost Westsiberian Plain. In: Volkova VS, Kul'kova LA, eds. *Environment and ligfe at the boundaries of Cenozoic epochs in SIberia and Far East.* Novosibirsk: Nauka, 172–184.

Gaiduchenko LL, Chkhikvadze VM. 1985. First record of chelydrid turtle from the Neogene sediments of Pavlodarian Priirtyshya. *Geologiya i geofizika* **(1)**:116–118.

Con formato: Alemán (Alemania)

Con formato: Alemán (Alemania)

Con formato: Alemán (Alemania)

Con formato: Alemán (Alemania)

Garcia-Porta J, Litvinchuk SN, Crochet PA, Romano A, Geniez PH, Lo-Valvo M, Lymberakis P, Carranza S. 2012. Molecular phylogenetics and historical biogeography of the west-palearctic common toads (*Bufo bufo* species complex). *Molecular Phylogenetics and Evolution* **63 (1)**:113–130.

Gnibidenko ZN, Volkova VS, Kuz'mina OB, Dolya ZA, Khazina IV, Levicheva AV. 2011. Stratigraphic, paleomagnetic, and palynological data on the Paleogene–Neogene continental sediments of southwestern West Siberia. *Russian Geology and Geophysics* **52 (4)**:466–473.

Gnibitenko ZN. 2006. *Cenozoic paleomagnetism of the West Siberian Plate.* Novosibirsk: Geo.

Goldfuss GA. 1820. *Handbuch der Zoologie.* Nürnberg: J. L. Schrag.

Gray JE. 1825. A synopsis of the genera of reptiles and Amphibia, with a description of some new species. *Annals of Philosophy, London* **10**:193–217.

Gray JE. 1870. *Supplement to the Catalogue of shield reptiles in the collection of the British Museum. Part 1. Testudinata (Tortoises).* London: Taylor & Francis.

Gubin YM. 1995. The First Find of Pelobatids (Anura) in the Paleogene of Mongolia. *Paleontologicheskiy zhurnal* **(4)**:73–76.

Gvoždík V, Moravec J, Klütsch C, Kotlík P. 2010. Phylogeography of the Middle Eastern tree frogs (*Hyla*, Hylidae, Amphibia) as inferred from nuclear and mitochondrial DNA variation, with a description of a new species. *Molecular Phylogenetics and Evolution* **55 (3)**:1146–1166.

Hodrova M. 1980. A toad from the Middle Miocene at Devínska Nová Ves near Bratislava. *Věstník Ústředního ústavu geologichého* **55 (5)**:311–316.

Hodrová M. 1987. Amphibians from the Miocene sediments of the Bohemian Karst. *Časopis pro mineralogii a geologii* **32 (4)**:345–356.

Hodrová M. 1988. Miocene frog fauna from the locality Devínska Nová Ves - Bonanza. *Věstník Ústředního ústavu geologichého* **63 (5)**:305–310.

Hoffstetter R, Gasc J-P. 1969. Vertebrae and rips of modern reptiles. In: Gans C, ed. *Morphology A, Biology of the Reptilia.* London, New York: Academic Press, 201–310.

Holman AJ. 1995. A New Species of *Emydoidea* (Reptilia: Testudines) from the Late Barstovian (Medial Miocene) of Cherry County, Nebraska. *Journal of Herpetology* **29 (4)**:548–553.

Iskakova K. 1969. Fossil amphibians from Priirtyshie. *Proceedings of Academy of Sciences of Kazakhian SSR, Series Biological* **(1)**:48–53.

Ivanov M. 2008. Early Miocene Amphibians (Caudata, Salientia) from the Mokrá-Western Quarry (Czech Republic) with comments on the evolution of Early Miocene amphibian assemblages in Central Europe. *Geobios* **41 (4)**:465–492.

Kirscher U, Prieto J, Bachtadse V, Abdul Aziz H, Doppler G, Hagmaier M, Böhme M. 2016. A biochronologic tie-point for the base of the Tortonian stage in European terrestrial settings: Magnetostratigraphy of the topmost Upper Freshwater Molasse sediments of the North Alpine Foreland Basin in Bavaria (Germany). *Newsletters on Stratigraphy* **49 (3)**:445–467.

Kordikova EG. 1994. Review of fossil Trionychid localities in the Soviet Union. *Courier Forschungsinstitut Senckenberg* **173**:341–358.

Kuzmin SL. 1995. *Die Amphibien Russlands und angrenzender Gebiete*. Magdeburg: Westarp Wissenschaften.

Laurenti JN. 1768. *Specimen medicum, exhibens synopsin reptilium emendatum cum experimentis circa venena et antidota Reptilium Austriacorum*. Viennae: Typ. Joan. Thom. nob. de Trattnern.

Con formato: Alemán (Alemania)

Con formato: Alemán (Alemania)

Li J-T, Wang J-S, Nian H-H, Litvinchuk SN, Wang J, Li Y, Rao D-Q, Klaus S. 2015. Amphibians crossing the Bering Land Bridge: Evidence from holarctic treefrogs (*Hyla*, Hylidae, Anura). *Molecular Phylogenetics and Evolution* **87**:80–90.

Linnaeus C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. L. Salvi: Stockholm.

Linnaeus C. 1761. *Fauna Svecica sisten Animalia Sveciae Regni Mammalia, Aves, Amphibia, Pisces, Insecta, Vermes. Distributa per Classes & Ordines, Genera & Species, cum Differentiis Specierum, Synonymis Auctorum, Nominibus Incolarum, Locis Natalium Descriptionibus Insectorum. Editio altera*. Stockholm: Laurentius Salvus.

Lucas SG, Bray ES, Emry RJ, Hirsch KF. 2012. Dinour eggshell and the Cretaceous-Paleogene boundary in the Zaysan Basin, Eastern Kazakstan. *Journal of Stratigraphy* **36 (2)**:417–435.

Lychev GF. 1990. Use of relative higth of the tooth crown of castorids as a indicator of geological time. In: Tleuberdina PA, Kojamkulova BS, Rajushkina GS, eds. *Vertebrate fauna and flora of the Mesozoic and Cenozoic of Kazakhstan*, vol. 11. Alma-Ata: Nauka, 54–60.

Lymberakis P, Poulakakis N, Manthalou G, Tsigenopoulos CS, Magoulas A, Mylonas M. 2007. Mitochondrial phylogeography of *Rana* (*Pelophylax*) populations in the Eastern Mediterranean region. *Molecular Phylogenetics and Evolution* **44 (1)**:115–125.

Malakhov DV. 2003. The earliest known record of *Mioproteus* (Caudata; Proteidae) from the Middle Miocene of Central Kazakhstan. *Biota* **4 (1-2)**:67–72.

Malakhov DV. 2004. Toads (Anura, Bufonidae) from the Middle Miocene in the Turgay Depression (Central Kazakhstan). *Biota* **5 (1-2)**:41–46.

Malakhov DV. 2005. The early Miocene herpetofauna of Ayakoz (Eastern Kazakhstan). *Biota* **6 (1-2)**:29–35.

Malakhov DV. 2009. Fossil amphibians and reptiles from Cenozoic of Kazakhstan: state of art and new materials. *Transactions of the Institute of Zoology MES RK* **50**:25–34.

Miklas PM. 2002. Die Amphibienfauna (Amphibia: Caudata, Anura) der obermiozänen Fundstelle Götzendorf an der Leitha (südliches Wiener Becken, Niederösterreich). *Annalen des Naturhistorischen Museums in Wien* **103A**:161–211.

Młynarski M, Szyndlar Z, Estes R, Sanchíz B. 1982. Lower vertebrate fauna from the Miocene of Opole (Poland). *Estudios geológicos* **38**:103–119.

Müller MJ, Hennings D. 2000. The Global Climate Data Atlas on CD-Rom. Flensburg and Köln.

Nikitina N, Ananjeva NB. 2009. Characteristics of dentition in gekkonid lizards of the genus *Teratoscincus* and other Gekkota (Sauria, Reptilia). *Biology Bulletin* **36 (2)**:193–198.

Nikitina NG. 2009. Pecularities of skull morphology and skin of geckos (Reptilia: Sauria: Gekkota) and their phylogenetic relevance, Zoological Institute of RAS.

Nilsson S. 1842. *Skandinavisk herpetologi eller beskrifning öfver de sköldpaddor, ödlor, ormar och grodor, som förekomma i Sverige och Norrige, jemte deras lefnadssätt, födoämnen, nytta och skada m.m*. Lund: Tryckt uti Borlingska Boktryckeriet.

Nokariya H. 1983. Comparative osteology of Japanese frogs and toads for paleontological studies (I): *Bufo*, *Hyla*, *Microhyla* and *Bombina*. *Bulletin of Natural Science Museum, Series C* **9 (1)**:23–40.

Oken L. 1816. *Lehrbuch der Naturgeschichte*. Leipzig, Jena: Reclam.

Oppel M. 1811. *Die Ordnungen, Familien und Gattungen der Reptilien als Prodrom einer Naturgeschichte derselben*. München: Joseph Lindauer.

Con formato: Inglés (Estados Unidos)

Con formato: Alemán (Alemania)

Con formato: Alemán (Alemania)

Pabijan M, Wandycz A, Hofman S, Węcek K, Piwczyński M, Szymura JM. 2013. Complete mitochondrial genomes resolve phylogenetic relationships within *Bombina* (Anura: Bombinatoridae). *Molecular Phylogenetics and Evolution* **69 (1)**:63–74.

Pomel A. 1853. *Catalogue méthodique et descriptif des vertébrés fossiles découverts dans le bassin hydrographique supérieur de la Loire*. Paris: J. B. Baillières.

Rafinesque CS. 1815. *Analyse de Nature, ou Tableau de l'Universe et des Corps Organisés*. Palermo: Jean Barravecchia.

Rage J-C. 1976. Les Squamates du Miocène de Béni Mellal, Maroc. *Géologie méditerranéenne* **3 (2)**:57–70.

Rage J-C. 2003. Oldest Bufonidae (Amphibia, Anura) from the Old World: a bufonid from the Paleocene of France. *Journal of Vertebrate Paleontology* **23 (2)**:462–463.

Rage J-C, Hossini S. 2000. Les Amphibiens du Miocène moyen de Sansan. *Mémoires du Muséum national d'histoire naturelle* **183**:177–217.

Ratnikov VY. 2001. Pliocene anurans of East-European platform. *Russian Journal of Herpetology* **8 (3)**:171–178.

Ratnikov VY. 2002. New find of amphibians and reptiles in type localities of Muchkapian, upper Don Basin. *Bulletin of Voronezh State University: Geology* **(1)**:73–79.

Ratnikov VY. 2010. A review of tailed Amphibian remains from Late Cenozoic sediments of the East European plain. *Russian Journal of Herpetology* **17 (1)**:59–66.

Ravkin YS, Bogomolova IN, Chesnokova SV. 2010. Amphibian and reptile biogeographic regions of Northern Eurasia, mapped separately. *Contemporary Problems of Ecology* **3 (5)**:562–571.

Ravkin YS, Yudkin VA, Tsybulin SM, Kuranova VN, Borisovich OB, Bulakhova NA, Patrakov SV, Shamgunova RR. 2008. Spatial-typological structure and mapping of reptile population of West Siberia. *Contemporary Problems of Ecology* **1 (2)**:214–220.

Recuero E, Canestrelli D, Vörös J, Szabó K, Poyarkov NA, Arntzen JW, Crnobrnja-Isailovic J, Kidov AA, Cogălniceanu D, Caputo FP, Nascetti G, Martínez-Solano I. 2012. Multilocus species tree analyses resolve the radiation of the widespread *Bufo bufo* species group (Anura, Bufonidae). *Molecular Phylogenetics and Evolution* **62 (1)**:71–86.

Reichenbacher B, Böhme M, Heissig K, Prieto J, Kossler A. 2004. New approach to assess biostratigraphy, palaeoecology and past climate in the South German Molasse Basin during the Early Miocene (Ottnangian, Karpatian). *Courier Forschungsinstitut Senckenberg* **249**:71–89.

Reichenbacher B, Krijgsman W, Lataster Y, Pippèrr M, Baak CC, Chang L, Kälin D, Jost J, Doppler G, Jung D, Prieto J, Abdul Aziz H, Böhme M, Garnish J, Kirscher U, Bachtadse V. 2013. A new magnetostratigraphic framework for the Lower Miocene (Burdigalian/Ottnangian, Karpatian) in the North Alpine Foreland Basin. *Swiss Journal of Geosciences* **106 (2)**:309–334.

Roček Z. 1984. Lizards (Reptili: Sauria) from the Lower Miocene locality Dolnice (Bohemia, Czechoslovakia). *Řada matematických a přirodních věd* **94 (1)**:4–69.

Roček Z. 2005. Late Miocene Amphibia from Rudabánya. *Palaeontographia Italica* **90**:11–29.

Roček Z, Wuttke M, Gardner J, Singh Bhullar B-A. 2014. The Euro-American genus *Eopelobates*, and a re-definition of the family Pelobatidae (Amphibia, Anura). *Palaeobiodiversity and Palaeoenvironments* **94 (4)**:529–567.

Con formato: Francés (Francia)

Con formato: Francés (Francia)

Con formato: Alemán (Alemania)

Sanchiz B, Schleich H. 1986. Erstnachweis der Gattung *Bombina* (Amphibia: Anura) im Untermiozän Deutschlands. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie* **26**:41–44.

Sanchíz B. 1998a. *Salientia*. München: Verlag Dr. Friedrich Pfeil.

Sanchíz B. 1998b. Vertebrates from the Early Miocene lignite deposits of the opencast mine Oberdorf (Western Styrian Basin, Austria). *Annalen des Naturhistorischen Museums in Wien* **99A**:13–29.

Sanchíz B, Młynarski M. 1979. Remarks on the Fossil Anurans from the Polish Neogene. *Acta zoologica cracoviensia* **24 (3)**:153–174.

Sanchíz B, Schleich H-H. 1986. Erstnachweis der Gattung *Bombina* (Amphibia: Anura) im Untermiozän Deutschlands. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie* **26**:41–44.

Sanchíz B, Schleich H-H, Esteban M. 1993. Water frogs (Ranidae) from the Oligocene of Germany. *Journal of Herpetology* **27 (4)**:486–489.

Savage JM. The geographic dstribution of frogs: patterns and predictions. In: *Val (Ed.) 1973 – Evolutionary biology of the anurans*, 351–445.

Scopoli GA. 1777. *Introductio ad historiam naturalem, sistens genera lapidum, plantarum et animalium hactenus detecta, caracteribus essentialibus donata, in tribus divisa, subinde ad leges naturae.* Prague: Apud Wolfgangum Gerle.

Shpanskiy AV. 2008. Pecularities of the development of the hipparion fauna of the Pavlodar Priirtyshe. In: Tleuberdina PA, Erzhanov NT, Zykin VS, eds.: Pavlodarian State University, 92–96.

Stöck M, Dubey S, Klütsch C, Litvinchuk SN, Scheidt U, Perrin N. 2008a. Mitochondrial and nuclear phylogeny of circum-Mediterranean tree frogs from the *Hyla arborea* group. *Molecular Phylogenetics and Evolution* **49 (3)**:1019–1024.

Stöck M, Moritz C, Hickerson M, Frynta D, Dujsebayeva T, Eremchenko V, Macey JR, Papenfuss TJ, Wake DB. 2006. Evolution of mitochondrial relationships and biogeography of Palearctic green toads (*Bufo viridis* subgroup) with insights in their genomic plasticity. *Molecular Phylogenetics and Evolution* **41 (3)**:663–689.

Stöck M, Sicilia A, Belfiore N, Buckley D, Lo Brutto S, Lo Valvo M, Arculeo M. 2008b. Post-Messinian evolutionary relationships across the Sicilian channel: Mitochondrial and nuclear markers link a new green toad from Sicily to African relatives. *BMC Evolutionary Biology* **8 (1)**.

Syromyatkova EV. 2014. The first record of *Salamandrella* (Caudata: Hynobiidae) from the Neogene of Russia. *Russian Journal of Herpteology* **21 (3)**:217–220.

Tempfer PM. 2005. The herpetofauna (Amphibia: Caudata, Anura; Reptilia: Scleroglossa) of the Upper Miocene locality Kohfidisch, Burgenland, Austria, Wien, Universität.

Tleuberdina PA, ed. 1993. *Faunistic and floristic complexes of Mesozoic and Cenozoic of Kazakhstan*. Almaty: Baspager.

Tleuberdina PA, Kozhamkulova GS, Kondratenko BS. 1989. *Catalogue of the Cenozoic mammals from Kazakhstan*. Alma-Ata: Nauka Kazakhian SSR.

Tleuberdina PA, Volkova VS, Lushczaeva TT, Lychev GF, Pita OM, Tjutkova LA, Chkhikvadze VM. 1993. Vertebrate fauna of Kalkaman (Pavlodar Priirtyshe). In: Tleuberdina PA, ed. *Faunistic and floristic complexes of Mesozoic and Cenozoic of Kazakhstan*, vol. 12. Almaty: Baspager, 132–157.

Con formato: Alemán (Alemania)

Con formato: Alemán (Alemania)

Con formato: Alemán (Alemania)

Con formato: Alemán (Alemania)

Tschudi JJv. 1838. *Classification der Batrachier, Mit Berucksichtigung der fossilen Thiere dieser Abtheilung der Reptilien*. Neuchâtel: Petitpierre.

Vangengeim EA, Pevzner MA, Tesakov AS. 2005. Ruscinian and Lower Villafranchian: age of boundaries and position in magnetochronological scale. *Stratigraphy and Geological Correlation* **13 (5)**:530–546.

Vasilyan D, Böhme M, Chkhikvadze VM, Semenov YA, Joyce WG. 2013. A new giant salamander (Urodela, Pancryptobrancha) from the Miocene of Eastern Europe (Grytsiv, Ukraine). *Journal of Vertebrate Paleontology* **33 (2)**:301–318.

Vasilyan D, Böhme M, Klembara J. 2016. First record of fossil *Ophisaurus* (Anguimorpha, Anguidae, Anguinae) in Asia (Russia and Kazakhstan). *Journal of Vertebrate Paleontology*:1–6.

Veith M, Kosuch J, Vences M. 2003. Climatic oscillations triggered post-Messinian speciation of Western Palearctic brown frogs (Amphibia, Ranidae). *Molecular Phylogenetics and Evolution* **26 (2)**:310–327.

Venczel M. 1999a. Fossil land salamanders (Caudata, Hynobiidae) from the Carpathian basin: relation between extinct and extant genera. *Acta Palaeontologica Romaniae* **2**:489–492.

Venczel M. 1999b. Land salamanders of the family Hynobiidae from the Neogene and Quaternary of Europe. *Amphibia-Reptilia* **20**:401–412.

Venczel M. 2000. Amphibians from the Lower Pleistocene Betfia 9 locality (Bihor country, Romania). *Satu Mare - Studii şi comunicări, seria stiintele naturale* **1**:28–37.

Venczel M. 2001. Anurans and squamates from the Lower Pliocene (MN 14) Osztramos 1 locality (Northern Hungary). *Palaeontologica Hungarica* **19**:79–90.

Venczel M. 2004. Middle Miocene anurans from the Carpathian Basin. *Palaeontographica Abt. A* **271**:151–174.

Venczel M. 2008. A new salamandrid amphibian from the Middle Miocene of Hungary and its phylogenetic relationships. *Journal of Systematic Palaeontology* **6 (1)**:41–59.

Venczel M, Codrea V, Fărcaş C. 2012. A new palaeobatrachid frog from the early Oligocene of Suceag, Romania. *Journal of Systematic Palaeontology* **11 (2)**:179–189.

Venczel M, Gardner JD, Codrea VA, Csiki-Sava Z, Vasile Ş, Solomon AA. 2016. New insights into Europe's most diverse Late Cretaceous anuran assemblage from the Maastrichtian of western Romania. *Palaeobiodiversity and Palaeoenvironments* **96 (1)**:61–95.

Venczel M, Hír J. 2013. Amphibians and Squamates from the Miocene of Felsötárkány Basin, N-Hungary. *Palaeontographica Abteilung A* **300 (1-6)**:117–147.

Vergnaud-Grazzini C, Młynarski M. 1969. Position systématic du genre *Pliobatrachus* Fejérváry 1917. *Comptes Rendus hebdomadaires des Séances de l'Académie des Sciences, Série D: Sciences naturelles* **268**:2399–2402.

Villa A, Roček Z, Tschopp E, Van den Hoek Ostende, Lars W., Delfino M. 2016. *Palaeobatrachus eurydices*, sp. nov. (Amphibia, Anura), the last western European palaeobatrachid. *Journal of Vertebrate Paleontology*:e1211664.

Volkova VS. 1984. Changes in the palinofloras of Siberia in the late Cenozoic. In: Volkova VS, Kul'kova LA, eds. *Environment and ligfe at the boundaries of Cenozoic epochs in SIberia and Far East*. Novosibirsk: Nauka, 54–69.

Con formato: Francés (Francia)

Con formato: Alemán (Alemania)

Wagler JG. 1830. *Natürliches System der Amphibien, mit vorangehender Classification der Säugethiere und Vögel . Ein Beitrag zur vergleichenden Zoologie*. München, Stuttgart, Tübingen: J.G. Cotta.

Wuttke M, Přikryl T, Ratnikov VY, Dvořák Z, Roček Z. 2012. Generic diversity and distributional dynamics of the Palaeobatrachidae (Amphibia: Anura). *Palaeobiodiversity and Palaeoenvironments* **92 (3)**:367–395.

Zykin VS. 1979. *Stratigraphy and unionids of the Pliocene of southern part of Western Siberian plain.* Novosibirsk: Nauka.

Zykin VS. 2012. *Stratigraphy and evolution of environments and climate during Late Cenozoic in the Southern West Siberia*. Novosibirsk: Geo.

Zykin VS, Zazhigin VS. 2004. A new biostratigraphic level of the Pliocene in Western Siberia and the age of the Lower-Middle Miocene stratotype of the Beshcheul Horizon. *Doklady Earth Sciences* **398 (7)**:904–907.

Zykin VS, Zazhigin VS. 2008. On the Neogene stratigraphy of Pavlodarian Priirtyshya. In: Tleuberdina PA, Erzhanov NT, Zykin VS, eds.: Pavlodarian State University, 15–21.

Zykin VS, Zykina VS, Zazhigin VS. 2007. Issues in separating and correlating Pliocene and Quaternary sediments of Southerwestern Siberia. *Archeology, Ethnology & Anthropology of Eurasia* **30 (2)**:24–40.

Con formato: Normal, No ajustar espacio entre texto latino y asiático, No ajustar espacio entre texto asiático y números