Neogene amphibians and reptiles (Caudata, Anura, Gekotta, Lacertilia, Testudines) from south of Western Siberia, Russia and Northeastern Kazakhstan (#12606)

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

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Background. Now-a-day territory of Western Siberia has the poorest diversity of amphibians and reptiles within the Palaearctic Realm, influenced by unfavourable climate. Less is known about the origi~~a~~n and emergence of it. Aside from better-explored European Neogene records of amphibians and reptiles, the Neogene herpetofauna of Western Asia is understudied. The few available studies on amphibian and reptile fossil assemblages need critical reviews and new interpretations considering the latest knowledge of the European record. The comparison with European record will provide data on palaeobiogeographic affiliations of the region as well as origin and emergence of the now-a-day fauna of Western Siberia. Beside these, a study providing overview about the earliest occurences of certain amphibian linages, that can be used for the calibration of the molecular clocks, is missing.

Methods and Results. The amphibian and reptile fauna from over 40 Western Siberian, Russia and Northeastern Kazakhian localities ranging from Middle Miocene to Early Pleistocene has been studied. In the study the published data has been considered and critically reviewed and newly interpreted. More then 50 amphibian and reptile taxa has been identified belonging to families Hynobiidae, Cryptobranchidae, Salamandridae, Palaeobatrachidae, Bombinatoridae, Pelobatidae, Hylidae, Bufonidae, Ranidae, Gekkonidae, Lacertidae and Emydidae. Palaeobiogeographic analysis for those group has been done. For 12 localities, palaeoprecipitation values have been estimated using the bioclimatic analysis of herpetofaunal assemblage.

Conclusions. The Neogene assemblage of West~~r~~en Sibera is dominated by groups (Palaeobatrachidae, *Bombina, Hyla*, *Bufo bufo*) with European affinities. A small part of assemblage includes Eastern Palaearctic taxa (e.g. Hynobiidae, *Tylototriton*, *Bufotes viridis, R*. *arvalis*). For several taxa (e.g. *Mioproteus, Hyla, Bombina*) the Western Siberian records ~~of~~ represent the most east Eurasian records of these groups. The most divers faunas are found in the Middle Miocene, whereas the poorest towards Early Pleistocene. This tendency could be referred to the progressive global cooling of the climate in Northern Hemisphere. Our results showed higher-amplitude changes of precipitation development in Western Siberia from Early Miocene to Pliocene, than earlier assumed.

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Abstract

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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 in the south (Fig. 1). The region comprises the drainage basin of the major Siberian rivers Irtysh and Ob, both flowing into the Kara Sea of the Arctic Ocean. Western Siberia is characterized by a highly continental climate and is 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 convective heating relatively labile, resulting in frequent torrential rainfalls. The mean annual range of temperature reaches 40 Kelvin 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; (*Müller & Hennings*, 2000)). The area is covered by the tundra (‘cold steppe’), taiga (coniferous forests) replaced by open landscapes in the north (tundra) and in the south (steppe). Region with studied Neogene outcrops belong to transition zone between dry more humid temperate biomes. Here taiga, forest-steppe and steppe are distributed (*Ravkin* et al., 2008).

Insert here Figure 1

Due to the strong continental climate, the Recent herpetofauna in the territory of Western Siberia has comparatively poor diversity. It is represented by about ten amphibian and seven reptile species. It is assumed that the present amphibian and reptile distribution in Western Siberia was strongly influenced by climatic fluctuation during the Quaternary (*Ravkin, Bogomolova & Chesnokova*, 2010). According to Borkin (*Borkin*, 1999), the Recent amphibian fauna of Western Siberia belongs to the Siberian region of amphibian distribution in the Palaearctic Realm. The region is inhabited by few amphibians, according to different authors (e.g. *Kuzmin*, 1995; *Amphibiaweb*, 2012) 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 *S. keyserlingii* and *Rana amurensis* are characteristic of the territory, but they are widely distributed and are found also with 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*, *Eremias arguta* (*Ananjeva* et al., 2006; *Ravkin, Bogomolova & Chesnokova*, 2010).

Insert here Table 1

Geology and stratigraphy

In Western Siberia, the Neogene sediments have widely distribution. Since many decades through the systematic palaeontological studies and research of the Neogene and Quaternary sediments of Western Siberia rich mollusks, small and large mammals fossil faunas are recovered (e.g. *Zykin*, 1979; *Zykin & Zazhigin*, 2008; *Zykin*, 2012). Based on the studies of the fossil small mammal fauna, the Neogene stratigraphy of the area is complemented by biochronologic 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 till the Quaternary (e.g. *Chkhikvadze*, 1984, 1989; *Tleuberdina* et al., 1993; *Malakhov*, 2005). The sedimentary basin is bordered in the west by the Ural Mountains, in the south by the Central Kazakhian Plain and Altai-Sayan Mountains, and in the east by the western margin of the Siberian Plateau, supplying clastic material into the basin. The Neogene sediments are represented by lacustrin, fluvial, alluvial and other continental formations overlaying marine Eocene sediments. The Neogene and Early Quaternary sediments have their maximal thickness of 300 m in the Omsk Basin. Neogene sediments crop out mainly in the interfluves of the rivers Irtysh and Ishym (*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 Irt~~h~~ysh 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 section and fossil localities are summarized in *Zykin* (1979); *Zykin* & *Zazhigin* (2004); *Gnibitenko* (2006); *Zykin* (2012).

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-Irthysh Interfluve is about 200 kyrs (Fig. 2, Suppls. 1 and 2). The main part of vertebrate localities ar~~ö~~e referred to certain svitas (e.g. Kalkaman, Pavlodar, Irtysh Svitas), however stratigraphic assignment of three localities Olkhovka 1A, 1B, 1C into svitas is not available (Fig. 2, Suppl. 1). Fossil material from the early Late Miocene deposits is entirely lacking.

Insert here Figure 2

State-of-art in palaeoherpetological studies in Western Siberia

The record on fossil amphibians and reptiles of the 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 fossil amphibians and reptiles data are given as short notes or mentioned in the faunal lists (e.g. *Bendukidze & Chkhikvadze*, 1976; *Chkhikvadze*, 1985; *Malakhov*, 2005). In the present study, apart from study of the new material, we restudy available for us fossil remains mentioned in those works.

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

The age of the locality Karashigar is unclear, Tleuberdina et al. (*Tleuberdina, Kozhamkulova & Kondratenko*, 1989) indicated its age as Late Oligocene, while *Lychev* (1990) as Middle Miocene, Kalkaman Svita (the list of the small mammal fauna see in the Suppl. 2). However, the mentioned amphibians taxa in *Iskakova* (1969) (*Bombina* cf. *bombina*, *Pelobates* cf. *fuscus*, *Bufo* cf. *viridis*, *Bufo* cf. *bufo*, *Rana* cf. *ridibundus*, *Rana* cf. *temporaria*) have been identified mainly based on the vertebra (cervical, trunk and sacral) morphology, which are not diagnostic in frogs for identification at this 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., *Coluber* sp. We did not study the material mentioned in those works and can not verify his taxonomic identification. The sample from the same locality studied in the present work (Suppl. 1), did not reveal any element listed in the earlier studies. *Chkhikvadze* (1984) summarised all known fossil amphibian and reptiles from the former USSR, including from Western Siberia~~n~~. For many of them accurate descriptions are still lacking. The Middle Miocene Kalkaman locality (*Tleuberdina*, 1993), now known as Malyi Kalkaman 1 (*Zykin*, 2012), provided a diverse herpetofauna. This fauna ha~~ve~~ been partially restudied by us and amended by newly collected material.

During last decade, a new attempt to study herpetofauna from the Western Siberian localities has been done (*Malakhov*, 2003, 2004, 2005, 2009). In these works, undescribed material from numerous Neogene localities of Kazakhstan has been summarized, revised and stud~~y~~, as well as provided a critical overview on known record. In spite of advances of the last years, the Neogene herpetofauna from the Western Asia is largely unknown and available material stays unsufficently studied. Thus, the main goal of the present study is description and taxonomic study of the new amphibian and reptile fossil material from the collections of V. Zazhigin, as well as faunistic anal~~sy~~s, and palaeobiogeographic and environmental interpretations. In addition, we summarize available literature data and include them into 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 fossil localities as well.

Meterials & Methods

The material of the present study was collected by VZ during his longtime excavations in different Western Siberian localities from 1960ies until 2008 by screen-washing of sediments.

The fossiliferous layers outcrop along the riverbanks of the Irtysh, Ishim and 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 have been identified in the available material. A part of them – snakes and anguine lizards, are to be published in ~~the~~ separate papers (e.g. *Vasilyan, Böhme & Klembara*, accepted). Further, in the present work the material collected from four fossil sites in Kazakhstan: loc. Akyspe (also known as Agyspe), Aral Horizon, leg. by Bendukidze in 1977; loc. Kentyubek, Turgai Basin; loc. Ryzhaya II (Ryzhaya Sopka), Zaisan Svita, Zaisan Basin, leg. in 1970; loc. Ayakoz (known also as Ayaguz), Zaisan Basin, leg. in 1970-1971; loc.

Petropavlovsk 1/2[1], leg. 1972 (Suppl. 1) has been studied. In addition to this, few literature data (after critical revision) has been included to amend the herpetofaunal assemblage of some localities as well as reassign and revise the stratigraphic position of these localities using biostratigraphic information of small and large mammal faunas (full list see in the Suppl. 2 and Suppl. 3).

The photographs of the fossil material are taken by a digital microscope LEICA DVM5000 (Tübingen) and inspect scanning electron microscope Inspect S (Madrid). The figure and tables are produced by the Adobe Photoshop and Illustrator. The osteological nomenclature of the salamander remains is given by *Vasilyan* et al. (2013), frogs *Sanchíz* (1998a), the lizard material is given by widely used lepidosaurian terminology of *Evans* (2008), additionally the standardized osteological nomenclature of *Daza, Aurich & Bauer* (2011) and *Daza & Bauer* (2010) is used for Gekkota.

Based on the herpetofaunal assembleges the palaeoprecipitation values for the fossil localities are 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 and more localities with age differences less than 100 kyr and/or belong to a single stratigraphic unit – svita, are considered as one. Those taxa added additionally to the herpetofaunal assemblage by range-through approach are indicated by grey colour in the Suppl. 1.

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[1] In town Petropavlovsk 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 Natulales, 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.

Anatomic abbreviations.

ao: antrum olfactorium; **alo**: antrum pro lobo olfactorio; **dl**: dental lamina; **ds**: dental shelf; **hl**: horizontal lamel; **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 lamel; **lf**: lacrimal facet; **lg**: longitudinal groove; **lh**: lamina horzontalis; **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**: prezygapohysis; **psz**: postzygapohysis; **pv**: paries verticalis; **pxp**: premaxillary process; **pyp**: pterygapophysis; **sac**: opening of superior alveolar canal; **sg**: symphyseal groove; **sf**: spleneal facet; **tpr**: transverse process.

RESULTS

Systematic palaeontology

Class **Amphibia** *Gray*, 1825

Order **Caudata** *Scopoli*, 1777

Family **Hynobiidae** *Cope*, 1859

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

Salamandrella sp.

(Figs. 3C)

Localities and material examined. Selety 1A, GIN 951/1001-AM01 – -AM03, 3 trunk and GIN 951/1001-AM04, 1 caudal vertebrae; GIN 951/1001-AM05, 1 extremity bone; Novaya Stanitsa 1A, GIN 948/2001-AM01 – -AM11, 11 trunk 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 trunk vertebrae; Lezhanka 2B, GIN 1130/2001-AM01, 1 trunk vertebra, GIN 1130/2001-AM02, 1 extremity bone; Olkhovka 1B, GIN 1111/2001-AM01, 1 trunk vertebra; Iskakovka 2A, GIN 1131/2001-AM01, 1 trunk vertebra; Andreievka – Speransko, GIN 1112/1001-AM01, 1 trunk vertebra; Lezhanka 1, GIN 1129/1001-AM01 – -AM02, 2 trunk and GIN 1129/1001-AM02, 1 caudal vertebra~~e~~; Beteke 1C, GIN 945/3001-AM01 – -AM02, 2 trunk vertebrae.

Description and comments. The vertebrae have an elongated to nearly slender form. The vertebra centrum is amphicoelous. A pair of subcentral foramina is situated at the basis of the transverse processes. The neural arch is tall in lateral view and relatively broad in dorsal view. The posterior edge of pterygapophysis is bifur~~a~~cated. Sometimes the neural spine is presen~~ce~~, but generally, the dorsal surface of the neural arch is plane. The pre- and postzygapophyses have elongate 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 small sizes of vertebrae with amphicoelous centrum; circular articular surfaces; neural spine, lacking notch on the posterior margin of neural arch; fused rib-bearers. Further, features characteristic for the genus *Salamandrella*: absence of the subcentral foramen; concave anterior margin of neural arch which reaches the middle part of prezygapophyseal articular facets (*Syromyatkova*, 2014), can be found on the vertebrae. 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.

Insert here Figure 3

Family **Cryptobranchidae** *Fitzinger*, 1826

Cryptobranchidae indet.

(Figs. 3A, 3B)

Localities and material examined. Pavlodar 1A (=Gusini Perelet), 1 fragmentary right dentary and 2 fragments of jaw bones, detail about the stratigraphic allocation see section ‘Cyptobranchidae’, unnr. PIN specimen.

Description and comments. Among the fragments a posteriodorsal portion of a large right dentary, 27 mm in length is present. In lingual view, the pars dentalis composes 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 concave surface, ventrally this surface possess a ridge, running parallel to the lamina horzontalis. The cross section of the dentary shows relatively low portion of cancellous bone and 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 for giant salamanders (*Vasilyan* et al., 2013).

Family **Proteidae** *Gray*, 1825

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

Mioproteus sp.

(Figs. 3D-3F)

Localities and material examined. Ryzhaya II (known also Ryzhaya Sopka), GNM unnr. specimen, 2 trunk vertebrae; Malyi Kalkaman 2, GIN 1107/2001-AM01, 1 right maxilla; Borki 1A, GIN 1115/1001-AM01, 1 trunk vertebra; Ayakoz, GNM unnr. specimen, 1 trunk vertebra; Akespe, unnr. HC specimens, 3 vertebrae; Petropavlovsk 1/2, GNM unnr. specimen, 22 vertebrae.

Description. The preserved left maxilla is fragmentary (Fig. 3F), the posterior process is broken off. In ventral view, the bone has rough surface. The pars dentalis of the maxilla is located at the anterior side of the bone. The crowns of pleurodont teeth are missing, only their pedicellar portions are present. 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 rising. The amphicoelous vertebrae are flat and wide. The centrum is dumb-bell in shape and narrows to the center. Two subcentral foramina are present at the central part of the vertebra 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 not forked posteriorly. 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 maxilla of the genus *Mioproteus* reported previously is impossible, due to lack or extremely scarce description of the skull elements attributed to *Mioproteus* in the publications (e.g. *Estes & Darevsky*, 1977; *Miklas*, 2002). Hence, we used unpublished material of *Mioproteus* sp. from the locality Grytsiv (Ukraine, earliest Late Miocene) (Fig. 3G) for the taxonomic identification of the fossil maxilla from Malyi Kalkaman 2 (Fig. 3F). Our comparison shows no differences in the maxilla 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 amphicolous centrum; (2) cranial margin of the neural arch is tall; (3) distinct wide depression at the anterior base of the transverse process (*Estes & Darevsky*, 1977; *Ivanov*, 2008).

Family **Salamandridae** *Goldfuss*, 1820

Subfamily **Pleurodelinae** *Tschudi*, 1838

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

Chelotriton sp.

(Figs. 3H, 3I)

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

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

The neural spine is tall and long, nearly as long as the vertebra 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 neural canal, has a triangular form. The roof of the neural canal, laterally on the both sides of the spine is plane.

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, 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 before and below the level of the diapophysis, due to which the transverse process becomes 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. 3H) is fragmentary preserved, the neural arch and left transverse process are lacking. The centrum is compact, short and wide. It possesses an elliptical central foramina. 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 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 for the first trunk vertebrae.

Comparison and comments. Earlier this vertebra has been described in Tleuberdina et al. (*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 also known in other salamanders, e.g. Recent species of *Tylototriton*, *Echinotriton*, *Cynops pyrrhogaster*, and *Lissotrit~~urus~~ boscai* (unnr. GPIT specimen), *Paramesotriton* (MNCN 23557, 13645), as well as fossil taxa *Archeotriton* (*Böhme*, 1998), aff. *Tylototriton* sp. (loc. Baikadam, this paper). The vertebra from the Malyi Kalkaman 1 resembles species of *Chelotriton*, *Paramesotriton*, *Tylototriton*, *Echinotriton,* and *Cynops pyrrhogaster* in 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* and *Cynops*); a longer neural spine with a 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 with the shape of massive rib-bearers and large dimensions (*Ivanov*, 2008) to this group too. It shows identical morphology of vertebra to *Chelotriton* sp., type II described from Mokrá-Western Quarry, 2/2003 Reptile Joint (Early Miocene, Czech Republic) (*Ivanov*, 2008).

The abundant European Cenozoic record of the genus showed (*Böhme*, 2008) that the vertebral morphology is insufficient for taxonomic identification as *Chelotriton* and most probably the genus has 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.

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

(Figs. 4A, 4B)

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

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 (same with dorsal wall of vertebrae centrum) canal is flat. In lateral view, the centrum is curved dorsally. The neural spine was most probably high, but does not reach the level of the pustular structure of the neural spine. 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 the neural spine was most probably bifurcated. The length of the neural spine without the 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 connection between the anterior bases of both prezygapophyses with the vertebra centrum. The posterolaterally directed transverse process is horizontally flattened and shows a bicapitate articulation surfaces with a rip. The diapophysis and parapophysis are widely 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 anterior (accessory alar process) and posterior (posterior alar process and dorsal lamina) laminar edges. The strait, 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 vertebra 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.

Comparison and comments. The vertebrae resemble morphology of pleurodeline salamanders *Echinotriton*, *Tylototriton*, *Cynops*, *Chelotriton* and *Paramesotriton* (for collection references see subsection 'Comparison' of *Chelotriton* sp., this paper) in characteristics such as: (1) presence of rugosities on the neural arch; (2) prezygapophysis and parapophysis connected with the accessory alar process, beside *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. The vertebrae with their general morphology resemble mainly the genus *Tylototriton*. Beside the similarities, the described salamander remains 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) lacking of a ridge connecting diapophysis with centrum; (7) a low and shallow posterior notch of the neural arch; (8) it differs from *Cynops* in having accessory alar process which reaches the parapophysis, contrary to *Cynops* where 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 differences of the vertebrae with other genera, we suggest that they belong to a new pleurodeline salamander genus, showing affinities with the genus *Tylototriton*. Based on present vertebra material we do not consider reasonable to describe a new form, unless cranial material of this salamander is available.

Insert here Figure 4

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

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

Palaeobatrachidae sp. indet.

(Fig. 5A)

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

Description. A very robust sphenethmoid lacks the posterior part. Two anterior cavities (antrum olfactorium) are shallower anteroposteriorlly, the posterior cavity (antrum pro lobo olfactorio) is deep and narrow. The olfactory foramen is larger than the orbitonasal one. The processus rostralis is elongate 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 (contact with the frontoparietal) shows a slightly striated surface. The lateral processes protrude laterally. The lamina supraorbitalis are 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. On the ventral face of the sphenethmoid from Novaya Stanitsa 1A, a narrow and long depression corresponds to the contact area with the cultriform process of the parasphenoid (parasphenoid facet).

Comparison and comments. The bone has strong similarities to palaeobatrachids. This group is characterized by: (1) a long sphenethmoid with frontoparietal fenestra more than half length of bone; (2) in ventral view, the articulation area of the parasphenoid is 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 beside the short septum nasi, which is long in the fossil bone. We presume that the frontoparietal fenestra was more than the 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.

Insert here Figure 5

Family **Bombinatoridae** *Gray*, 1825

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

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

(Figs. 6A, 6B)

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 ~~of~~ is based on the ilium from Selety 1A, since the specimens from the localities Malyi Kalkaman 1 and Cherkal are strongly damaged. In lateral view, the iliac shaft is almost straight and lacking 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 slighly constricted, the ventral base of the corpus ossi possesses a preacetabular fossa. The ventral ridge of 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 vexilium, a weakly developed tuber superior is characteristic for the genus *Bombina* (*Böhme*, 1977). The ilium differs from *Bombina orientalis* by weaker developed tuber superior. The ilium from Selety 1A distinguishes from *Bombina variegata* and resembles *Bombina bombina* in having: (1) a developed pars descendes; (2) a posteroventral ridge of the pars descendes projecting ventrally rather than posteriorly (*Böhme*, 1977); (3) a developed preacetabular fossa (*Sanchíz & Młynarski*, 1979). However, due to the absence of the well-preserved material of the fire-bellied toads from Selety 1A, we tentatively assign the bone to *Bombina bombina*. The specific assignment of the ilia from Malyi Kalkaman 2 and Cherlak is impossible due to their fragmentary preservation, thus we describe them as *Bombina* sp.

Insert here Figure 6

Family **Pelobatidae** *Bonaparte*, 1850

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

Pelobates sp.

(Fig. 6C)

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 composes a larger lower and a smaller upper portions. Between these portions a well-developed interiliac tubercle is visible. The lower portion is ventroposteriorlly oblique, whereas the upper one is flat, less rugose and has 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 absence of a dorsal crest and dorsal tubercle, presence of an oblique spiral groove on the dorsal surface (*Roček* et al., 2014). The bone shows following characters of the genus *Pelobates*: (1) high and long pars ascendes; (2) well-developed spiral groove (*Böhme*, 2010); (3) lack of the dorsal crest of the iliac shaft (*Folie* et al., 2013), 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.

Family **Hylidae** *Rafinesque*, 1815

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

Hyla savignyi *Audouin*, 1827

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

(Figs. 6D, 6E)

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 sca~~lupa~~, 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 a 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 above the anterior corner of the acetabulum. The preserved iliac shaft is nearly cylindric 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.

Comparison and comments. The Siberian fossil tree frog differs from already described fossil and some recent species of the genus *Hyla*. 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* (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 arbor~~ae~~* (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 a low and broad processus gleinoidalis. The Recent *H. savignyi* is the only tree frog showing a fossa supragleinoidalis like the studied remains. The Recent *H. savignyi* possesses also some similarity to fossil tree frog in having a slender junctura ilioischiadica, the same position of the tuber superior, comparable acetabular tubers and 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 interiliac facet; whereas *H. savigyni* has: (1) a dorsally and laterally significantly prominent tuber superior; (2) a shallow and small fossa supragleinoidalis; (3) the interiliac facet devoid 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), resembles a similar morphology of ilium with Siberian fossil in orientation of the tuber superior and in the form of the junctura ilioischiadica. 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*.

Family **Bufonidae** *Gray*, 1825

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

Bufo bufo (*Linnaeus*, 1758)

(Figs. 6F-6I)

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 trunk 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 trunk vertebra; Olkhovka 1C, GIN 1111/3001-AM01, 1 left scapula, GIN 1111/3001-AM02, 1 trunk 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 trunk vertebrae; Isakovka 1B, GIN 1131/3001-AM01, 1 left ilium; Isakovka 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 trunk 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 b~~oar~~d 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 ~~e~~scendens. The ventral edge of the pars descendens is thin and lamelliform. The preacetabular fossa is absent. In posterior view, the anterolateral edge of acetabular is strongly curved; the junctura ilioischiadica shows a higher acetabular ventral tuber than 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 from 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 pars acromialis is nearly straight, the wall is thin.

In several localities, isolated large sized frog vertebrae and urostyle (Figs. 6H, 6I) in association with (e.g. Olkhovka 1C) or without (e.g. Pehsniovo 3) diagnostic elements (ilia and scapula). They indicate individuals of the same size and according to the size they can be assigned to the large *Bufo bufo*. The morphological traits described above (e.g. lack of angular fossa on scapula and preacetabular fossa on ilium, general outline, form and size of the scapula and ilium) as well as bone dimentions are found in the common toad *Bufo bufo* (*Blain, Gibert & Ferràndez-Cañadell*, 2010).

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

Bufotes viridis *Laurenti*, 1768

(Figs. 6J, 6K)

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 – -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 an uni- or bilabated 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 absence of well-preserved material, we prefer tentatively assignment of 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 for genus *Bufo* morphology, the iliac shaft without the dorsal crest, 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 descentens is ventromedial directed.

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

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

Pelophylax sp.

(Figs. 6L, 6M)

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

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

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

(Figs. 6N, 6O)

Localities and material examined. 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; Ayakoz, unnr. HC specimens, numerous 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 ilium of *Pelophylax* sp., is low. The tuber superior projects dorsolaterally, the pars descendens medially. The middle portion of two scapulae, without proximal parts of 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.

Comments. The ilia and scapulae morphology strongly resembles that of the brown frogs (*Böhme*, 1977). Due to fragmentary preservation of the bone material, any precise taxonomic identification of frogs from nearly all localities is impossible. The comparison with recent species (e.g. *Rana temporaria* (unnr. GPIT specimen), *Rana dal~~am~~tina* (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 rather with European and Western Asiatic species than with Eastern Asiatic brown frogs.

Only the locality Malyi Kalkaman 1 provides adequate material for specific identification. The ilia and scapulae from here resemble the recent species *Rana arvalis*, which has the widest distribution among the brown frog in Eurasia. The fossil bones of brown frogs from other Western Siberian localities we describe here as *Rana* sp.

Ranidae indet.

Localities and material examined. Kentyubek, unnr. HC specimens, 2 left ilia.

Class **Reptilia** *Laurenti*, 1768

Order **Squamata** *Oppel*, 1811

Suborder **Gekkota** *Cuvier*, 1817

Family **Gekkonidae** *Gray*, 1825

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

Alsophylax sp.

(Fig. 7)

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 from 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. 7B1, 7D1). Rarely, the cusps of maxilla teeth are posteriorly oriented. The most complete dentary contains at least 17 (in total 20?) teeth, counted by both teeth and their alveoles (Fig. 7B).

Dentaries. The dentary is a slender and elongate bone. In the symphyseal region, the bone is slightly curved medially. The paries ventralis is enlarged, due to which the bone increases in height posteriorly. The dentary is characterized 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, 7B1, 7B2). The Meckelian canal is open posteriorly at about the 15-16th teeth position. The spleneal facet on the dentary – the anterior margin of Meckelian opening, shows a light concave and elongated surface (Figs. 7B, 7C). 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 anterioposterior direction, changing also in form – 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. 7C). 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 lower. Its margin is rounded but not prominent. A shallow and anteriorly extending dental shelf divides lamina horizontalis from the dental lamina (Fig. 7B1). Posteriorly the bone is nearly L-shaped in transverse section. The paries horizontalis is always destroyed in the preserved bone.

The caudal portion of the paries verticalis shows bifurcation (Fig. 7C), which corresponds to the coronoid inseration.

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 posteriorly a small distinct longitudinal groove, running parallel to the lamina horizontalis (Figs. 7D and 7E). 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 expends laterally just under the tip of the lacrimal facet (? = at its midsection) and builds a palatine facet (Figs. 7D and 7E). 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. 7E1). The maxillary lappet is damaged; its base is preserved. The internal wall surface of the maxilla contains few rugosities. Here an anteroposteriorlly 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. 7F2 and 7G2) 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. 7I). 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, maxillae and dentaries bearing numerous pleurodont, isodont, densely packed, cylindrical, and slender monocuspid teeth; medially extended dental shelf of the maxilla; lingually closed Meckelian canal allow the identification as a member of the 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 (a distinct and longer horizontal lamel, reduced symphyseal groove). The Recent genus *Phelsuma* can be excluded from consideration, since these geckos are restricted to the islands of the south-west 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 presence of the prefrontal process, short row of foramina of the trigeminal nerve, which terminates under the prefrontal process. Due to lack of 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). Re-study of the material reveals that the posterior fragment of a right maxilla shows a morphology similar to *Alsophylax* sp. from Cherlak in having a lingual longitudinal groove, absence of foramina at the posterior portion of the bone and a round tooth apex, but it is different with its larger size (Fig. 7J). Taking this into account we tentatively consider the Mynsualmas record as cf. *Alsophylax* sp. Probably, this fossil represents a larger *Alsophylax* species than in Western Siberia.

Insert here Figure 7

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 generalized (*Lacera* sensu lato) and shows very few characteristic features (bone and teeth morphology) of detailed taxonomic assignment (*Böhme*, 2010; *Böhme & Vasilyan*, 2014).

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, 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 increase 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 ventrally with the dorsal margin of the splenial and gradually narrows posteriorly. The articulation surface is exposed lingually. The crista dentalis (sensu Roček (1984)) is not high but is longer than the ventral margin of the lamina horizontalis. The ventral margin of the crista dentalis at its posterior half bears an articulation surface with the ventral margin of the coronoid. A lingually exposed articulation surface of the splenial is located at the posterior portion of the ventral surface of the lamina horizontalis. In labial view, up to eight small foramina are present.

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

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 denteries possess ca. 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 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 lenght, higher and broader anterior portion of the lamina horizontalis, a shorter cirsta dentalis and a lower Meckelian groove.

Insert here Figure 8

Lacerta **s.l. sp.**

Material. 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, the anterior portion of the frontal process a shallow but broad groove is present. The large foramen of the fifth cranial (trigeminal) nerve opens at the ventral surface of the lamina 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 preserved and its comparison between different localities is impossible. 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.

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

Eremias sp.

(Fig. 8C)

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

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 like 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.

In lateral view, a single preserved vertebra has a rectangular form. 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 posteriorly builds a rounded process, projecting over the posterior margin of the arch. The centrum is compressed anteroposteriorlly and possesses two shallow subcentral grooves with a subcentral foramina in each. The condylus 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 robust frontal, better pronounced grooves at the anteroventral bone surface, lack of the lateral extension of the prefrontal facet; (2) *Acanthodactylus* by a flat posterioventral bone surface, a less curved outline in lateral view. The preserved single vertebra resembles strongly morphology found in *Eremias* (*Rage*, 1976).

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.

Order **Testudines** *Linnaeus*, 1758

Suborder **Cryptodira** *Cope*, 1868

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

Genus ***E~~ym~~doidea*** *Gray*, 1870[2]

Emydoidea sp.

(Figs. 8D, 8E)

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 of a width of 54.3 mm is preserved (Fig. 8D). Probably it belongs to a middle size individual with a total length of the

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

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 4 (medially from the bridge) to 7.2 mm (behind the bridge). 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 from the hypoplastron fragment is found. The bone is slender and bent (Fig. 8E). 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 reconstructed total body-sizes from both elements (ca. 30 cm), we consider the remains to belong to one taxon of the genus *Emydoidea*.

Testudines indet.

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 taxonomic interpretation.

DISCUSSION

Neogene evolution of amphibian and reptile assemblages in Western Siberia

In general, amphibian and reptile faunas from the Neogene of Asia are very little known, while the European record is well-studied. This is mainly caused on one hand by less explored Neogene deposits from the Asian Continent, which are not extensively studied, on another hand, although small mammals were studied intensely by many scholars, the amphibians and reptile remains retained entirely unstudied. The Western Siberian localities provide an exceptional opportunity to fill the lack of these studies and to explore both the unknown diversity of Asian herpetofaunal assemblages and the palaeobiogeographic affinities of 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 careful. The unbiased comparison and analysis of our data is also hindered by scarce record of the Asian Neogene fossil faunas. For the comparison with the European record we used already published data on amphibian and reptile groups (families, genus, species etc.) summarized in the fosFARbase database (*Böhme & Ilg*, 2003). These data are given in the Suppl. 5. As 'Europe' record, we consider all known fossil records from Western, Central and Eastern Europe as well as 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.

Insert here Figure 9

Hynobiidae

The asiatic salamanders (*Salamandrella* sp.) have the most abundant and frequent record among studied Western Siberian localities. They appear here at 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.

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

In Central Europe, hynobiids (genus *Parahynobius*) appear at the terminal Middle Miocene and are present until Early Pleistocene (*Venczel*, 1999a, 1999b; *Venczel & Hír*, 2013). 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 coincides both with Central European and Western Siberian records of hynobiids, which most probably was a time characterised with favourable conditions for their distribution. Taking into account their oldest records, most probably their origin is in the early Miocene of Eastern Asia. Detailed study on Cenozoic record of fossil Hynobiidae including 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 overlaying 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 originate from the basal horizon of the Pavlodar Svita, overlaying the ‘Aral clays’ = limnic clays of the Kalkaman Svita. In *Gaiduchenko* (1984) and *Gaiduchenko & Chkhikvadze* (1985) a giant salamander (Cryptobranchidae indet.) has been mentioned from a locality named Detskaya Zheleznaja Doroga (engl. Children Railway) (Fig. 2, Suppl. 1, Suppl. 3) – a sand pit located 10 km south-east from the ‘Gusini Perelet’ [=Pavlodar 1A]. The age of the of the fossilizerous horizon may be near the Miocene-Pliocene boundary, more on geology, age and accompanying fauna see in Suppl. 2. 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, Suppl. 1) (*Chkhikvadze*, 1984; *Böhme, Vasilyan &*

Winklhofer, 2012). The remains are assigned by Chkhikvadze (*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, Suppl. 1). In the Middle Miocene, they occur in several localities in southern Russia and northern Kazakhstan (Suppl. 1). 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 lack of complete fossil skeletons and unclear taxonomic assignments of the fossil records, preferred to refer all known specimen of *Mioproteus* to the '*Mioproteus caucasicus* complex', including *Mioproteus* from Ashut, Kazakhstan, *M*. *caucasicus* from type locality, as well as from the Late Miocene of Czech Republic, *M*. *wezei* from the Pliocene of Poland and Lower Pleistocene of Moldavia (*Malakhov*, 2003). Later on, *Roček* (2005) considered *M*. *wezei* as a junior synonym of *M*. *caucasicus*. However, as mentioned already by *Malakhov* (2003), an adequate material including cranial and postcranial elements is necessary to solve the taxonomic problems of the genus. *Malakhov* (2003) suggested also an Asiatic origin for the '*Mioproteus caucasicus* complex' and their later distribution into Europe. To sum up, the oldest Late Oligocene record of *Mioproteus* (*Mioproteus* sp.) from Akespe, Kazakhstan and other localities of younger age suggest that: (1) their probable Asian origin of the genus; (2) it was continuously present in Central Asia / Western Siberia until early Pliocene; and (3) in the Early Miocene they migrated into Europe.

Salamandridae

As already known, *Chelotriton* is a busket taxa (*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) (Suppl. 1), making their Asiatic record older then known.

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), *Tylototriton* (cf. *Tylototriton* sp. and *Tylototriton* sp. nov.) have 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 an 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 reached also Anatolia, where they existed since latest Oligocene 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 characterized by a four-million-year-long (ca. 5.6-9.78 Ma) gap in the palaeobatrachids record in 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, *Böhme & Ilg* (2003)), also in those localities, which are characterized by environment, favourable for their life. After this gap, they occur near the Mio- – Pliocene transition in localities of Italy (Ciabot Cagna (*Cavallo* et al., 1993)) and Hungary (Ostramoc 1C (*Venczel*, 2001)), they disappeared in the Pliocene from Western and Central Europe and are present exclusively in Eastern Europe (Poland – European Russia). Their most east distribution never reached east from the Ural Mountains – the locality Apastovo in Russia (Late Pliocene, (*Wuttke* et al., 2012)), where they occur is still 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, also 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 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 *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 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 (*Bombina* sp.) in the Middle Miocene of Central Europe (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 presented 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, Suppl. 5).

In Western Siberia, they are known from three localities: Malyi Kalkaman 2, Selety 1A, 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 coincides 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 Europe at least from the later part of the Early Miocene, and later in the Middle Miocene, they expanded into Western Asia, reaching east from the Ural Mountains. The Western Siberian fossil *Bombina* can be separated osteologically from a species *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 area eastern from the Ural Mountains in Russia and north Kazakhstan (*Kuzmin*, 1995). The family, showing Laurasian affinities, is known since the Late Cretaceous of North America. From the Early Eocene they appeared in Europe and were present here with a fossil genus *Eopelobates* (Middle Eocene – late Pliocene), as well as 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. from: (1) the localities of the Zaisan Basin from the Upper Aksyr Svita[3], early Priabonian; rare founds in the Kusto Svita and basal horizon of Buran Svita[4], late Priabonian and earliest Rupelian; abundant occurrence in the Buran Svita[5], early Rupelian; (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, due to the lack of the description and illustrations of the material as well as access to it, was not possible. Nevertheless, taking into account the Paleogene fossil records we infer that spadefoot toads might dispers from Europe to Western

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

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

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

Asia during the Late Eocene – Early Oligocene. Whether *Pelobates* sp. from the Selety 1A (late Tortonian, Miocene) is a European or Asian migrant can not be clearly asserted.

Hylidae

The family of tree frogs Hylidae has wide distribution in Eurasia and is represented by a monophyletic genus *Hyla*. The most recent phylogenetic study of the genus *Hyla* by *Li* et al. (2015) recognized in Eurasia two closely related clades West Palaearctic *arborea*-group and East Palaearctic *chinensis*-group, 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 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, Central Europe and Balkan) + *H. orientalis* (Southeastern Europe, Georgia, Armenia, Iran) have wide distribution 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, 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 arbor~~ae~~* (*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 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 of 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 fossil record of the tree frogs, we conclude that in Western Eurasia two large clades split during the Middle Miocene of Europe. Our comparison showed older ages for the first fossil occurrences of these clades than the molecular data of two recent studies (*Gvoždík* et al., 2010; *Li* et al., 2015) estimated. Thus, *Gvoždík* et al. (2010)[6] suggested split of *H*. *orientalis/arborea* and *H*. *savignyi* at 11.1 Ma (early Late Miocene, early Tortonian), which is ca. three million years younger than the first fossil occurrence of *H*. cf. *arborea* (Suppl. 5). 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, the interpretation on 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 following distribution pattern for West Palaearctic *arborea*-group: entering Eurasia from the East via Beringian from the North America in the Paleogene, 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 here; apparently, the Western Siberian Late Miocene and Early Pliocene records represent the most east expansion of the European genus, when the climatic conditions were still favourable for their distribution; it is conceivably for us that the *H*. *savignyi*

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[6] 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.

may have potentially uncovered fossil occurrences in the Miocene of Eastern Europe and/or south from the Caucasus.

Bufonidae

Two groups of toads are found in the studied Western Siberian localities the common (*Bufo bufo*) and green (*Bufotes* cf. *viridis*) toads (Suppl. 1, Figs. 7F-7K). The toads of both groups are the most frequent elements with abundant occurrences among frogs of fossil localities.

Common toads. *Bufo bufo* is a Recent species with the widest (Central, Southern, Eastern Europe and Western and Eastern Asia) distribution 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 western group of the genus, having their near relatives – the eastern group *Bufo 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 found 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 again 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* are yielded from a Late Pliocene (3.0-3.8 Ma) age locality Apastovo, 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. (*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 South into Eastern Europe. Most probably in these areas, theye were present permanently until present times. Lack of their fossil record in the Late Pliocene and Quaternary sites can be explaned by sampling bias. Although those two species do not occur sympatricly nowadays, in two Middle Pleistocene localities Koziy Ovrag and Yablonovets from Russia (see more in Suppl. 5) 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 Europe via Anatolia). Indeed, the works did not consider entire fossil record (including the oldest record of the groups from the Middle Miocene of Slovakia (*Hodrova*, 1980)) of the species group for both calibration of the molecular clock and palaeogeographic considerations, thus update 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 group ancestors. Although for the calibration of molecular clock not the entire fossil record of the group has been used, the results on mtDNA sequence seems to provide reliable data on evolutionary rates within the *Bufo bufo* species group, which can be proved by first appearances of the fossils related to the each of 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 recognized 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 taxonomic identification are established (*Blain, Gibert & Ferràndez-Cañadell*, 2010), hence no precise specific assignment of any fossil material is possible. As Blain et al. (*Blain, Gibert & Ferràndez-Cañadell*, 2010) showed until the most recent past (1.1-1.3 Ma, Early Pleistocene) green toads were also present in the Iberian Peninsula and as suggested became extinct due to climatic changes and/or competition. In studied Western Siberian localities, 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 (Suppl. 1). In the youngest localities (Olkhovka 1A, Lebiazhie 1A, Lebiazhie 1B), they are found as the sole taxon. Further fossils assigned to the family Bufonidae (Bufonidae indet.) are reported already 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 an early Early Miocene (20.4-22.5 Ma, Aquitanian) locality Ayakoz, north-eastern Kazakhstan (Fig. 1, Suppl. 1). *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 in 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 probable, loc. Córcoles (17-18 Ma), Spain (*Sanchíz*, 1998a). Once they entered Europe, they became regular element of the European Neogene and Quaternary herpetofaunal assemblages (Fig. 9). Beside *Bufotes* (aff.) *viridis* European record includes another species *Bufotes priscus* from four localities of latest Early Miocene to earliest Late Miocene age (see Suppl. 5). Taken together *B. viridis* Neogene records and bufonid record from the Eurasian Paleogene, we suggest that the group arriving the Old World in the Paleocene (*Rage*, 2003), entered Central Asia in the Early Oligocene and diversified. 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 Kazakhian Early Oligocene record to green toads seems most probable. Apparently, the Early Oligocene forms were ancestral for the *Bufotes viridis* lineage evolved in Central Asian in the Early Miocene. This assumption is also supported by molecular data suggesting that: (1) green toad clade diversification in Asia during the Oligocene/early Miocene and (2) high genomic and specific diversity found within the Central Asian green toads (*Stöck* et al., 2006). Present in the Central Asian fossil record since the Early Miocene, they dispersed consequently via Anatolia in the early Burdigalian into Europe in the middle Budigalian. 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 indicating 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 stratrigraphically well-dated localities; (2) exploring the Miocene record of Anatolian and South-eastern Europe as well as 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.

Ranidae

The family of true frogs Ranidae are ~~re~~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 then the brown frogs. Both frog genera are common amphibians in the Recent herpetofauna of the area. Beside this record, further true frog (Ranidae indet.) finds are reported from early Rupelian age fossil sites (see section 'Pelobatidae') of the Buran Svita, Zaisan Basin, which taxonomic validity we are not able to revise due to unfigured fossils and inaccessibility of the material.

Green frogs. The genus *Rana* includes 21 Recent species of aquatic frogs having wide distribution ranging from northern Africa, Europe to Eastern Asia. Two genetically distinct clades Western Palaearctic and Far East are recognized within green frogs *Pelophylax*

(*Lymberakis* et al., 2007). The oldest green frog found (*Pelophylax* sp.) in the Western Siberian record is dated by the late Middle Miocene, coinciding stratigraphically with the Eastern Siberian record of green frogs (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 fragmentary preservation of the studied bones as well as lack of other informative elements of skeleton (e.g. frontoparietals), any assignment to the recent green frog species is impossible. Though considering the present distribution of two green frog clades, 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 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 (Suppl. 5). 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 spit from the sister Far East clade in the Eocene;

diversify in the territory of Europe and/or Western Asia in Oligocene; dispersed 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)) comprise more than 15 species distributed over the Eurasia. Similar to green frogs, among brown frog species two lineages the Western and Eastern Palaearctic are known (*Veith, Kosuch & Vences*, 2003). Based on osteological characters, the studied Western Siberian brown frog remains can be related to the Western Asiatic lineage of the genus *Rana*. Among the late Paleogene and Early Miocene frog fossils (*Böhme & Ilg*, 2003), which generic identification is unclear (*Rana* vel *Pelophylax*), only the frog remain from Dietrichsberg, Germany, Early Miocene (*Böhme*, 2001)) have been definitely referred to the brown frogs *Rana* cf. *temporaria*, representing the oldest fossil of the group known so far. As suggested already by *Böhme* (2001) brown frogs migrated to Europe from the possible centre of origin in Western or Central Asia during the second half of the Early Miocene. The brown frog finds from an Aquitanian age locality Ayakoz in Kazakhstan, which is stratigraphically older then the Dietrichsberg frog, confirms this hypothesis. Further arguments for the Asiatic origin of the brown frogs is their present-day biogeography and diversity: presence of a distinct Eastern Palaearctic lineage in Eastern Asia and 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 via Anatolia into Europe 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 arvalis*, representing herewith the oldest fossil record of the species. Previously the earliest form close to *R. arvalis* was considered from the late Pliocene of Slovakia (*Hodrová*, 1981). *R. arvalis* has the widest distribution among the brown frogs, reaching in the east the territory of Eastern Siberia and overlaps with the areas of the Eastern and Western Palaearctic brown frog species (*Kuzmin*, 1995). The fossil record of the species accords with the results of the molecular analysis, suggesting also an Asiatic origin of the species and their later dispersal into Europe (*Babik* et al., 2004).

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 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 better understanding of relationships between these groups, as well as revealing the origin and palaeobiogeographic history of the groups, it will be interesting to revises the Paleocene record of frogs finds (Ranidae indet.) reported from the early Rupelian fossil sites (see section ‘Pelobatidae’) of the Buran Svita, Zaisan Basin (*Chkhikvadze*, 1998). This was not possible to do in the present work, due to lack of figures of the fossils and inaccessibility of the material.

Gekkonidae

The family Gekkonidae is present in 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 4 degrees north of their present occurrence, suggests a shift of 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 in the present but also in the past.

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.

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* (*Chkhikvadze*, 1980); loc. Pantishara (8.7-9.2 Ma), Georgia (*Chkhikvadze*, 2003)). The Siberian record indicates their occurrence in Asia also during the Late Miocene, which is located interestingly much north then their Middle Miocene record form 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 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 summarized 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 with aquatic 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 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 the tortoises since the late Late Miocene in Western Siberia and in 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. The last chelonids present in Western Siberia (since late Late Miocene) are emydid and chelydrid aquatic turtles, indicating not necessarily only 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 themal buffer) in comparison to tortoises, and consequently are able to populate higher poleward latitudes.

Insert here Table 2

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.

Our analysis suggests a (Western) Asiatic origin for Hynobiidae, Proteidae, aff. *Tylototriton*, *Bufotes viridis* species group and brown frogs *Rana*, including *R*. *arvalis.* The green toads and brown frogs dispersed coincidentally in the earliest Miocene, and at least for *Bufotes viridis* group Anatolia was involved. Anatolia played also an important role in 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 the both Asian and European Continents are necessary.

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. Beside amphibians, some West Siberian reptiles like glass lizards and snakes from the Middle Miocene, show European affinities, resembling the Central European faunas (*Vasilyan, Böhme & Klembara*, accepted).

The amphibian genera *Bombina*, *Hyla*, *Bufo*, *Rana* and *Pelophylax* resemble a comparable (palaeo-) biogeographic pattern: molecular genetic data showed 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 Europe (see Fig. 9, Suppl. 5). To explain this common pattern, we hypothesise that western and eastern clades split already in the Paleogene, most probably in the western or central parts of Asia, and subsequently dispersed into Europe.

The Western Siberian fossil *Mioproteus*, *Chelotriton*, *Bombina*, Paleobatidae, *Hyla*, *Bufo bufo* and *Rana arvalis* represent the most east Eurasian records of those groups found in the 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) stays unclear. Considering the geographic location of the fossil site, its relation to the Recent genus *Pelobates* seems most possible.

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 a climate of the Sarybulak Svita (early late Miocene) by a mean annual temperature (MAP) of not less than 14.8 °C (*Böhme*, 2003).

In summary, Western Siberia (Central Asia) can be hypothesized 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 arvalis*. The Neogene herpetofauna of Western Siberia and adjacent areas has significant similarities with the European amphibian and reptile assemblages. Western Palaearctic elements from Europe entered gradually the Siberian territory across Middle Miocene to Early Pliocene, shaping strongly the herpetofauna of Western Siberia, and retaining partially 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*, able to survive in less favourable environments and form the main part of the Western Siberian present-day herpetofauna, are present in the Pliocene fossil record.

Palaeobiogeographic analysis of the recent amphibian faunas of the Western Asia (*Savage*, 1973; *Garcia-Porta* et al., 2012) hypothesizes 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 progressive change of environmental conditions – climate and vegetation, during the Miocene (*Arkhipov* et al., 2005). Along Early to Late Miocene warm and humid climate has been replaces by 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)

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 (Suppl. 4). 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 and well-documented herpetofaunal assemblages are necessary from those deposits for further environmental reconstructions.

For a better palaeoclimatic understanding we estimate palaeoprecipitation values for 12 data point – those localities, which provide six and more amphibian and reptile taxa, applicable for the bioclimatic analysis (*Böhme* et al., 2006). Even so, our data do not enable to reconstruct in high temporal coverage the climate development over Middle Miocene to earliest Pleistocene in Western Siberia. Thus, climate development only for several short intervals can be reconstructed and discussed. Nevertheless, our estimations show rather dynamic climate development in the Neogene of Western Siberia with large amplitudes ranging from 158 to over 1.500 mm per year (Suppl. 1, Fig, 10) than estimated using palynological data (*Arkhipov* et al., 2005). Apart from the fluctuating character of humidity, in general mean annual precipitation (MAP) is significantly above the present day values (reaching 550 % of the present-day values). Only two localities are characterised by drier climates, at the late Serravallian (ca. 12.1 Ma) and the late Messinian (5.9 Ma), having present-day or below present-day levels.

Insert here Figure 10

Reliability of precipitation estimates

The accuracy of precipitation estimates based on bioclimatic analysis of herpetofauna (*Böhme* et al., 2006) depend primarily on taxon counts and the assumption of low (stochastic) taphonomic bias. For West Siberia we document some cases were a rich aquatic herpetofauna, e.g. with freshwater turtles, giant salamanders, proteids, etc. is present, but small terrestrial forms (e.g. lizards, anguids, etc.) are lacking, indicating 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 – humity relation is calibrated, see detailed in Böhme et al. (*Böhme* et al., 2006)). In these cases we restrict our estimates to a limit of 1.500 mm.

Aquitanian

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

Akzhar Svita

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

Late Serravallian

In contrast to already known climate development suggested by Arkhipov *et al.* (2005), our data point to a strong humidity fluctuations within in 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 compare to our Malyi Kalkaman 2 results (MAP 884 mm).

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 however give lower estimates (400-450 mm; Arkhipov *et al.* 2005).

Rytov Svita

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

Miocene-Pliocene transition (Detskaya Shelzna Daroga)

Even though the precise taxonomic identification of the Western Siberian and Zaisan cryptobranchids is unclear at the generic or species level, their occurrences indicate a high rainfall > 900 mm MAP (*Böhme, Vasilyan & Winklhofer*, 2012) during the Burdigalian in the Zaisan Basin and the Miocene-Pliocene transition of Western Siberia. Beside 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 of Western Siberia.

Earliest Pliocene (Olkhovka 1A-1C)

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), which indicate 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 from more then 40 Western Siberian localities ranging from the Middle Miocene to Pleistocene (Suppl. 1). The late Middle Miocene localities have the most diverse faunas including all major groups of herpetofauna. According to our analysis, the fauna contains taxa showing an Asian (Eastern Palaearctic) origin Hynobiidae, Proteidae, *Bufotes viridis* species group and *Rana* (including *R. arvalis*), *Varanus* and Agamidae. The main part of the herpetofaunal assemblage, including Palaeobatrachidae, Paleobatidae, genera *Chelotriton*, *Bombina* (i.e. *Bombina* (cf.) *bombina*), *Hyla* (i.e. *Hyla* (cf.) *savignyi*), *Pelophylax* ?, *Bufo bufo* species group, *Ophisaurus* sp. (*Vasilyan, Böhme & Klembara*, accepted) has European (Western Palaearctic) affinities. The Western Siberian records of *Mioproteus*, *Chelotriton*, *Bombina*, Paleobatidae, *Hyla*, *Bufo bufo* and *Rana arvalis* represent the most east Eurasian records of these groups. 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 this scope, it will be important to study in the future in detail the Neogene record of the amphibian and reptiles faunas in Anatolia and regard them in the palaeobiogeographic context. According to our study, the precipitation development in Western Siberia shows high-amplitude changes during the studied intervals. Aside from certain time-periods (late Seravalian, late Messinian), the palaeorainfall in Western Siberia was significantly above the present-day values. The best data with stratigraphic and climate data we are able to reconstruct for time period 6.6 to ~4.5 Ma. They show: a humid climate during early Messinian; a dry climate during late Messinian; a very humid climate during Miocene-Pliocene transition; and humid climate during the earliest Pliocene (Suppl. 4, 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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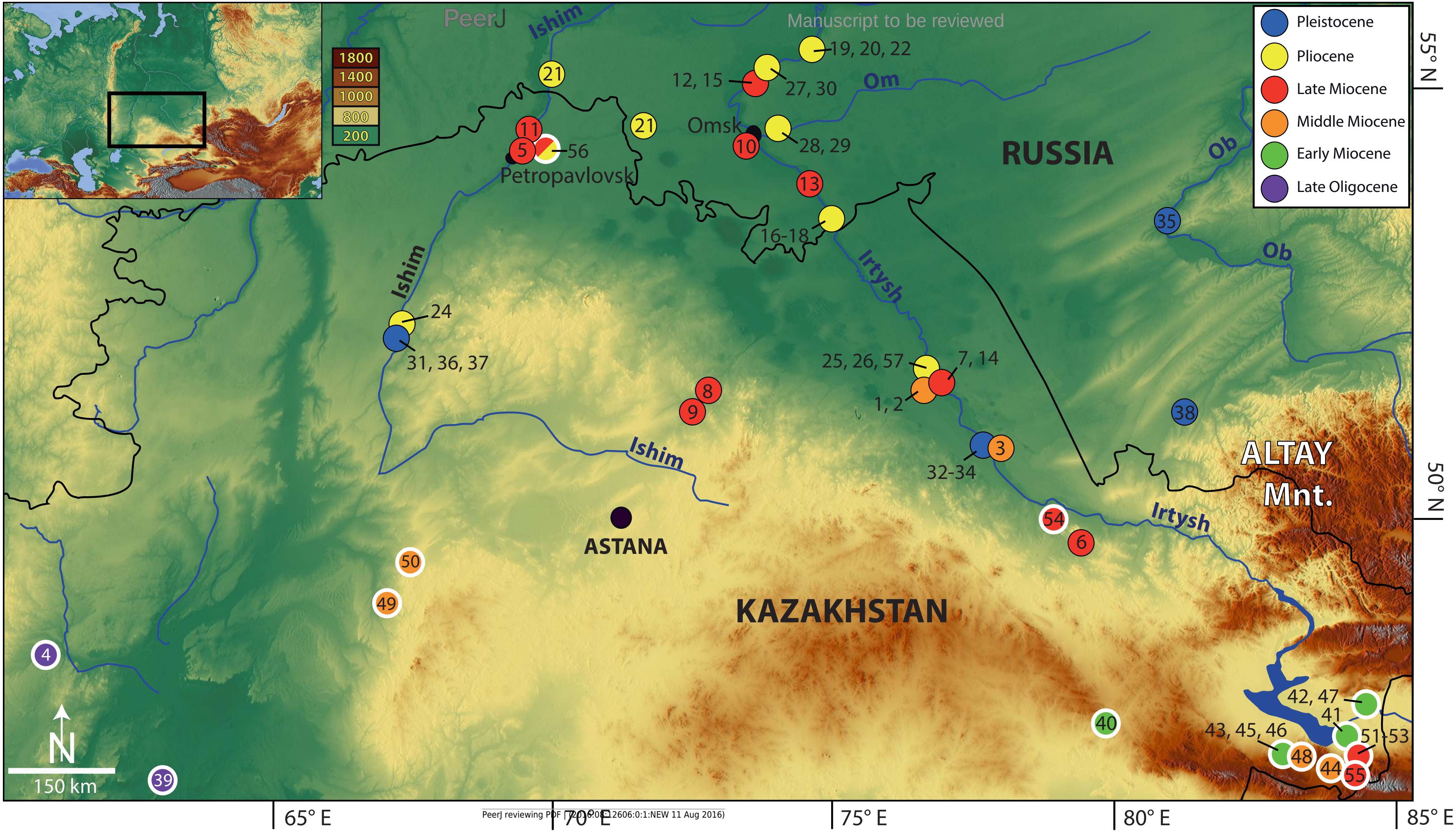
Figure 1(on next page)

Map showing location of Western Siberian studied fossil sites (1-37; black–thin outlined circles) as well as localities known from literature (38-49; white – thick outlined circles).

1, Baikadam; 2, Malyi Kalkaman 2; 3, Malyi Kalkaman 1; 4, Shet-Irgyz 1; 5, Petropavlovsk 1; 6, Znamenka; 7, Pavlodar 1A; 8, Selety 1A; 9, Kedey; 10, Novaya Stanitsa 1A; 11, Borki 1A; 12, Lezhanka 2A; 13, Cherlak; 14, Pavlodar 1B; 15, Lezhanka 2B; 16, Olkhovka 1A; 17, Olkhovka 1B; 18, Olkhovka 1C; 19, Iskakovka 2A; 20, Isakovka 1A; 21, Peshniovo 3; 22, Isakovka 1B; 23, Kamyshlovo; 24, Beteke 1B; 25, Pavlodar 2B; 26, Pavlodar 3A; 27, Lezhanka 1; 28, Andreievka-Speransko; 29, Andreievka 1; 30, Livenka; 31, Beteke 1C; 32, Lebiazhie 1A; 33, Lebiazhie 1B; 34, Podpusk 1; 35, Beteke 2; 36, Beteke 4; 37, Kamen-na-Obi; 38, Razdole; 39, Akespe; 40, Ayakoz; 41, Golubye Peski; 42, Zmei Gorynych; 43, Vympel; 44, Poltinik; 45, Zaezd; 46, Tri Bogatyrja; 47, Kaymanovaja cherepakha; 48, Ryzhaya II; 49, Kentyubek; 50, Ashut; 51, Point “Y”; 52, Sarybulak Svita; 53, Kalmakpai Svita; 54, Karabastuz; 55, Kalmakpai; 56, Petropavlovsk 1/2; 57, Detskaya zheleznaja doroga. Map data © 2016 Google.


Pleistocene
Pliocene
Late Miocene
Middle Miocene
Early Miocene
Late Oligocene
1800
1400
1000
800
200
Ishim
Om
Ob
Irtysh
RUSSIA
KAZAKHSTAN
ALTAY Mnt.
Omsk
Petropavlovsk
ASTANA
19, 20, 22
12, 15
27, 30
21
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28, 29
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16-18
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25, 26, 57
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150 km
55° N
50° N
65° E
70° E
75° E
80° E
85° E

Figure 2(on next page)

Compiled stratigraphy of the Middle Miocene – Early Pleistocene studied localities in Western Siberia grouped in the svitas and relative to their geographic positions.

The localities without assignment into a certain svita are given in coloured (according to age) frames In the right column the small mammalian biochronologic data (species or lineages) used for age estimations are given, the numbers accompanying the species refer the locality numbers. The arrows left from the small mammal taxa indicates its/their first appearance. Abbreviations: klm – Kalkaman, ish – Ishim, pv – Pavlodar, kd – Kedey, nst – Novaya Stanitsa, rt – Rytov, is – Isakov, psh – Peshnev, krt – Krutogor, bt – Betekey, liv – Levetin, irt – Irtysh, kar – Karagash.

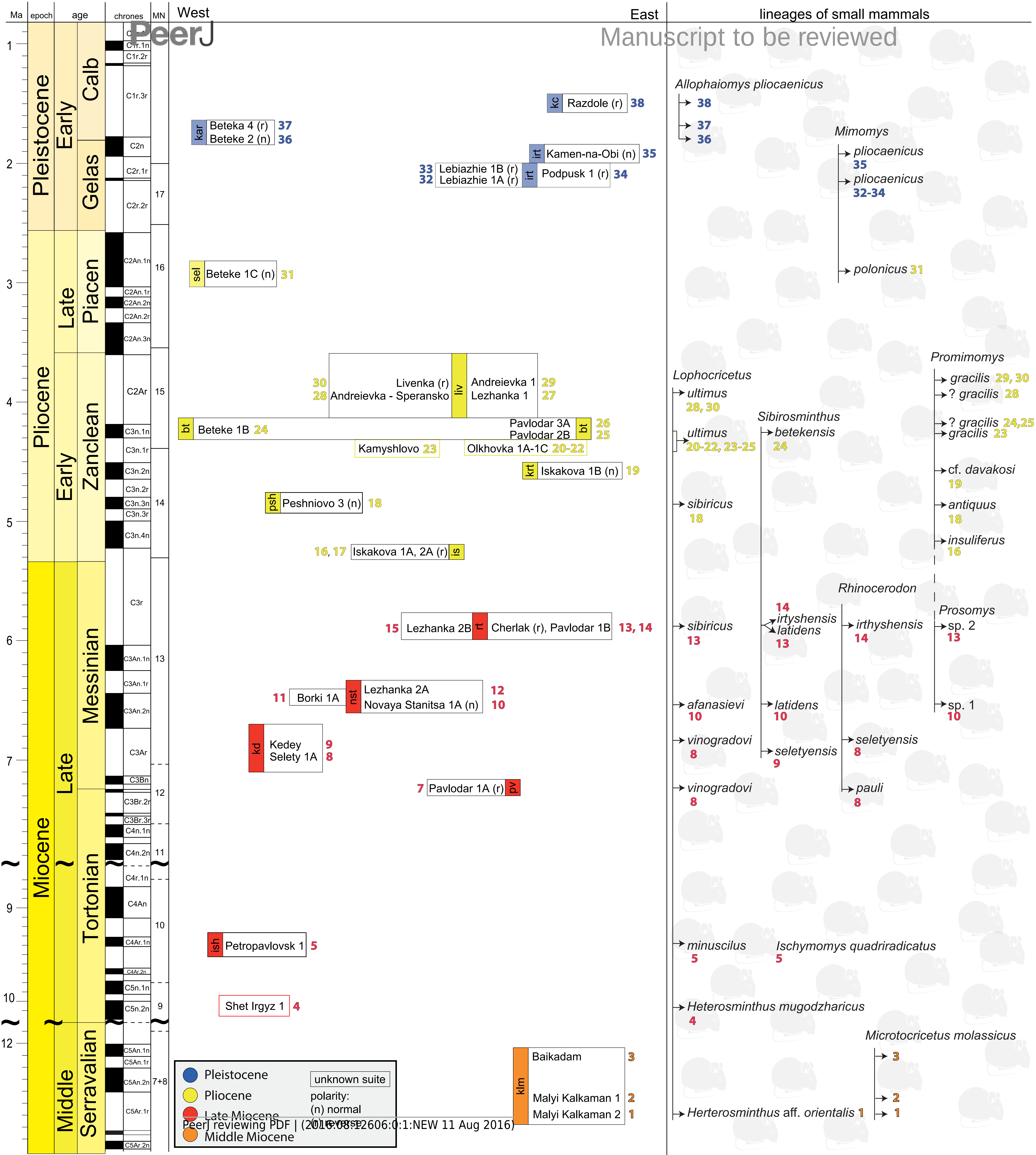
Ma
epoch
age
chrones
MN
West
East
lineages of small mammals
Pleistocene
Early
Calb
Gelas
Pliocene
Late
Piacen
Early
Zanclean
Miocene
Late
Messinian
Tortonian
Middle
Serravalian
1
2
3
4
5
6
7
9
10
12
C1r.1n
C1r.2r
C1r.3r
C2n
C2r.1r
C2r.2r
C2An.1n
C2An.1r
C2An.2n
C2An.2r
C2An.3n
C2Ar
C3n.1n
C3n.1r
C3n.2n
C3n.2r
C3n.3n
C3n.3r
C3n.4n
C3r
C3An.1n
C3An.1r
C3An.2n
C3Ar
C3Bn
C3Br.2r
C3Br.3r
C4n.1n
C4n.2n
C4r.1n
C4An
C4Ar.1n
C4Ar.2n
C5n.1n
C5n.2n
C5An.1n
C5An.1r
C5An.2n
C5Ar.1r
C5Ar.2n
17
16
15
14
13
12
11
10
9
7+8
kc Razdole (r) 38
kar Beteka 4 (r) 37
Beteke 2 (n) 36
irt Kamen-na-Obi (n) 35
33 Lebiazhie 1B (r)
32 Lebiazhie 1A (r)
irt Podpusk 1 (r) 34
sel Beteke 1C (n) 31
30 Livenka (r)
28 Andreievka - Speransko
liv
Andreievka 1 29
Lezhanka 1 27
bt Beteke 1B 24
Pavlodar 3A
Pavlodar 2B
bt 26 25
Kamyshlovo 23
Olkhovka 1A-1C 20-22
krt Iskakova 1B (n) 19
psh Peshniovo 3 (n) 18
16, 17 Iskakova 1A, 2A (r) is
15 Lezhanka 2B rt Cherlak (r), Pavlodar 1B 13, 14
11 Borki 1A
nst Lezhanka 2A 12
Novaya Stanitsa 1A (n) 10
kd Kedey 9
Selety 1A 8
7 Pavlodar 1A (r) pv
ish Petropavlovsk 1 5
Shet Irgyz 1 4
klm Baikadam 3
Malyi Kalkaman 1 2
Malyi Kalkaman 2 1
Pleistocene
Pliocene
Late Miocene
Middle Miocene
unknown suite
polarity:
(n) normal
(r) reverse
Allophaiomys pliocaenicus
38
37
36
Mimomys
pliocaenicus
35
pliocaenicus
32-34
polonicus 31
Promimomys
gracilis 29, 30
? gracilis 28
? gracilis 24,25
gracilis 23
cf. davakosi
19
antiquus
18
insuliferus
16
Lophocricetus
ultimus
28, 30
ultimus
20-22, 23-25
sibiricus
18
sibiricus
13
afanasievi
10
vinogradovi
8
vinogradovi
8
minuscilus
5
Sibirosminthus
betekensis
24
14
irtyshensis
latidens
13
latidens
10
seletyensis
9
Rhinocerodon
irthyshensis
14
seletyensis
8
pauli
8
Prosomys
sp. 2
13
sp. 1
10
Ischymomys quadriradicatus
5
Heterosminthus mugodzharicus
4
Microtocricetus molassicus
3
2
1
Herterosminthus aff. orientalis 1

Figure 3

Salamander remains from Western Siberian localities.

A-B, Cryptobranchidae indet. from loc. ? Gusiny Perelet, unnr. PIN specimens; **A1,** fragmentary right dentary, natural cross-section; **A2,** the same dentary, in lingual view; **B,** a jaw fragment, lingual view; **C,** *Salamandrella* sp., Lezhanka 2A, GIN 1130/1001-AM01, trunk vertebra; **D-~~F~~,** *Mioproteus* sp.; **D,** loc. Ayakoz, trunk vertebra, GNM unnr. specimen; **E,** trunk vertebra, Borki 1A, GIN 1115/1001-AM01; **F,** right maxilla, Malyi Kalkaman 2, GIN 1107/2001-AM01; **G,** left maxilla loc. Grytsiv (Ukraine), unnr. MNMHK specimen; **H,** trunk vertebrae of aff. *Chelotriton* sp., loc. Ayakoz, GNM unnr. specimen; **I,** *Chelotriton* sp. from Malyi Kalkaman 2, GNM unnr. specimen; **C1, D1, E1, F1, G1, H1, I,** dorsal view; **C2, D2, E2, F2, G2, H2,** ventral view; **C3, D3, E3, H3,** lateral view; **C4, D4, H4,** anterior view; **D5, H5,** posterior view. Scale bars: A, B = 5 mm; C = 0.5 mm; D, E, F, G, H, I = 1 mm.

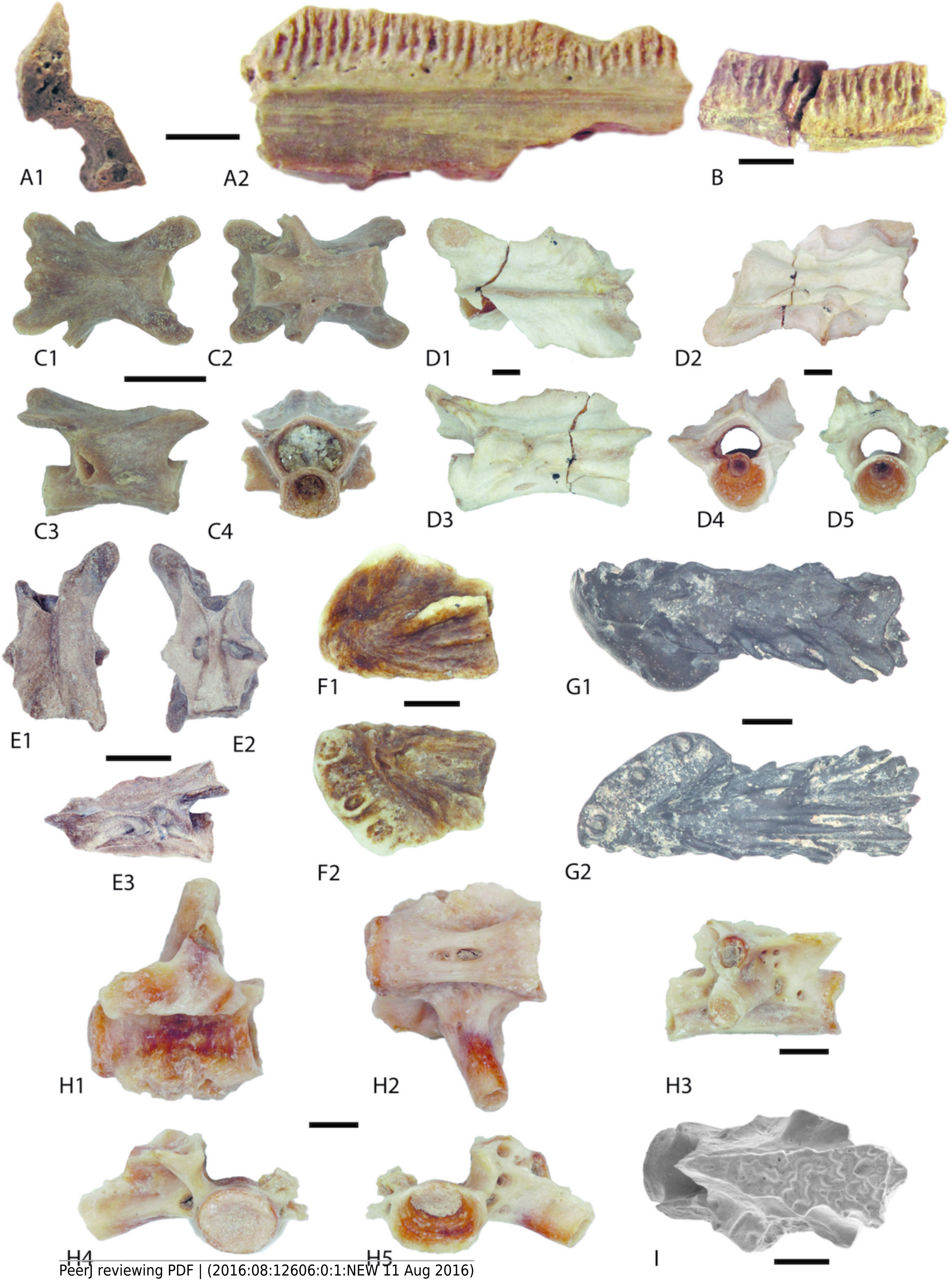
A1
A2
B
C1
C2
D1
D2
C3
C4
D3
D4
D5
E1
E2
F1
G1
E3
F2
G2
H1
H2
H3
H4
H5
I

Figure 4

Trunk vertebrae of *Tylototriton, Echinotriton* and *Cynops*.

A, aff. *Tylototriton* sp., locality Ayakoz, GNM unnr. specimen; **B´,** and **B,** GIN 950/2001-AM14 and GIN 950/2001-AM01, loc. Baikadam; **C,** *Tylototriton verrucosus*, GPIT unnr. specimen; **D,** *Tylototriton shanjing*, GPIT unnr. specimens; **E,** *Echinotriton andersoni*, GPIT unnr. specimen; **F,** *Cynops pyrrhogaster*, GPIT unnr. specimen; **A1-F1,** lateral view; **A2-F2,** dorsal view; **A3-F3,** ventral view; **A4-F4,** anterior view; **A5-F5,** posterior view. Scale bars = 2 mm.

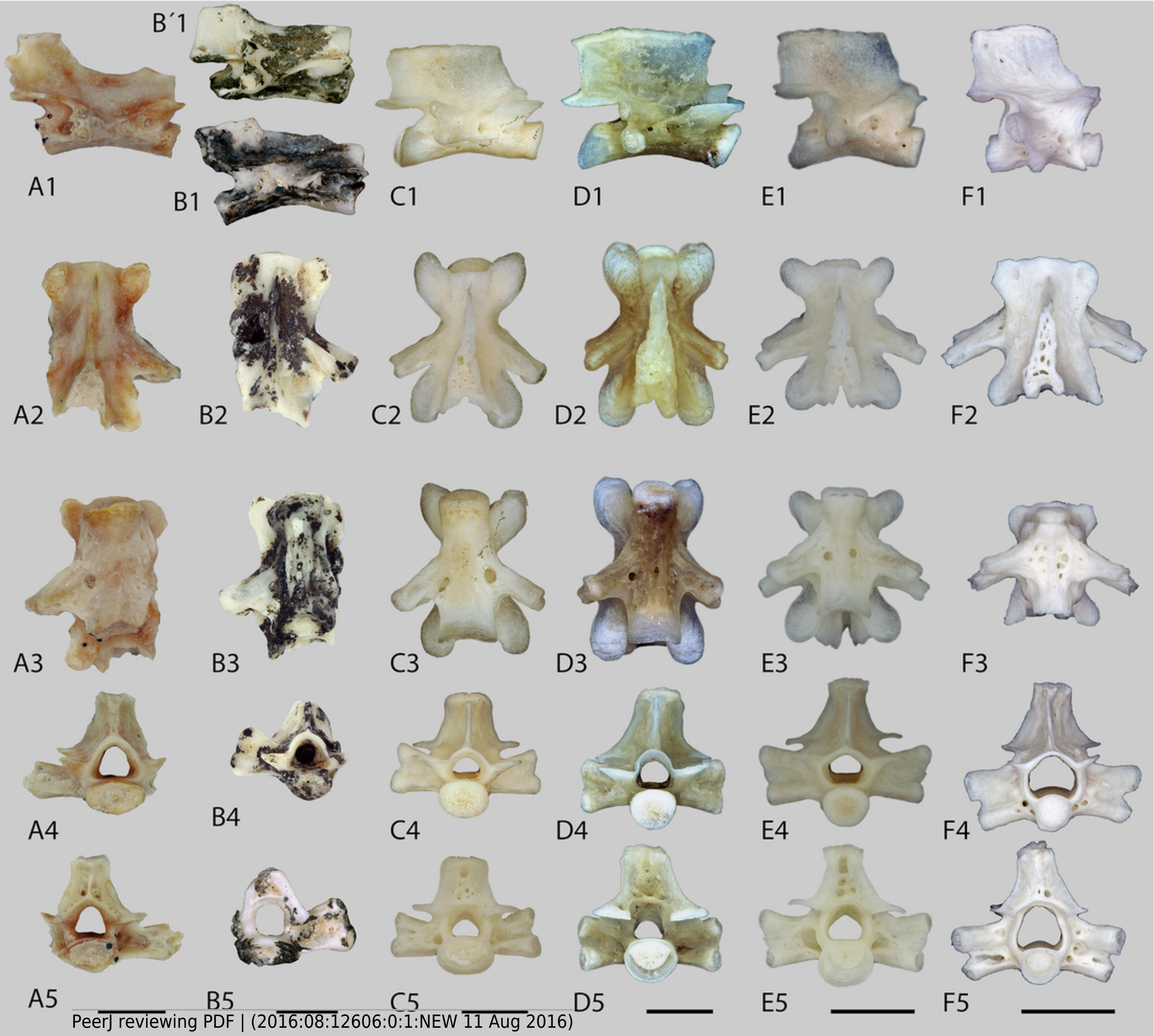

Figure 5

Palaeobatrichid sphenethmoids.

A, Palaeobatrachidae indet., Novaya Stanitsa 1A, GIN 948/2001-AM12; **B,** *Palaeobatrachus* sp. from Grytsiv (Ukraine), unnr. NMNHK specimen; **1,** ventral view; **2,** dorsal view; **3,** anterior view; **4,** lateral view. Abbreviations: ao, antrum olfactorium; alo, antrum pro lobo olfactorio; is, incisura semielliptical; ff, frontoparietal facet; lp, lateral processes; ls, lamina supraorbitalis; nf, nasal facet; onf, orbitonasal foramina; olf, olfactory foramina; pf, parasphenoid facet. Scale equals 1 mm.

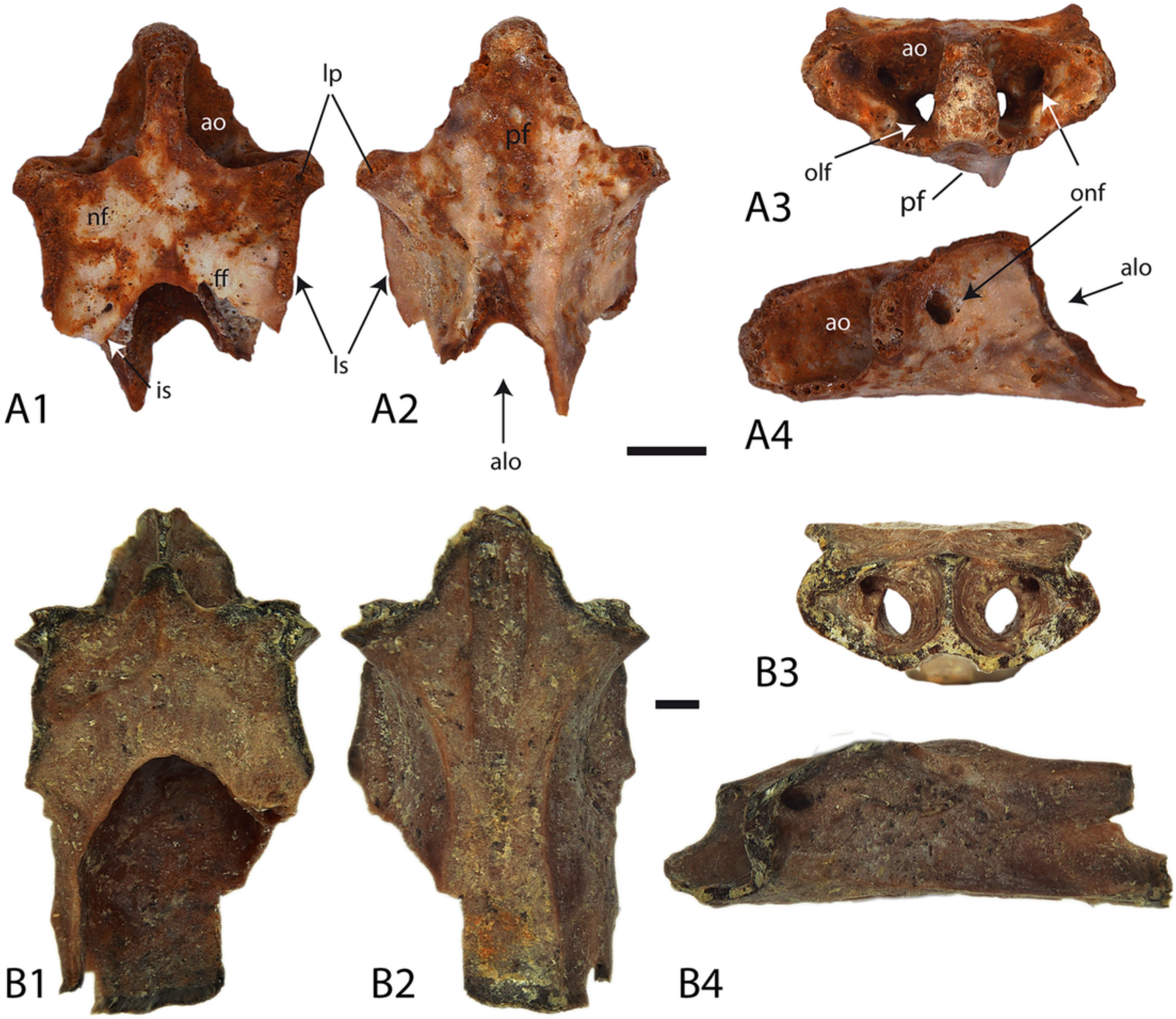
lp
ao
pf
ao
nf
ff
is
ls
onf
olf
pf
alo
ao
alo
A1
A2
A3
A4
B1
B2
B3
B4

Figure 6

Fossil frogs from Western Siberia.

A-D, F, J, L, N, Ilia; **A** *Bombina* cf. *bombina*, Selety 1A, GIN 951/1001-AM06; **B,** *Bombina* sp., Cherlak, GIN 1110/2001-AM13; **C,** *Pelobates* sp., Selety 1A, GIN 951/1001-AM07; **D,** *Hyla* gr. *H*. *savignyi*, Lezhanka 2A, GIN 1130/1001-AM29; **F,** *Bufo bufo*, Olkhovka 1B, GIN 11 11/2001-AM03; **J,** *Bufotes* cf. *viridis*, Pavlodar 1A, GIN 640/5001-AM01; **L,** *Pelophylax* sp., Lezhanka 1, GIN 1129/1001-AM05; **N,** *Rana arvalis*, Malyi Kalkaman 1, GIN 1107/1001-AM10; **A1-D1, F1, J1, L1, N1,** in lateral view; **A2-D2, F2, L2, N2,** in proximal view; **A3-D3, F3, J3, L3, N3,** in medial view; **E, G, K, M, O,** Scapulae of frogs; **E,** *Hyla* gr. *H*. *savignyi* from Lezhanka 2A, GIN 1130/1001-AM33; **G,** *Bufo bufo*, Olkhovka 1C, GIN 1111/3001-AM01; **K,** *Bufotes* cf. *viridis*, Pavlodar 1A, GIN 640/5001-AM63; **M,** *Pelophylax* sp., Lezhanka 1, GIN 1129/1001-AM07; **O,** *Rana arvalis*, Malyi Kalkaman 1, GIN 1107/1001-AM01; **E1, G1, K1, M1, O1,** dorsal view; **E2, G2, K2, M2, O 2,** ventral view; **E3, G3, K3, M3, O3,** posterior view; **H,** trunk vertebra of *Bufo bufo*, Olkhovka 1C, GIN 1111/3001-AM02; **H1,** anterior view; **H2**, lateral view; **I,** urostyle of *Bufo bufo*, Olkhovka 1C, GIN 1111/3001-AM03, dorsal view. The arrows show position of angular fossa. Scale bars: A-F, L-M, O = 1 mm, G-K, N = 2 mm.

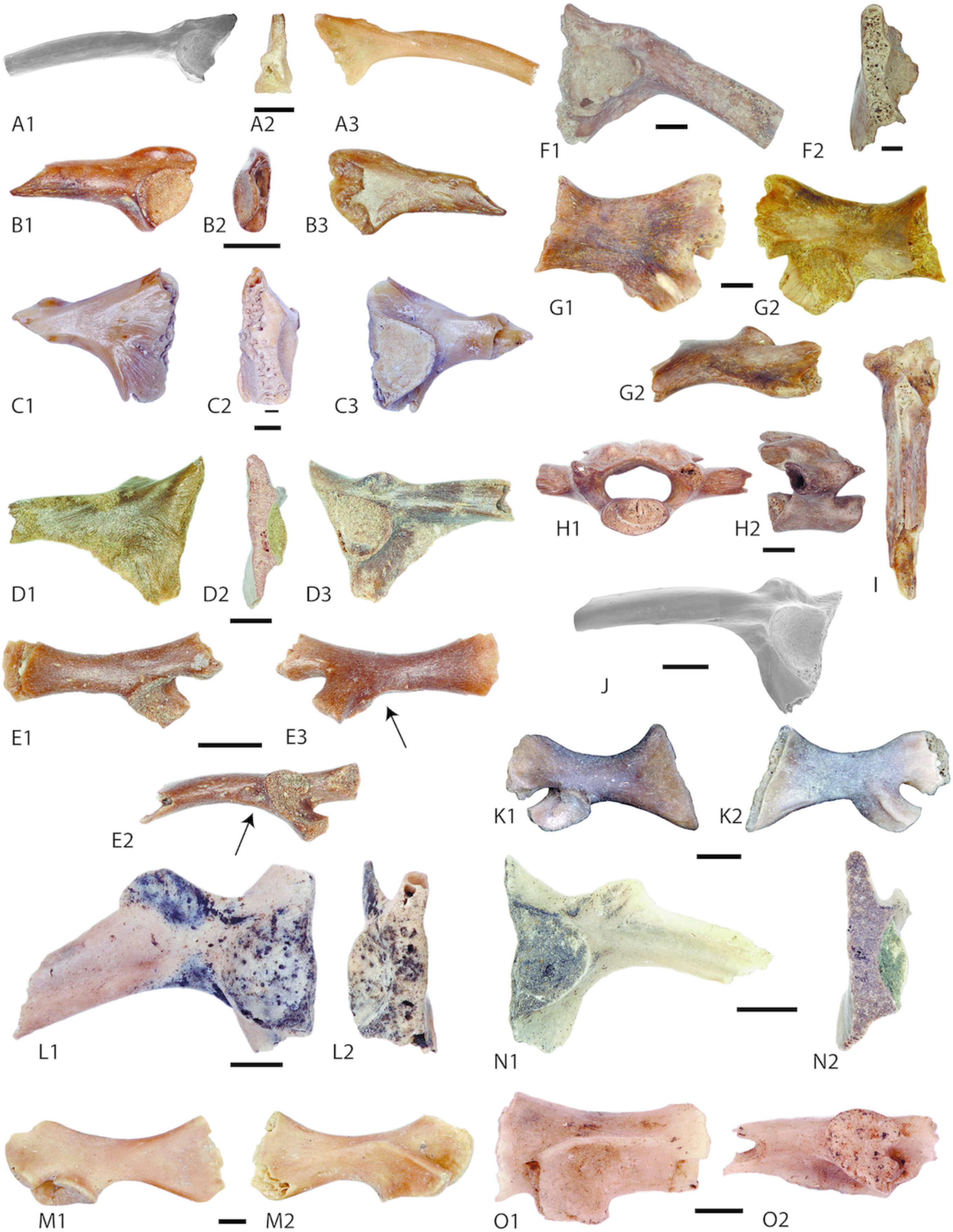
A1
A2
A3
F1
F2
B1
B2
B3
G1
G2
C1
C2
C3
G2
D1
D2
D3
H1
H2
I
E1
E3
J
E2
K1
K2
L1
L2
N1
N2
M1
M2
O1
O2

Figure 7

Alsophylax sp. from locality Cherlak (A-I) and Mynsualmas-MSA 3 (J).

A-C, two left dentaries; **A, B,** left dentary, GIN 1110/2001-RE11; **A,** mirrored labial view; **B,** lingual view; **B1,** symphyseal region in lingual view; **B2,** the same region in ventral view, both display the symphyseal groove; **C,** posterior fragment of left dentary, GIN 1110/2001-RE12, lingual view; **D-H**, five maxillae; **D**, left maxilla, GIN 1110/2001-RE26, lingual view; **E**, right maxilla, GIN 1110/2001-RE40, lingual view; **F,** right, GIN 1110/2001-RE41 and **G,** left maxillae GIN 1110/2001-RE27; **F1, G1,** lingal view; **F2, G2,** labial view; **H,** left maxilla, GIN 1110/2001-RE28, labial view; **I,** cervical vertebra, GIN 1110/2001-RE45; **I1,** anterior view; **I2,** left lateral view; **I3,** posterior view; **J**, right dentary, unnr. GPIT specimen, lingual view. Abbreviations: dl, dental lamina; ds, dental shelf; 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 horzontalis; mc, Meckelian canal; na, neural arch; nc, neural canal; nf, nasal facet; pfc, palatine facet; ph, paries horizontalis; prz, prezygapohysis; psz, postzygapohysis; pv, paries verticalis; pxp, premaxillary process; pyp, pterygapophysis; sac, opening of superior alveolar canal; sg, symphyseal groove; sf, spleneal facet; tpr, transverse process.

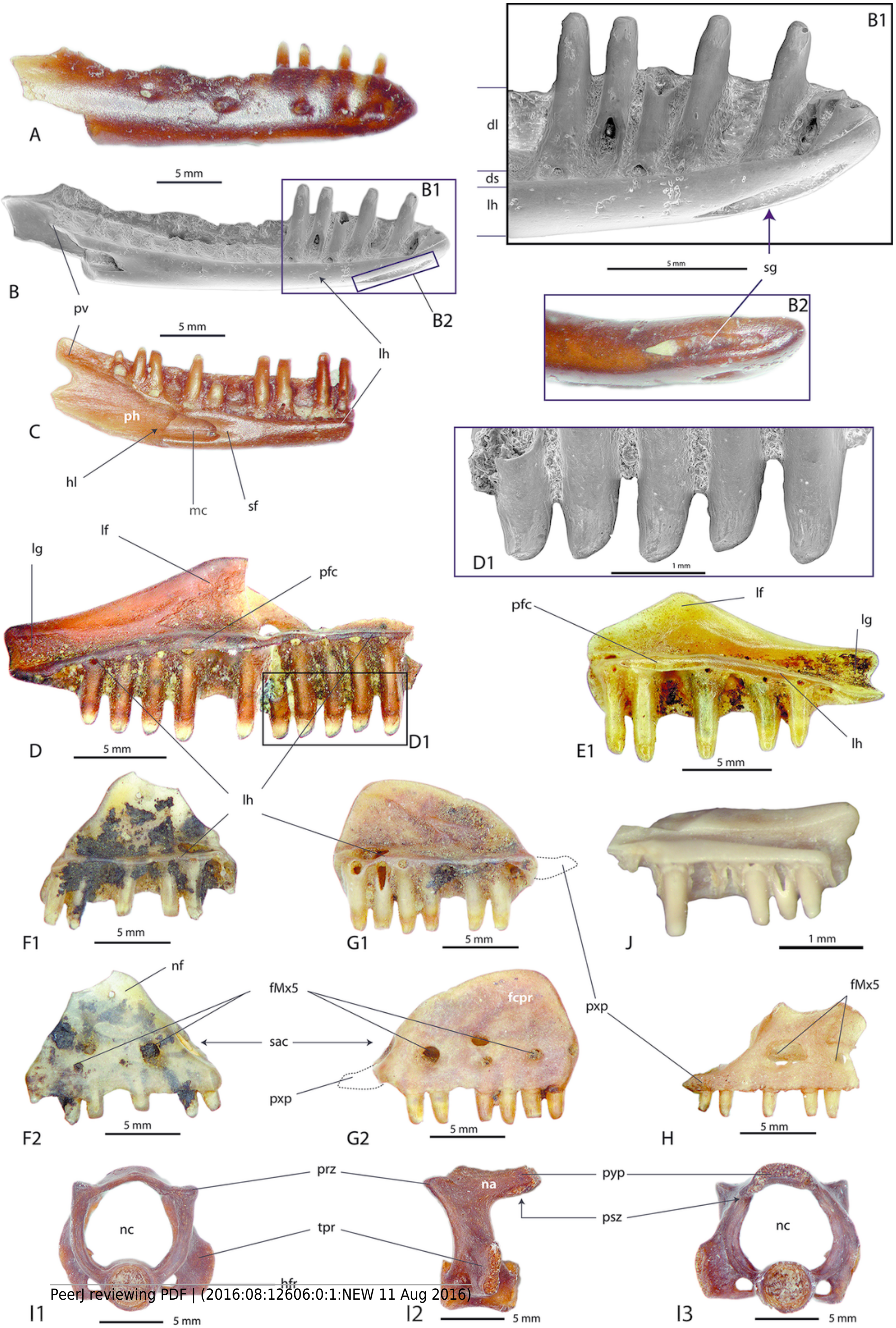
A
5 mm
B
B1
B2
pv
lh
5 mm
C
ph
hl
mc
sf
B1
dl
ds
lh
5 mm
sg
B2
D1
1 mm
lg
lf
pfc
D
5 mm
D1
pfc
lf
lg
lh
E1
5 mm
lh
F1
5 mm
G1
5 mm
J
1 mm
nf
fMx5
sac
pxp
fcpr
pxp
fMx5
F2
5 mm
G2
5 mm
H
5 mm
prz
pyp
na
psz
nc
tpr
nc
hfr
I1
5 mm
I2
5 mm
I3
5 mm

Figure 8

Lizard and turtle remains from the Western Siberian localities.

A, *Lacerta* s.l. sp. 1, left dentary, Pavlodar 1A, GIN 640/5001-RE01, lingual view; **B,** *Lacerta* s.l. sp. 2, right dentary, Pavlodar 1A, GIN 640/5001-RE34, lingual view; **C,** *Eremias* sp., frontal, Pavlodar 2B, GIN 1108/2001-RE01; **C1,** dorsal view; **C2,** ventral views; **D,** *Emydoidea* sp., fragment of right hypoplastron, GIN 948/2001-RE01, ventral view; **E,** *Emydoidea* sp., left femur, GIN 948/2001-RE02; **E1** cranial view; **E2,** ventral view. Scale bars: A, C = 2 mm; B = 1 mm; D, E = 1 cm.

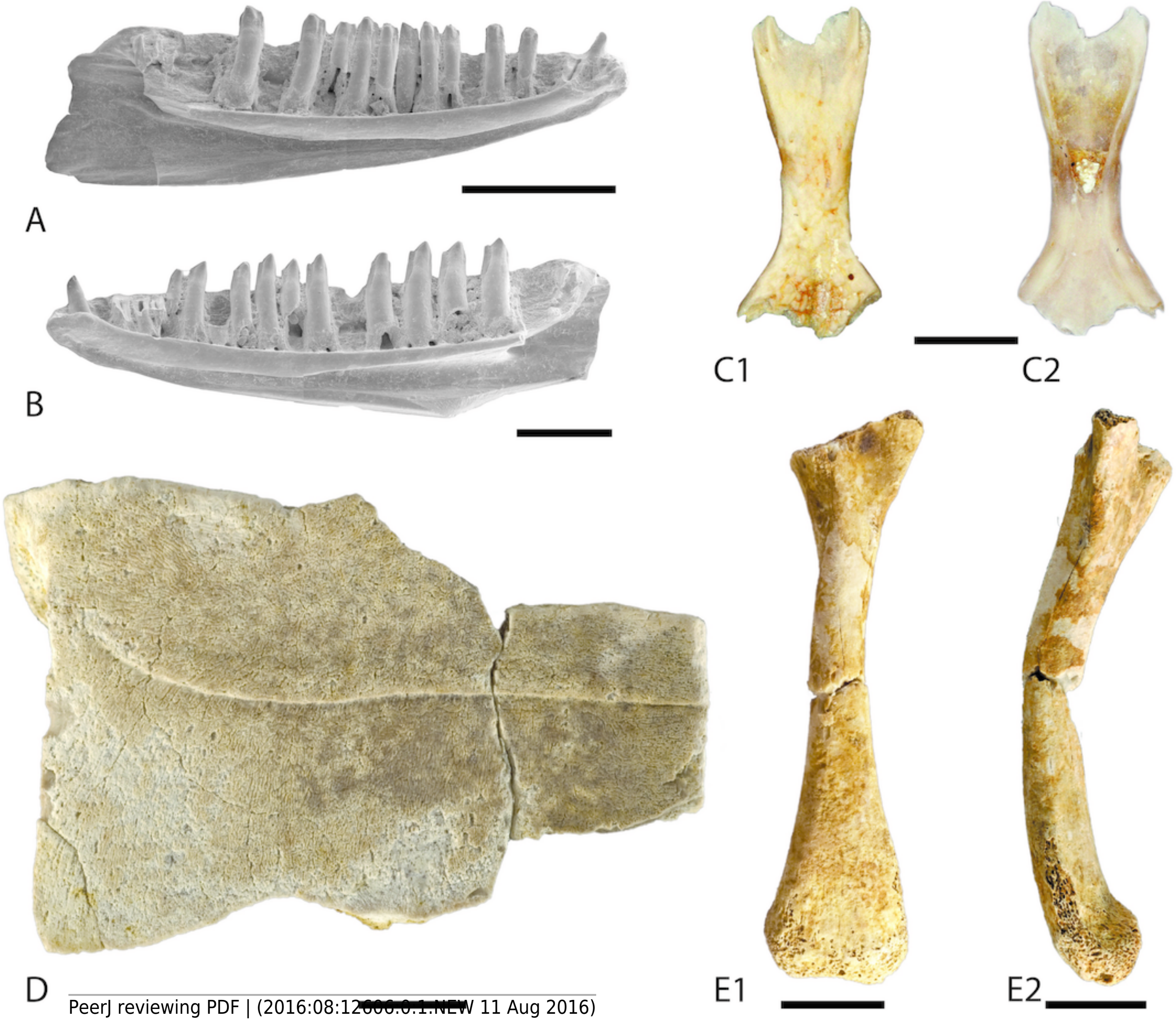

Figure 9(on next page)

The European (Suppl. 5) and Western Siberian (present study) Neogene fossil record of the studied amphibian groups.

Detailed list of the localities see the Additional file 3 and for the family Cryptobranchidae – Böhme *et al.* (2012; table 1). The occurrences of each group in Europe and Western Siberia are given in the same colour. The Paleogene records of the groups are indicated with arrows. Abbrevations: Hyn, Hynobiidae; Cry, Cryptobranchidae; Prot, Proteidae; Chel, *Chelotriton*; Tylt, *Tylototriton*; Bomb, *Bombina*; red balk, *Bombina* (cf.) *variegata*; black balk, *Bombina* (cf.) *bombina*; Palbr, Palaeobatrachidae; Pelb, Pelobatidae; Hyla, *Hyla*; white balk, *Hyla* (cf.) *arborea*; Bbuf, *Bufo bufo* (group); Bvir, *Bufotes* (cf.) *viridis* / group of *Bufotes viridis*; Rana, *Rana* (cf.) *temoraria*; Pelx, *Pelophylax*.

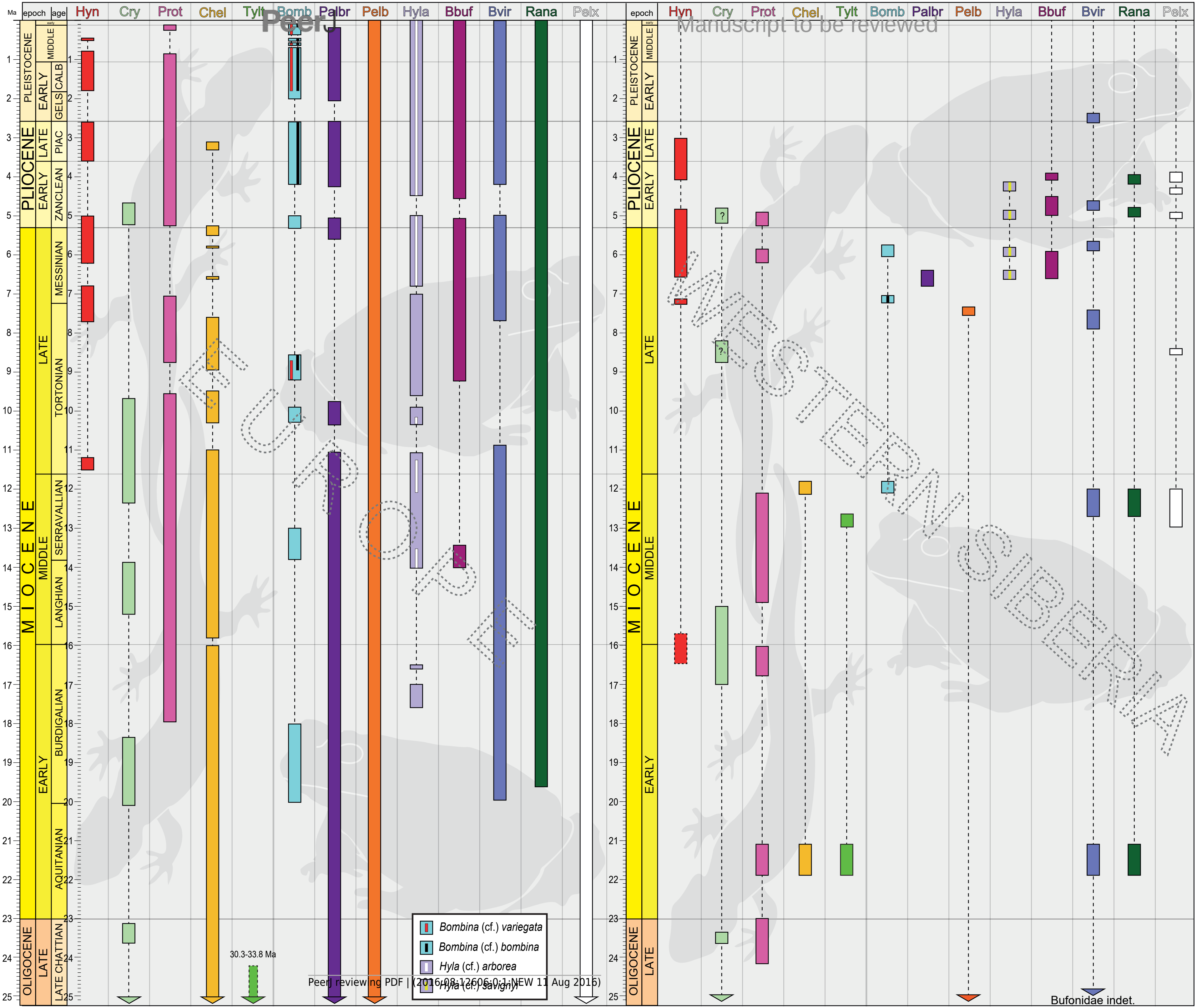
Ma
epoch
age
Hyn
Cry
Prot
Chel
Tylt
Bomb
Palbr
Pelb
Hyla
Bbuf
Bvir
Rana
Pelx
PLEISTOCENE
PLIOCENE
MIOCENE
OLIGOCENE
early
MIDDLE
EARLY
LATE
CALB
GELS
PIAC
ZANCLEAN
MESSINIAN
TORTONIAN
SERRAVALLIAN
LANGHIAN
BURDIGALIAN
AQUITANIAN
CHATTIAN
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
EUROPE
WESTERN SIBERIA
30.3-33.8 Ma
?
Bombina (cf.) variegata
Bombina (cf.) bombina
Hyla (cf.) arborea
Hyla (cf.) savignyi
Bufonidae indet.

Figure 10(on next page)

Palaeoprecipiation development of Western Siberia including the Zaisan Basin.

A, curve displaying the development of the absolute values of mean annual precipitation (MAP); **B,** the ratio of MAP to recent precipitation value (MAP/MAP$_{recent}$100%), dashed black line (100 %) indicates the recent precipitation values. Localities: 1, Ayakoz; 2, Vympel; 3, Poltinik; 4, Tri Bogatyrja; 5, Kentyubek; 6, Malyi Kalkaman 2; 7, Malyi Kalkaman 1; 8, Baikadam; 9, Novaya Stanitsa 1A; 10, Cherlak; 11, Detskaya zheleznaya doroga; 12, Olkhovka 1B.

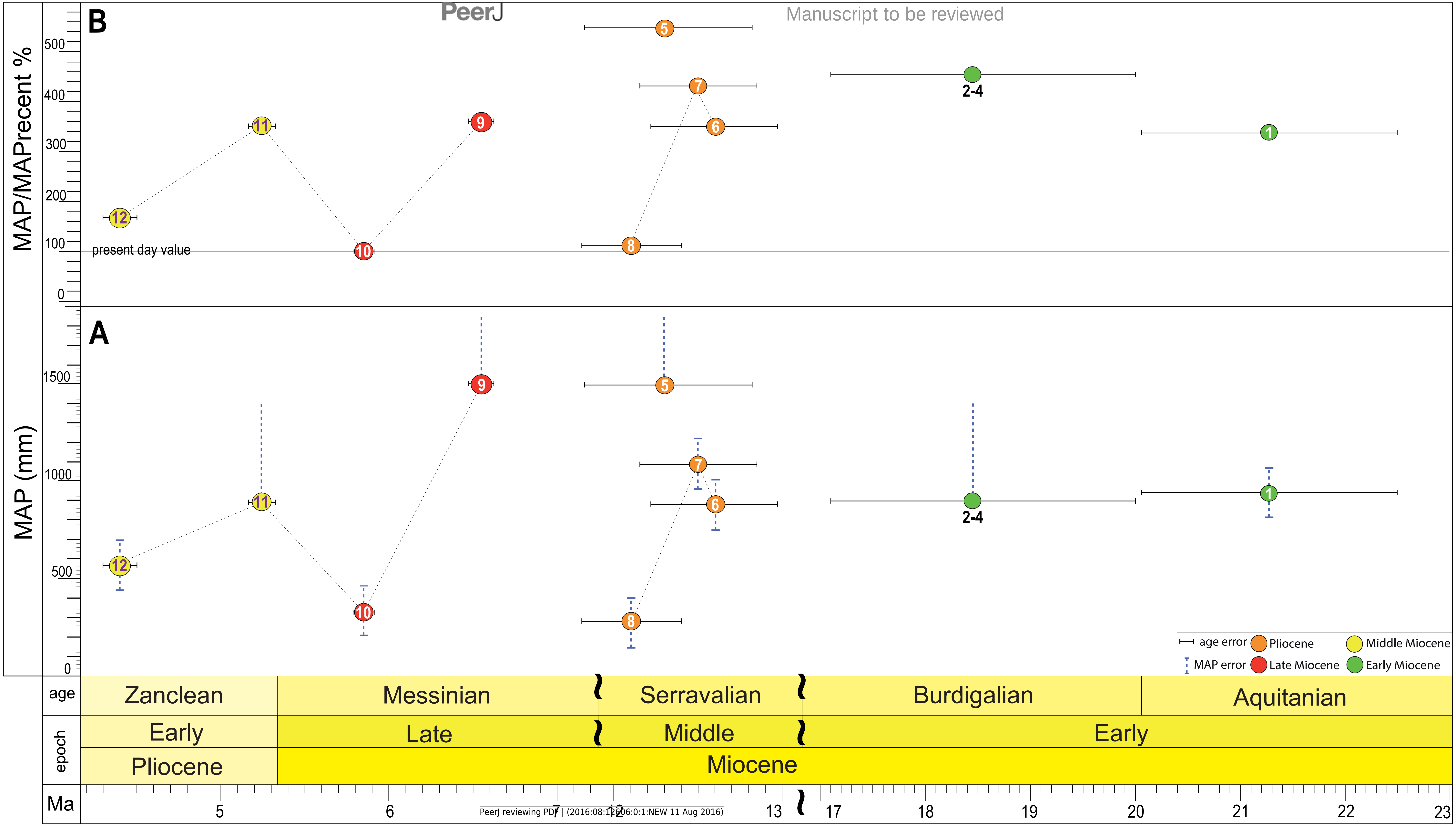
B
MAP/MAPrecent %
500
400
300
200
100
0
present day value
5
7
6
2-4
1
11
9
12
10
8
A
MAP (mm)
1500
1000
500
0
9
5
7
6
2-4
1
11
12
10
8
age error
MAP error
Pliocene
Late Miocene
Middle Miocene
Early Miocene
age
Zanclean
Messinian
Serravalian
Burdigalian
Aquitanian
epoch
Early
Late
Middle
Early
Pliocene
Miocene
Ma
5
6
7
12
13
17
18
19
20
21
22
23

Table 1(on next page)

Recent herpetofauna of south-western part of Siberia (Ob and Irtysh River drainages) according to different authors.

References: 1 - *Kuzmin* (1995) ; 2 - *Borkin* (1999) ; 3 - *Ravkin, Bogomolova & Chesnokova* (2010) ; 4 - *Ananjeva* et al. (2006) ; 5 - *Amphibiaweb* (2012) . Abbreviation: is – insular occurrence.

Taxa		References				
		1	2	3	4	5
Caudata	*Salamandrella keyserlingii*	+	+	+	+	
	Lissotriton vulgaris	is	+	-	+	
Anura	*Rana arvalis*	+	+	+	+	
	Rana amurensis	+	+	+	+	
	Rana dybowskii	+	-	-	+	
	Rana temporaria	+	-	+	+	
	Pelophylax ridibundus	is	-	+	is	
	Bufotes viridis	is	+	+	is	
	Bufotes variabilis	-	-	-	+	
	Bufo bufo	+	+	+	+	
	Bufo gargarizans	-	?	-	is	
Lacertoidea	*Lacerta agilis*					+
	Zootoca vivipara					+
Serpentes	*Elaphe dione*					+
	Natrix natrix					+
	Viperus berus					+
	Viperus renardi					+
	Gloydius halys					+

Table 2(on next page)

Neogene testudinoid fauna of Western Siberia and the Zaisan and Turgay Basins.

According to *Chkhikvadze* (1989) , as well as the superscriptions before the taxa indicate the references: * *Kordikova* (1994) ; ** *Danilov, Cherepanov & Vitek* (2013) , *** Kentyubek fauna (Suppl. 3), *$^{-}$ Chkhikvadze (1989) and *$^{+}$ *Tleuberdina* et al. (1993) , ^{K} *Kuznetsov* (1982) , ^{O} our results. The aquatic families are indicated with blue and terrestrial families with dark yellow colour. Abbreviations: Ty – Trionychidae, Cy – Chelydridae, Pl – Platysternidae, Ts – Testudinidae, Ey – Emydidae, Gey – Geoemydidae.

Stage		Zaisan Basin			Turgay Basin	Western Siberia
		Suite	Turtle “Stage”*$^{-}$	taxa	taxa	taxa
Pliocene						*Chelydropsis kuznetsovi*(Cy), ?*Sakya* sp. (Ey)
Miocene	Late	Karabulak		**Protestudo illiberalis* (Ts)		^{O}*Emydoidea* sp. (Ey)
		Kalmakpai		*Protestudo kegenica* (Ts)		^{K}*Protestudo karabastusica* (Ts)
	Middle	Sarybulak	up.	**Protestudo darewskii* (Ts)	****Chrysemys* sp. (Ey), ?*Ocadia* sp. (Gey), *Emydoidea tasbaka* (Ey), *Kazakhemys zaisanensis* (Pl), ?*Chelydropsis* sp. (Cy)	*$^{+}$ *Chrysemy* sp. (Ey), *Ocadia* sp. (Gey)
			low.	**Pelodiscus jakhimovitchae* (Ty) ***Baicalemys moschifera* (Ey)		
		Zaisan	up.			
			low.	(**)*Baicalemys* sp. (Ey)		
	Early	Akzhar	up.	*Protestudo* sp. (Ts)		
			midd.	*$^{-}$ *Chelydropsis poena* (Cy)		
				**Pelodiscus* sp. (Ty)		
				*$^{-}$ *Kazakhemys zaisanensis* (Pl)		
				***Baicalemys jegalloi* (Ey)		
				***Ocadia iliensis* (Gey)		
			low.	*$^{-}$*Protestudo alba* (Ts)		
				Emydidae gen. indet. (Ey)		