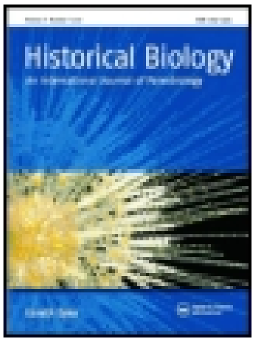

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Miocene snakes from northeastern Kazakhstan: new data on the evolution of snake assemblages in Siberia

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ABSTRACT
The Neogene snake fauna from the central and eastern regions of Eurasia is still largely unknown. This paper reports on a unique snake fauna from the late middle Miocene of the Baikadam and Malyi Kalkaman 1 and 2 localities, northeastern Kazakhstan, which represents the best-documented Miocene snake assemblage in Central Asia. Previous studies admitted that snake fauna could be homogeneous over a large part of Eurasia during the Miocene, with the late middle to early late Miocene assemblages similar to snake assemblages that inhabited Europe in the late early and early middle Miocene. This assumption is partially supported by the presence of *Texasophis bohemiacus* and *Coluber* cf. *hungaricus*, as well as vipers of the '*V. aspis*' complex. However, the presence of taxa which are (1) probably not related to European representatives ('Colubrinae' A and B), (2) probably never occurred in Central and Western Europe and (3) are closely related to species recently inhabiting southern Siberia (*Elaphe* aff. *dione*, *Gloydius* sp.) indicates that faunal dissimilarity was relatively high within Eurasia during the late middle Miocene. This assumption is in accordance with studies of small mammal assemblages which show a decreasing homogenity in the Eurasia in the course of the middle Miocene.

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Snakes; palaeobiogeography; palaeoecology; middle Miocene; Siberia

Introduction

The Neogene snake fauna from the central and eastern regions of Eurasia is still largely unknown. Only a few localities with fossil snakes have been reported from central and eastern Eurasia:

1. The Tagay (Togay) locality, middle Miocene (14–13 Ma), Ol'khon Island, Baykal Lake, Russia (Rage and Danilov 2008; Daxner-Höck et al. 2013);
2. Mizunami (Akeyo Formation), late early Miocene, Japan (Holman and Tanimoto 2004);
3. Builstyn Khudang, late Miocene, central Mongolia (Böhme 2007);
4. Shantung (Shanwang Formation), middle Miocene, China (Sun 1961);
5. numerous Neogene localities of the Zaisan Basin, Eastern Kazakhstan (Chkhikvadze 1984, 1985; Zerova and Chkhikvadze 1984), as well as a few localities from Northern Kazakhstan e.g. Ayakoz and Maly Kalkaman (Tleuberdina et al. 1993; Malakhov 2005, 2009);
6. Ertemte, latest Miocene (6–5 Ma) Ertemte, Inner Mongolia, northeastern China (Schlosser 1924).

All remaining Neogene localities providing snake remains come from western and southern Asia: Anatolia (Rage and Sen 1976; Paicheler et al. 1978; Szyndlar and Rage 1999; Szyndlar and Hoşgör 2012), Saudi Arabia (Thomas et al. 1982), the Siwalik beds of Pakistan and India (Rage et al. 2001; Head 2005), Burma (Swinton 1926) and Thailand (Rage and Ginsburg 1997). This paper reports on a snake fauna from the late middle Miocene (13–12 Ma; Vasilyan et al. 2017) of the Baikadam and Malyi Kalkaman 1 and 2 localities. All the localities are situated in northeastern Kazakhstan close to the southern border of the Siberia geographical region (Figure 1).

Geological settings and localities

The geographical region of Western Siberia is restricted to the territories of Russia and parts of Northern Kazakhstan. Over this area, there is a Cenozoic sedimentary basin, which extends between the Ural Mountains in the west, the Central Siberian Plateau in the east, and the Kazakh Plain and Altay Mountains, including the Zaisan Lake, in the south. In this basin, the continental sedimentation began after the late Eocene closure of the Turgai Strait and covered the time span from the Oligocene until the Pleistocene (e.g. Chkhikvadze 1984, 1989; Tleuberdina et al. 1993; Malakhov 2005). The Neogene sedimentary sequences are represented by lacustrine, fluvial, alluvial and other continental sedimentation in the overlying of Eocene marine deposits. The

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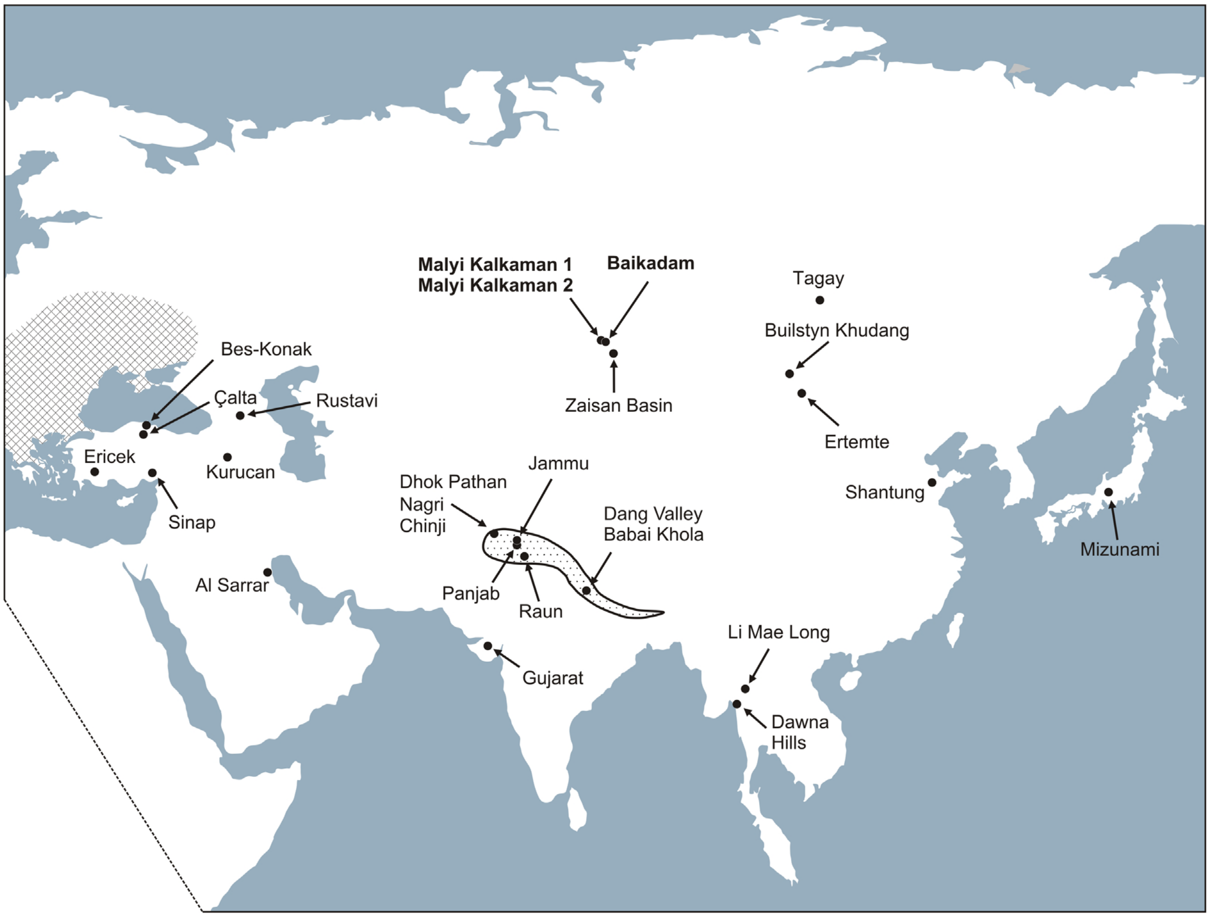

Figure 1. Map of Eastern Europe and Asia showing the locations of published Neogene (Miocene and Pliocene) snake bearing Asiatic localities, including Western Siberian fossil sites (bold). Dotted area – Siwalik Group; hatched area – well-documented area of Eastern Europe (map source (modified): http://freedesignfile.com; data according to Sun 1961; Rage et al. 2001; Head 2005; Rage and Danilov 2008; Szyndlar and Hoşgör 2012; van den Hoek Ostende et al. 2015).

source of clastic sedimentation occurs in the surrounding regions (Borisov 1963; Vasilyan et al. 2017).

Most of the Neogene localities occur in the interfluves of the Irtysh and Ishim rivers (Gnibidenko 2006; Zykin 2012). The sedimentary content of all the sections is formed by terrestrial fluvial and alluvial facies where numerous fossiliferous layers produced rich faunas (Zykin 2012). The areas along the Irtysh River and its tributaries are particularly abundant regarding vertebrate-bearing deposits. The detailed geological descriptions of the stratigraphic sections and fossil localities were summarised by Zykin (1979), Zykin and Zazhigin (2004), Gnibidenko (2006), and Zykin (2012).

The stratigraphic subdivision is based mainly on the Russian concept of svitas. A svita has lithological, biochronological, and genetic (sedimentological) significance; however, there is no precise equivalent in western stratigraphic theory or terminology (Lucas et al. 2012).

Localities

Malyi Kalkaman 1 and 2: These localities are situated in the Pavlodar District near the western margin of Malyi Kalkaman Lake close to the village of Solvetka. The bone remains from the original locality (Malyi Kalkaman 1) have been known since the 1930s, and the first list of fossil fauna from this site was published by Lychev (1963). In 1978 a fossiliferous horizon with numerous bones of different vertebrate groups was discovered and published in Tleuberdina (1988, 1989). This fossiliferous layer is located in the upper part of the section and composed of sands with pebbles. The description of snake fauna from this sampling was given by Chkhikvadze and Gutiyeva (in Tleuberdina et al. 1993), who reported as the only snake species *Elaphe* cf. *dione* (Pallas, 1773). Later another fossiliferous layer (Malyi Kalkaman 2) was found at the base of the section. Both localities belong to the Kalkaman Svita and are dated to the late middle Miocene, 13–12 Ma (MN 7 + 8), by their small mammal assemblages (*Heterosminthus* aff. *orientalis* Schaub, 1930; *Microtocricetus molassicus* Fahlbusch & Mayr, 1975 in Malyi Kalkaman 2 and *Microtocricetus molassicus* in Malyi Kalkaman 1). The amphibian, reptile (excluding snakes), and small and large mammal assemblages are discussed in detail in Vasilyan et al. (2016, 2017).

Baikadam: The Baikadam (Podpusk 2) locality is situated 8.4 km north of the village of Podpusk on the right bank of the Irtysh River. The fossiliferous layer is located at the base of the upper half of the section, in the sands of the Kalkaman Svita. The locality provides only small vertebrate remains (Zykin 2012; Vasilyan et al. 2016, 2017). The small mammal fauna contains the cricetid remains of *Microtocricetus molassicus*, which are relevant to biochronology. Based on the position of the fossiliferous layers relative to Malyi Kalkaman, Baikadam is somewhat younger than Malyi Kalkaman 1 and 2 (Vasilyan et al. 2017).

Material and methods

The fossil material of snakes of the Malyi Kalkaman 1 and 2 localities comes from excavations from 1980, 1987 and 2001, and of the Baikadam locality from 1989 and 2001. All the material of small vertebrates was obtained by screen-washing. The snake material is represented almost exclusively by isolated vertebrae that are rather fragmentary and mostly poorly preserved. The identification at the species level, therefore, remains problematic in many instances. The cranial morphology follows Ivanov (1999); the vertebrae terminology follows Hoffstetter and Gasc (1969) and Szyndlar (1984). Leica MZ 16 stereomicroscope equipped with a Leica DFC 480 digital camera (5 mpx) were used for examination and photographs of the isolated fossil material. The material from all three localities is housed in the collection of the Geological Institute of the Russian Academy of Sciences under the collection numbers: GIN 950/2001 (Baikadam), GIN 1107/1001 (Malyi Kalkaman 1), and GIN 1107/2001 (Malyi Kalkaman 2).

Abbreviations: Institutes: GIN, Geological Institute of the Russian Academy of Sciences, Moscow. Measurements (see Szyndlar 1984): n, number of specimens; cl, centrum length; naw, centrum width; or, observed range.

Systematic part

Alethinophidia NOPCSA, 1923
Booidea GRAY, 1825
Boidae GRAY, 1825
Erycinae BONAPARTE, 1831
Albaneryx HOFFSTETTER & RAGE, 1972
Albaneryx* cf. *volynicus ZEROVA, 1989
(Figures 2A-H)

Material: Baikadam: three trunk vertebrae (GIN 950/2001-RE16-1-3).

Description

Trunk vertebrae. All three preserved trunk vertebrae are fragmentary with damaged synapophyses; the posterior part of the neural arch of one vertebra (GIN 950/2001-RE16-3) is missing. The vertebrae are as high as they are long, or slightly higher than they are long. In lateral view, the middle trunk vertebra (Figures 2(A)–(E)) has a rather low neural spine. Its anterior margin arises at the level of the posterior termination of the zygosphene. The anterior margin of the neural spine is almost vertical, but in one specimen the neural spine is inclined anteriorly. The

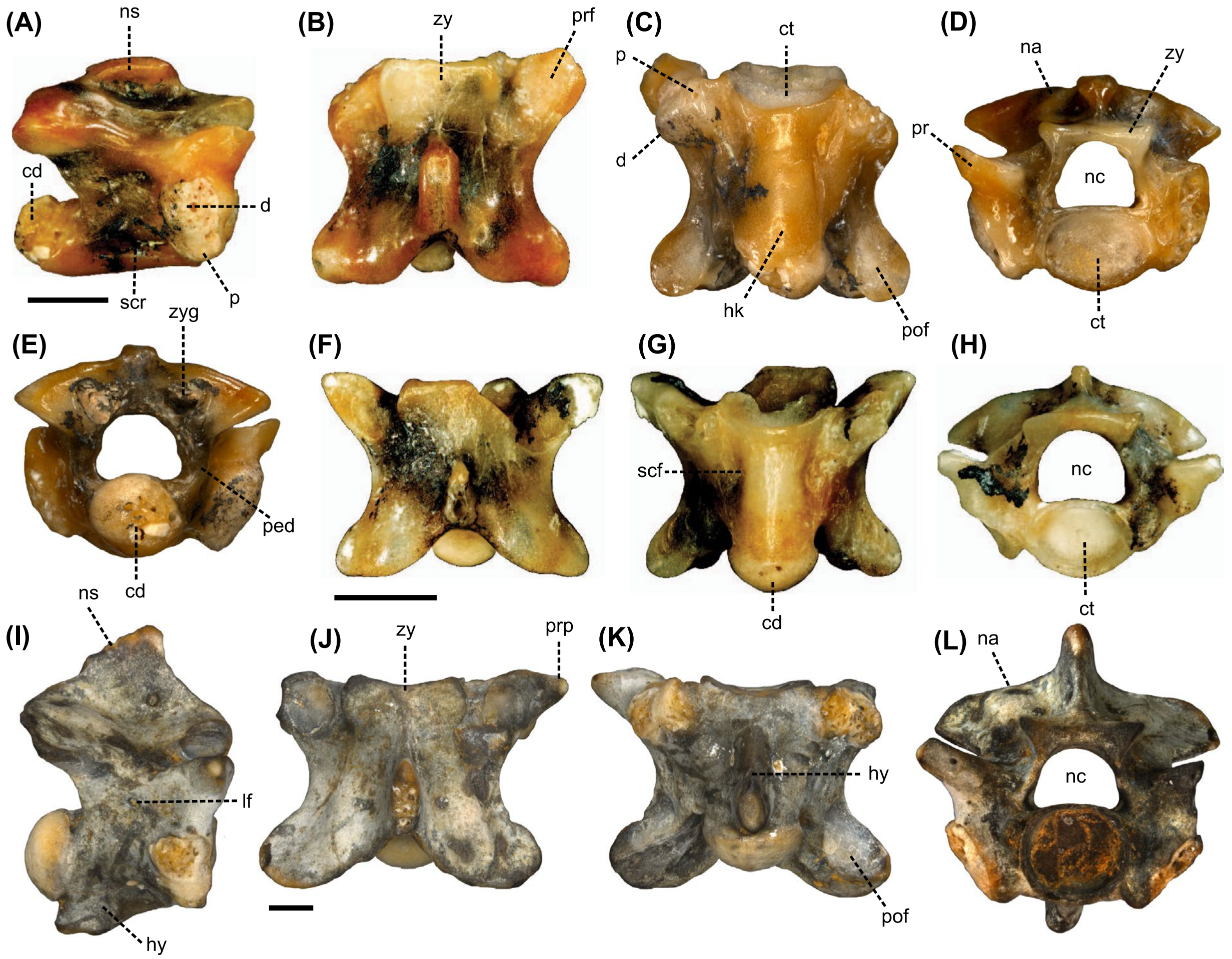

Figure 2. *Albaneryx* cf. *volynicus*, A-E, GIN 950/2001-RE16-1 (Baikadam), middle trunk vertebra in right lateral (A), dorsal (B), ventral (C), cranial (D) and caudal (E) views; F-H, GIN 950/2001-RE16-2 (Baikadam), trunk vertebra in dorsal (F), ventral (G) and cranial (H) views. Boidae gen. et sp. indet., I-L, GIN 950/2001-RE16-4 (Baikadam), cervical vertebra in right lateral (I), dorsal (J), ventral (K) and cranial (L) views. Abbreviations: cd, condyle; ct, cotyle; d, diapophysis; hk, haemal keel; hy, hypapophysis; lf, lateral foramen; na, neural arch; nc, neural canal; ns, neural spine; p, parapophysis; ped, pedicele; pof, postzygapophyseal articular facet; pr, prezygapophysis; prf, prezygapophyseal articular facet; prp, prezygapophyseal process; scf, subcentral foramen; scr, subcentral ridge; zy, zygosphene; zyg, zygantrum. Scale equals 1 mm.

height of the neural spine decreases caudally together with the rising caudal part of the neural arch. The dorsal margin of the neural spine is clearly thickened. The lateral foramina are large and situated below the short and relatively blunt interzygapophyseal ridges approximately close behind the dorsal margin of the synapophyses. Although the synapophyses are not completely preserved, they were probably subsquare without apparent division into the para- and diapophyses. The diapophyses are larger than the parapophyses. The relatively short and blunt subcentral ridges are vaulted dorsally. They vanish at the level of the caudal margin of the pedicle far from the anterior margin of the condyle. In dorsal view, the vertebra is as wide as it is long or slightly wider. The only preserved right prezygapophyseal articular facet is slightly damaged. It was elongated suboval or subtriangular. The distal tip of the prezygapophyseal process is damaged, although it was obviously extremely short and hardly visible in dorsal view. The cranial margin of the zygosphene is almost straight in the largest specimen; however, in two smaller vertebrae, the cranial margin of the zygosphene is slightly convex with small but well-developed lateral lobes. The epizygapophyseal ridges are underdeveloped. The condyle is situated on the relatively long neck. The caudal margin of the neural arch forms a shallow and wide notch. In ventral view, the relatively shallow subcentral grooves are developed along the distinct and extremely wide haemal keel. The subcentral grooves are developed only in the anterior part of the vertebra. The subcentral foramina are small but well visible in ventrolateral view. They are situated at the base of the haemal keel at about one-third of the vertebral centrum length. The postzygapophyseal articular facets are suboval. The diapophyses are directed laterally. In cranial view, the neural arch is slightly vaulted. The neural canal is rounded with short and relatively narrow lateral sinuses. The prezygapophyses were tilted dorsally. The cranial margin of the zygosphene is straight with slightly dorsally raised lateral lobes. The ventral margin of the synapophyses does not reach below the ventral margin of the cotyle. The cotyle with a damaged cotylar rim was slightly depressed dorsoventrally. Deep subtriangular depressions occur on either side of the cotyle. The paracotylar foramina are missing. In caudal view, the neural arch is developed on the wide pedicle. The zygantral area is wide. The condyle is slightly depressed dorsoventrally. The measurements of the largest vertebra are as follows: cl = 2.42 mm; naw = 2.45 mm.; cl/naw = 0.99.

Remarks: The middle trunk vertebrae of this tiny boid snake clearly refer to the subfamily Erycinae based on the following combination of characteristics (Rage 1984): 1 – the small dimensions with a centrum length of less than 3 mm; 2 – the depressed neural arch developed on the high pedicle; 3 – the low neural spine; 4 – the distinctly short prezygapophyseal processes which are hardly visible in the dorsal view; 5 – the absence of paracotylar foramina. Although the caudal vertebrae are not preserved, the vertebrae from Baikadam differ from the middle trunk vertebrae of the extant genera *Eryx* (Szyndlar and Schleich 1994; Blain 2016) and *Gongylophis* [*Gongylophis conicus* (Schneider, 1801); MNHN 1907-138] by the dorsally thickened neural spine that rises behind the zygosphene at the posterior half of the neural arch. The presence of a markedly wide haemal keel and the caudal position of the neural spine concur with those of *Albaneryx volynicus* Zerova, 1989 reported from the early late Miocene of Grytsiv, Ukraine (Zerova 1989). The middle trunk vertebrae differ from *Albaneryx depereti* Hoffstetter & Rage, 1972 reported from the late middle Miocene of La-Grive-Saint-Alban, France (Hoffstetter and Rage 1972) by the absence of the dorsal bending of the haemal keel in lateral view, as well as in the position of the neural spine behind the zygosphene and the longer condylar neck. *Albaneryx* cf. *volynicus* from Baikadam differs from the type of material reported by Zerova (1989, p. 31, fig. 11) by the distinctly longer condylar neck.

Boinae GRAY, 1825
Boinae gen. et sp. indet.
(Figures 2I-L)

Material: Baikadam: one cervical vertebra (GIN 950/2001-RE16-4).

Description

Cervical vertebra. A single fragmentary vertebra is preserved with the broken-off distal tip of the neural spine, hypapophysis and damaged synapophyses. In lateral view, the vertebra is relatively short but clearly high. The neural spine is high and its base rises at the level of short and almost circular zygosphenal facets. The cranial margin of the neural spine is vertical with the exception of its base, which slopes anteriorly as far as the close vicinity of the zygosphenal lip. The caudal margin of the neural spine is damaged, but its preserved basal portion indicates that it is slightly inclined posteriorly. The large paired foramina occur at the base of the neural spine. The posterior portion of the flat neural arch is steeply lifted dorsally. The blunt interzygapophyseal ridges are very short. The large lateral foramina occur in the middle of the neural arch length. There is no depression around the foramina. The subcentral ridges are short. The condyle is developed on the short neck. The hypapophyseal base indicates that the relatively short hypapophysis was bent caudally. In dorsal view, the vertebra is wider than it is long. The cranial margin of the short zygosphene is concave. The right prezygapophyseal articular facet is oval. The pointed prezygapophyseal process is rather short but well visible. The interzygapophyseal constriction is well-developed. The median notch on the posterior border of the neural arch is deep. In ventral view, the short subcentral ridges are blunt. The short subcentral grooves are wide and shallow, vanishing close behind the synapophyses. The diapophyses were probably somewhat larger than the parapophyses. The large subcentral foramina occur at the base of the wide hypapophysis. The only preserved left postzygapophyseal articular facet is subtriangular. In cranial view, the neural arch is rather flat. The dorsal termination of the neural spine is not thickened. The massively built zygosphenal lip is slightly concave with tilted up zygosphenal facets. The neural canal is rounded to subsquare, outlining the short and narrow lateral sinuses. The diameter of the neural canal is smaller than the diameter of the rounded cotyle. The prezygapophyses are clearly tilted dorsally. The prezygapophyseal facets occur well above the cotylar rim. No paracotylar foramina occur within the deep depressions at either sides of the cotyle. In caudal view, the wide zygantral area is gracile. The condyle is rounded. The measurements of the vertebra are as follows: cl = 3.90 mm; naw = 4.32 mm; cl/naw = 0.90.

Remarks: The relatively large vertebra has a flat neural arch and well-developed interzygapophyseal constriction, which enables its distinction from the family Pythonidae (Szyndlar and Rage 2003; Ivanov and Böhme 2011). The strongly dorsally inclined prezygapophyses, the presence of the short prezygapophyseal processes, as well as the position of the prezygapophyseal facets clearly above the cotylar rim all correspond to the boine snake *Bavarioboa* Szyndlar & Schleich, 1993 (Szyndlar and Rage 2003). Although the vertebra partially resembles that of *Bavarioboa hermi* Szyndlar & Schleich, 1993 reported from the early to early middle Miocene of Europe (Szyndlar and Schleich 1993; Szyndlar and Rage 2003; Ivanov and Böhme 2011), there are differences including the strongly concave and extremely short zygosphene in the dorsal view and the almost circular zygosphenal facets. The paired foramina that occur at the base of the neural spine are most probably a result of taphonomic processes. Despite the absence of the paracotylar foramina in the cervical vertebra from Baikadam, it is possible that a posterior trunk vertebra of an indeterminate Boinae reported from the middle Miocene of Tagay (Togay), Olʹkhon Island, Baykal Lake (Rage and Danilov 2008) could represent the same taxon, which displays the same development of concave zygosphene and a similar position of the neural spine.

Colubroidea OPPEL, 1811
Colubridae OPPEL, 1811
'Colubrinae'
***Coluber* (s.l.)** LINNAEUS, 1758
Coluber* cf. *hungaricus (BOLKAY, 1913)
(Figure 3A-I)

Material: Baikadam: eight trunk vertebrae (GIN 950/2001-RE16-5-12).

Description

Trunk vertebrae. All vertebrae are at least partially fragmentary, with broken-off prezygapophyseal processes. In lateral view, the neural spine of the best-preserved vertebra is about twice as long as it is high. Its cranial margin is vertical or slightly inclined posteriorly and the caudal margin is low and inclined caudally. The zygosphenal facets are oval in outline. The interzygapophyseal ridges are short and blunt. The lateral foramina, which are usually large, are situated within depressions at the posterior margin of the prezygapophyses just below the interzygapophyseal ridges. The parapophyses are somewhat smaller than the diapophyses. The subcentral ridges, which are only moderately developed in the anterior trunk vertebrae, are blunt and slightly dorsally vaulted. In the posterior trunk vertebrae, the straight subcentral ridges are conspicuous and extend as far as the close vicinity of the condyle. The condylar neck is short. In dorsal view, the zygosphene is strongly convex with small but rather distinct lateral lobes. In the anterior trunk vertebrae, the interzygapophyseal constriction is shifted to the anterior half of the vertebra. The prezygapophyseal articular facets are oval to subtriangular in outline. A partially preserved left prezygapophyseal process in one vertebra (Figure 3(F)) indicates that the process was probably of equal length or slightly shorter than the prezygapophyseal facet. The epizygapophyseal spines are moderately developed. The median notch on the posterior border of the neural arch is deep. In ventral view, the cotylar rim is smooth without subcotylar tubercles. The haemal keel is thin along its entire length in the anterior trunk vertebrae. In the posterior trunk vertebrae (Figure 3(G)), the haemal keel is wide and flattened. The posterior margin of the haemal keel is situated far from the anterior margin of the condyle. The subcentral grooves are wide and well-expressed only in the posterior trunk vertebrae. The small subcentral foramina are situated at the base of the haemal keel. They occur close behind the level of the posterior margin of the posterolaterally directed diapophyses. In cranial view, the neural arch is vaulted. The neural canal is rounded with small but distinct lateral sinuses. The zygosphenal lip is thin and strongly convex. The prezygapophyses are directed laterally. The paracotylar foramina occur within deep depressions on either side of the circular to slightly dorsoventrally depressed cotyle. The parapophyses reach close below the ventral margin of the cotylar rim. In caudal view, the zygantral area is wide. The condyle is rounded or slightly depressed dorsoventrally. Measurements are as follows (n = 6): cl: or = 3.41–4.25 mm; naw: or = 2.49–3.16 mm; cl/naw: or = 1.31–1.41, mean 1.35 ± 0.04.

Remarks: The vertebrae are typical by their elongated centrum not exceeding a length of 4.30 mm, the relatively high neural spine and the relatively long prezygapophyseal processes. These features make it possible to determine this small colubrine snake as belonging to the small colubrine snakes referred to as *Coluber* s.l. (*sensu* Szyndlar 2009). The trunk vertebrae closely resemble *Coluber hungaricus* reported from the Central European early middle Miocene (Germany, Griesbeckerzell; Ivanov and Böhme 2011) to the early Pliocene (Hungary, Osztramos 1; Venczel 2001) by the following combination of features: 1 – the same length of the prezygapophyseal processes; 2 – the zygosphenal lip is wider than the cotyle and clearly dorsally vaulted with a distinct wide median lobe and small lateral lobes (Venczel 1994; Venczel and Ştiucă 2008); 3 – the subcentral ridges are blunt and subcentral grooves shallow; and 4 – the parapophyses are smaller than the diapophyses. The morphology of the preserved vertebrae is strongly affected by the intracolumnar variability. The anterior trunk vertebrae are typical in their relatively sharp haemal keel and shallow subcentral grooves, whereas the posterior trunk vertebrae are characterized by the flat ventral surface of the haemal keel and prominent subcentral ridges, as well as the deep subcentral grooves. Moreover, the pointed prezygapophyseal processes of these vertebrae are directed anteriorly rather than laterally. The degree of development of the structures coincides with the description by Szyndlar (2005), who reported *Coluber hungaricus* from the early late Miocene of Rudabánya, Hungary.

Texasophis HOLMAN, 1977
Texasophis bohemiacus SZYNDLAR, 1987
(Figures 4A-H)

Material: Baikadam: 22 trunk vertebrae (GIN 950/2001-RE16-13-34).

Description

Trunk vertebrae. All preserved vertebrae are at least partially fragmentary, usually with broken-off prezygapophyseal processes and strongly damaged synapophyses. In lateral view, the vertebrae are typical with a rather low neural spine that is at least four times longer than it is high. The cranial margin of the neural spine is inclined anteriorly and rises to about the middle of the

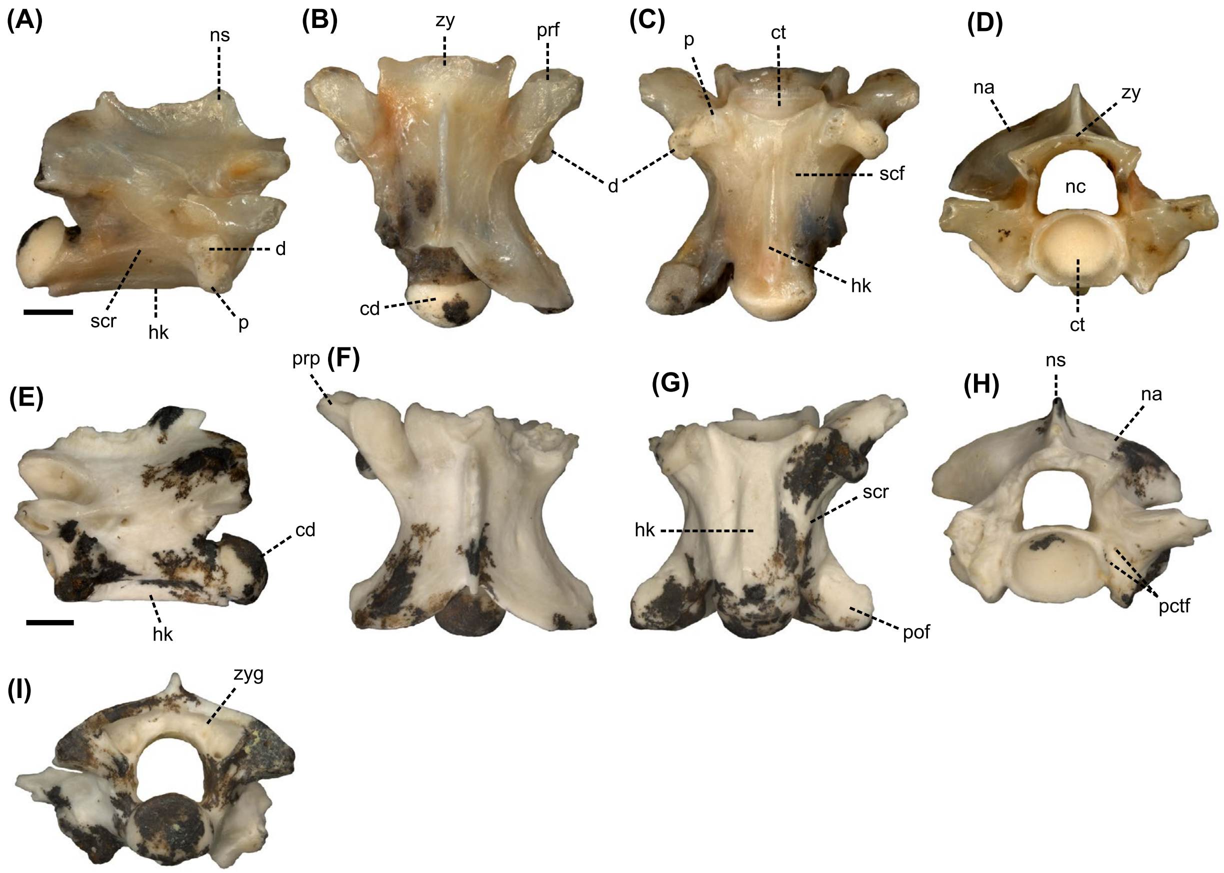

Figure 3. *Coluber* cf. *hungaricus*, A-D, GIN 950/2001-RE16-7 (Baikadam), middle trunk vertebra in right lateral (A), dorsal (B), ventral (C) and cranial (D) views; E-I, GIN 950/2001-RE16-10 (Baikadam), posterior trunk vertebra in left lateral (E), dorsal (F), ventral (G), cranial (H) and caudal (I) views. Abbreviations: cd, condyle; ct, cotyle; d, diapophysis; hk, haemal keel; na, neural arch; nc, neural canal; ns, neural spine; p, parapophysis; pctf, paracotylar foramina; pof, postzygapophyseal articular facet; prf, prezygapophyseal articular facet; prp, prezygapophyseal process; scf, subcentral foramen; scr, subcentral ridge; zy, zygosphene; zyg, zygantrum. Scale equals 1 mm.

zygosphenal lip length. The posterior margin of the neural spine is rather low and inclined posteriorly forming a short tip. The zygosphenal facets are elongated and oval in outline. The lateral foramina are very small and are situated in shallow depressions close below the blunt interzygapophyseal ridges. The synapophyses are well-divided into para- and diapophyses, both of equal length. The relatively sharp subcentral ridges, strongly expressed in the posterior trunk vertebrae, extend as far as the proximity of the anterior margin of the condyle. These ridges are indistinctly vaulted dorsally; however, in the posterior trunk vertebrae they are straight. The condyle is situated on the relatively long neck (Figures 4(A) and (D)). In dorsal view, the vertebrae are elongated with a cylindrical neural arch. The caudal notch of the neural arch is deep. The prezygapophyseal articular facets are subtriangular and are situated far from the lateral margins of the zygosphene (Figure 4(E)). The prezygapophyseal processes are sharp and directed anterolaterally. In the posterior trunk vertebrae, the distal tips of the prezygapophyseal processes are bent anteriorly. The wide medial lobe and small lateral lobes occur on the cranial margin of the zygosphenal lip. The epizygapophyseal spines are absent. In ventral view, the centrum is long and narrow with straight subcentral ridges. The haemal keel is usually robust and well-expressed. The keel has the same width along its entire length, or it becomes slightly wider posteriorly. The width of the haemal keel is variable, depending on the position of the vertebra in the vertebral column. In the anterior trunk vertebrae, the haemal keel is narrow and either sharp or blunt. In the posterior trunk vertebrae, the haemal keel is flat with a slight widening of its caudal termination. The subcentral ridges are well-expressed mainly in the posterior trunk vertebrae. The subcentral grooves are distinct and deep. The tiny subcentral foramina occur at the base of the haemal keel. The ventral margin of the cotylar rim is smooth, or indistinct subcotylar tubercles occur in the posterior trunk vertebrae. The postzygapophyseal articular facets are square in outline. In cranial view, the neural arch is moderately vaulted. The zygosphenal lip is almost straight; however, in the posterior precaudal vertebrae, it is slightly convex. The neural canal is rounded to subsquare with wide lateral sinuses. The prezygapophyses are developed high above the cotylar rim and are directed clearly laterally. The only completely preserved right prezygapophyseal process of the best-preserved vertebra is inclined ventrolaterally. The ventral margin of the parapophyses is situated close below the level of the ventral margin of the cotylar rim. The paracotylar foramina are situated within wide depressions on either side of the dorsoventrally compressed cotyle. In caudal view, the zygantral area is wide. The condyle is slightly compressed dorsoventrally. The measurements are as follows ($n = 4$): cl: or = 3.77–4.69 mm; naw: or = 2.52–3.08 mm; cl/naw: or = 1.42–1.52, mean 1.49 ± 0.05.

Remarks: Texasophis represents a small-sized colubrine snake (Holman 1977; Szyndlar 1987, 1991a). The trunk vertebrae from Baikadam resemble *Texasophis* by the same combination of

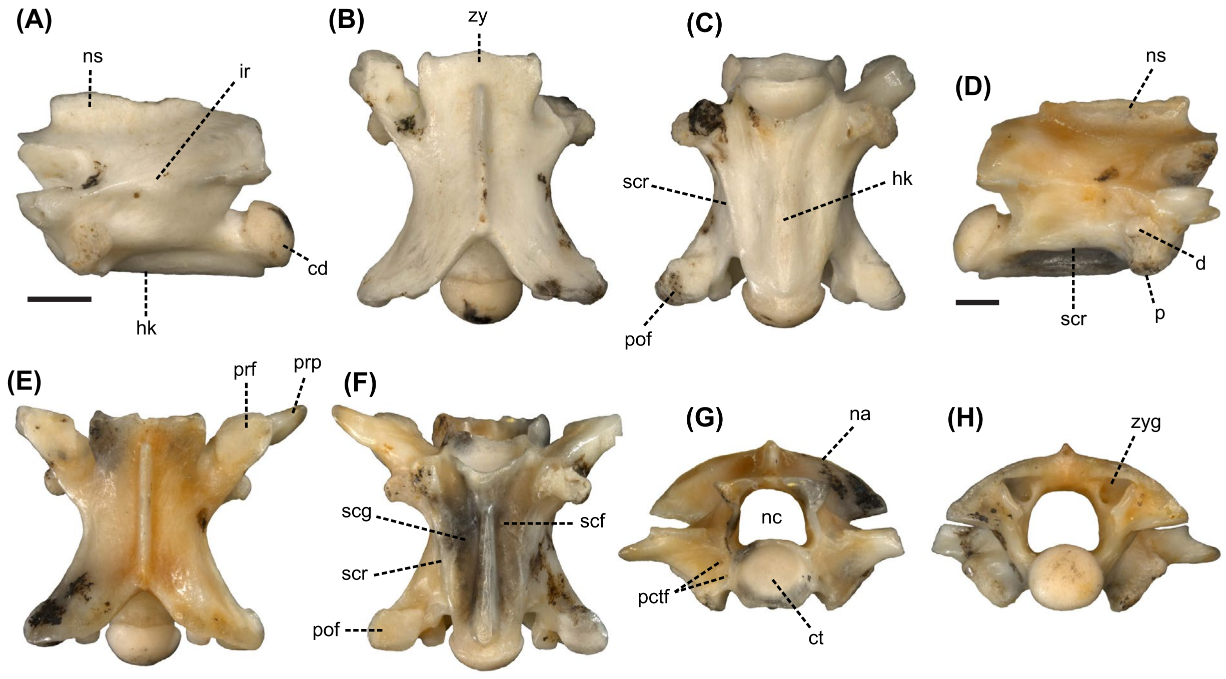

Figure 4. *Texasophis bohemiacus*, A-C, GIN 950/2001-RE16-15 (Baikadam), middle trunk vertebra in left lateral (A), dorsal (B) and ventral (C) views; D-H, GIN 950/2001-RE16-20 (Baikadam), posterior trunk vertebra in right lateral (D), dorsal (E), ventral (F), cranial (G) and caudal (H) views. Abbreviations: cd, condyle; ct, cotyle; d, diapophysis; hk, haemal keel; ir, interzygapophyseal ridge; na, neural arch; nc, neural canal; ns, neural spine; p, parapophysis; pctf, paracotylar foramina; pof, postzygapophyseal articular facet; prf, prezygapophyseal articular facet; prp, prezygapophyseal process; scf, subcentral foramen; scg, subcentral groove; scr, subcentral ridge; zy, zygosphene; zyg, zygantrum. Scale equals 1 mm.

features reported by Holman (1977, 2000): 1 – the elongated centrum; 2 – the moderately vaulted neural arch; 3 – a distinct but low neural spine; 4 – the rather robust haemal keel; 5 – the distinct subcentral ridges that are straight from the lateral view and have distinct subcentral grooves. *T. bohemiacus* from Baikadam differs from the most similar *Texasophis wilsoni* Holman, 1984 from the late middle to early late Miocene of Kansas by its smaller dimensions and lower neural spine, which does not overhang posteriorly (see Szyndlar 1987). The Baikadam material is identical to the type material of *T. bohemiacus* from the Czech early Miocene Dolnice locality (Szyndlar 1987), as well as to the material reported from the German early Oligocene Ehrenstein 12 locality (Szyndlar 1994).

Elaphe FITZINGER, 1833
Elaphe* aff. *dione (PALLAS, 1773)
(Figures 5A-O)

Material: Baikadam: four cervical vertebrae (GIN 950/2001-RE16-35-38), 16 trunk vertebrae (GIN 950/2001-RE16–39–56); Malyi Kalkaman 1: seven trunk vertebrae (GIN 1107/1001-RE03-1-7).

Description

Cervical vertebrae. Several preserved cervical vertebrae are rather fragmentary with broken-off hypapophyses (Figures 5 (A)–(E)). Usually, the posterior portion of the neural arch is also damaged. The vertebrae are typically with short centra. In lateral view, the best-preserved vertebra has a developed high neural spine. Although the cranial margin of the neural spine is not preserved, most probably it was as high as it was long. The caudal margin of the neural spine inclines posteriorly. The zygosphenal facets are elongated and oval in outline. The synapophyses are rather small with the diapophysis slightly bigger than the parapophysis. The short parapophyseal process is directed anteriorly. The interzygapophyseal ridges are short and indistinct. The lateral foramina are large. The short subcentral ridges are poorly developed. The posteroventrally directed hypapophysis is broken-off close to its base. The condyle is developed on a rather short neck. In dorsal view, the neural arch is cylindrical with a conspicuously deep furrow in its caudal part, reaching to almost half of the vertebra length. The zygosphenal lip is almost straight with small lateral sinuses. The large prezygapophyseal articular facets are suboval. The only preserved laterally directed right prezygapophyseal process is pointed and small, reaching one third of the length of the prezygapophyseal facet. In ventral view, the diapophyses are directed posterolaterally and the parapophyseal processes project anteriorly before the cotylar rim. The subcentral grooves are wide and shallow. The subcentral foramina are small. The postzygapophyseal articular facets are circular in outline. In cranial view, the neural arch is vaulted. The zygosphenal lip is also vaulted dorsally. The neural canal is rounded with wide lateral sinuses. The prezygapophyses are directed laterally. The paracotylar foramina are situated on either side of the cotyle within deep depressions. Small subcotylar tubercles occur at the ventral margin of the cotylar rim. In caudal view, the zygantral area is wide. The condyle is slightly compressed laterally.

Trunk vertebrae. All preserved vertebrae are damaged (Figures 5(F)–(O)). In lateral view, in the best-preserved vertebra (Figures 5(H)–(L)), a relatively high neural spine occurs that is about one and a half times longer than it is high. Its cranial margin was originally vertical or slightly inclined anteriorly. The damaged caudal margin was inclined posteriorly. The neural spine rises at about the middle of the zygosphenal facet length.

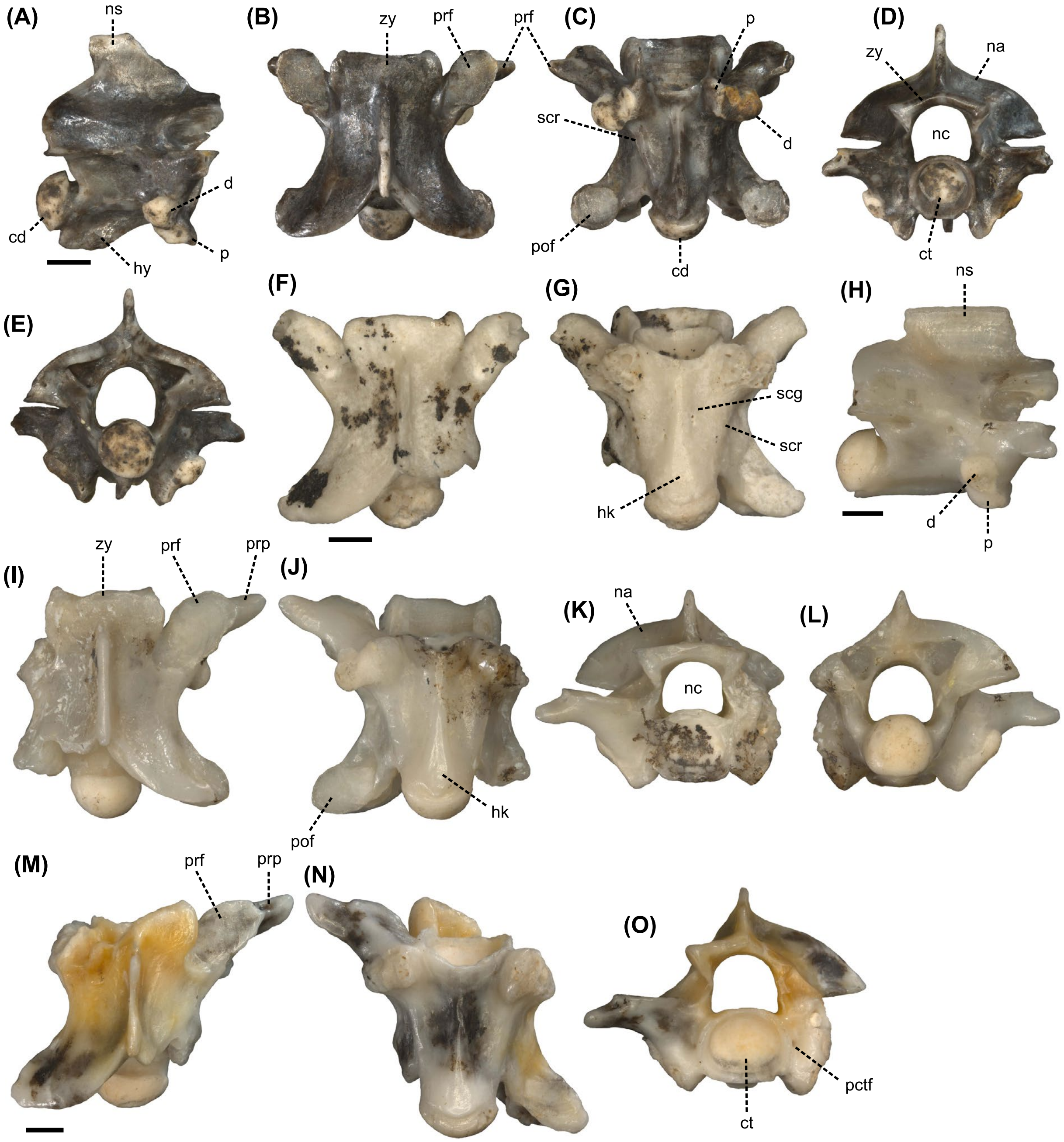

Figure 5. *Elaphe* aff. *dione*, A-E, GIN 950/2001-RE16-36 (Baikadam), cervical vertebra in right lateral (A), dorsal (B), ventral (C), cranial (D) and caudal (E) views; B, GIN 950/2001-RE16-41 (Baikadam), anterior trunk vertebra in dorsal (F) and ventral (G) views; H-L, GIN 950/2001-RE16-45 (Baikadam), middle trunk vertebra in right lateral (H), dorsal (I), ventral (J), cranial (K) and caudal (L) views; M-O, GIN 950/2001-RE16-47 (Baikadam), posterior trunk vertebra in dorsal (M), ventral (N) and cranial (O) views. Abbreviations: cd, condyle; ct, cotyle; d, diapophysis; hk, haemal keel; hy, hypapophysis; na, neural arch; nc, neural canal; ns, neural spine; p, parapophysis; pctf, paracotylar foramen; pof, postzygapophyseal articular facet; prf, prezygapophyseal articular facet; prp, prezygapophyseal process; scg, subcentral groove; scr, subcentral ridge; zy, zygosphene. Scale equals 1 mm.

The lateral foramina occur within depressions closely below the short and blunt interzygapophyseal ridges. The diapophyses are only slightly larger than the parapophyses. The ventral margin of the parapophyses is slightly rounded. The subcentral ridges are moderately developed (underdeveloped in the anterior trunk vertebrae) and dorsally vaulted. The condyle occurs on the short neck. In the dorsal view, the cranial margin of the zygosphenal roof is either almost straight with small lateral lobes, or has a developed indistinct wide medial lobe (Figure 5(I)). The right prezygapophyseal articular facet is oval in outline. The pointed prezygapophyseal process reaches to about a half of the prezygapophyseal facet length. The interzygapophyseal constriction is short but well-developed. The only preserved right diapophysis is directed posterolaterally. The epizygapophyseal spines are indistinct. In ventral view, the subcentral grooves are wide and shallow. The subcentral foramina are rather small and situated at the base of the haemal keel in the middle of the vertebral centrum length. The haemal keel is distinctly developed only in the anterior half of the vertebra but becomes wide and markedly low caudally. In the anterior trunk vertebrae, the caudal margin of the haemal keel is clearly spatulate (Figure 5(G)). The slightly laterally elongated right postzygapophyseal articular facet is subrectangular in outline. In cranial view, the zygosphenal lip is slightly vaulted dorsally. The neural arch is vaulted and the neural canal is rounded with distinct narrow lateral sinuses. The right prezygapophysis is inclined slightly dorsally; in other vertebrae, it can be directed laterally. The paracotylar foramina are situated in depressions at both sides of the rounded cotyle. In caudal view, the zygantral area is wide and the condyle is rounded to moderately depressed laterally. The measurements are as follows ($n = 5$): cl: or = 3.65–4.51 mm; naw: or = 2.85–3.63 mm; cl/naw: or = 1.18–1.28, mean 1.23 ± 0.04.

Remarks: The small dimensions of the middle trunk vertebrae with cl/naw > 1, the presence of paracotylar foramina and the presence of haemal keel instead of the hypapophysis all indicate that the vertebrae belonged to a small colubrine snake. The determination of small colubrines is difficult and usually impossible even at the generic level based exclusively on vertebrae (Szyndlar 1991a). The following character combination, including: 1 – the centrum slightly convex ventrally; 2 – the moderately vaulted neural arch with a relatively high neural spine; 3 – the rounded neural canal with narrow lateral sinuses; 4 – the indistinct subcentral ridges which are absent in the anterior trunk vertebrae, 5 – a deep posteriorly widened haemal keel which is rounded (even sharp) and never flat, enables the determination of the vertebrae as possibly belonging to *Elaphe dione* (Ratnikov 2002, 2004). However, unlike extant *E. dione*, the neural spine was probably only slightly inclined anteriorly and the condyle is developed on a short neck.

cf. *Elaphe* sp.
(Figures 6A-G)

Material: Malyi Kalkaman 1: one trunk vertebra (GIN 1107/1001-RE03-7); Malyi Kalkaman 2: one cervical vertebra (GIN 1107/2001-RE03-1), one trunk vertebra (GIN 1107/2001-RE03-2)

Description

Cervical vertebra. The only preserved cervical vertebra is rather fragmentary with a broken-off neural spine, a hypapophysis, a right parapophyseal process and a left postzygapophysis (Figures 6(A)–(C)). In lateral view, the neural spine rises in the posterior half of the zygosphene. The lateral foramen is situated within a shallow depression below the short interzygapophyseal ridge. In dorsal view, the vertebra is short with distinct interzygapophyseal constriction. The zygosphene is wide with distinct lateral lobes. The medial lobe was probably absent. The left prezygapophyseal articular facet is elongated and is oval in outline. The anterolaterally directed prezygapophyseal process is slender and reaches to about a half of the prezygapophyseal surface length. In ventral view, the subcentral ridges are blunt. The small subcentral foramina are situated at the base of the gracile hypapophysis. In cranial view, the neural arch is vaulted. The zygosphenal lip is vaulted dorsally. The neural canal is subsquare in outline. The laterally directed prezygapophyses are situated clearly above the dorsal margin of the cotylar rim. The small paracotylar foramina are situated on either side of the rounded cotyle.

Trunk vertebrae. The more completely preserved vertebra is partially fragmentary with a broken-off left prezygapophysis, a left synapophysis and a zygosphene (Figures 6(D)–(G)). In lateral view, the neural spine is about twice as long as it is high. Its cranial margin with unpreserved anterodorsal termination rises at the level of a half of the zygosphenal length. The caudal margin of the neural spine is inclined caudally. The well visible lateral foramen is situated within a shallow depression below the

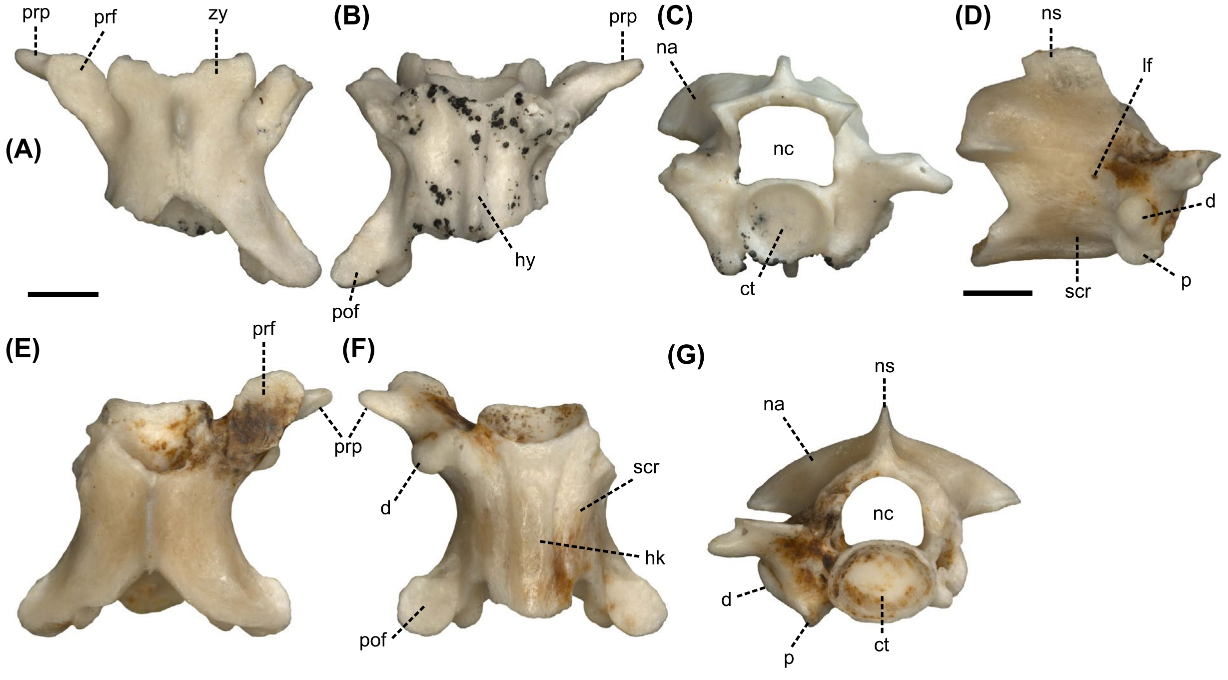

Figure 6 cf. *Elaphe* sp., A-C, GIN 1107/2001-RE03-1 (Malyi Kalkaman 2), cervical vertebra in dorsal (A), ventral (B) and cranial (C) views; D-G, GIN 1107/2001-RE03-2 (Malyi Kalkaman 2), posterior trunk vertebra in right lateral (D), dorsal (E), ventral (F) and cranial (G) views. Abbreviations: ct, cotyle; d, diapophysis; hk, haemal keel; hy, hypapophysis; lf, lateral foramen; na, neural arch; nc, neural canal; ns, neural spine; p, parapophysis; pof, postzygapophyseal articular facet; prf, prezygapophyseal articular facet; prp, prezygapophyseal process; scr, subcentral ridge; zy, zygosphene. Scale equals 1 mm.

blunt interzygapophyseal ridge. The synapophysis is relatively small with the diapophysis of equal length to the parapophysis. The subcentral ridge is well-developed only in the anterior half of the vertebral centrum. The condyle is connected to a short neck. In dorsal view, the fragmentary right prezygapophyseal articular facet was probably oval. The anterolaterally directed right prezygapophyseal process is long (almost as long as the prezygapophyseal facet) and slender with an acute distal termination. The postzygapophyses are rather small in comparison to the preserved prezygapophysis. The epizygapophyseal ridges are indistinctly developed. In ventral view, the centrum is long and weakly convex. The haemal keel is wide and spatulate in distal termination (GIN 1107/1001-RE03-7). The subcentral ridges are blunt and do not reach the posterior margin of the pedicle. The subcentral grooves are moderately developed only in the anterior part of the centrum. The tiny subcentral foramina occur at the base of the blunt haemal keel. In cranial view, the neural arch is moderately vaulted. The neural canal is rounded with small but distinct lateral sinuses. The prezygapophysis is tilted dorsally. The paracotylar foramina occur on both sides of the slightly dorsoventrally compressed cotyle.

Remarks: The centrum of the trunk vertebrae was relatively short with distinct interzygapophyseal constriction, slender and relatively short prezygapophyseal processes, blunt subcentral ridges and indistinctly developed subcentral grooves. These characteristics allow the identification of the vertebrae as possibly belonging to the genus *Elaphe*. The better preserved posterior (or posterior-most) trunk vertebra has a wide haemal keel with a craniocaudally enlarged medial depression. This morphology indicates the possible presence of the haemapophyses in the subsequent cloacal vertebra. A more precise determination is impossible because of the incomplete preservation of the vertebrae.

'Colubrinae' A
(Figures 7A-E)

Material: Baikadam: one trunk vertebra (GIN 950/2001-RE16-57); Malyi Kalkaman 2: one trunk vertebra (GIN 1107/2001-RE03-3).

Description

Trunk vertebrae. The more completely preserved vertebra has a damaged neural spine and distal tips of the prezygapophyseal processes (Figures 7(A)–(E)). In lateral view, the preserved base of the relatively short neural spine indicates that it was well developed. The zygosphenal articular facets are regularly oval. The left lateral foramen is large, whereas the right one is small. Both foramina are situated within shallow depressions below the relatively

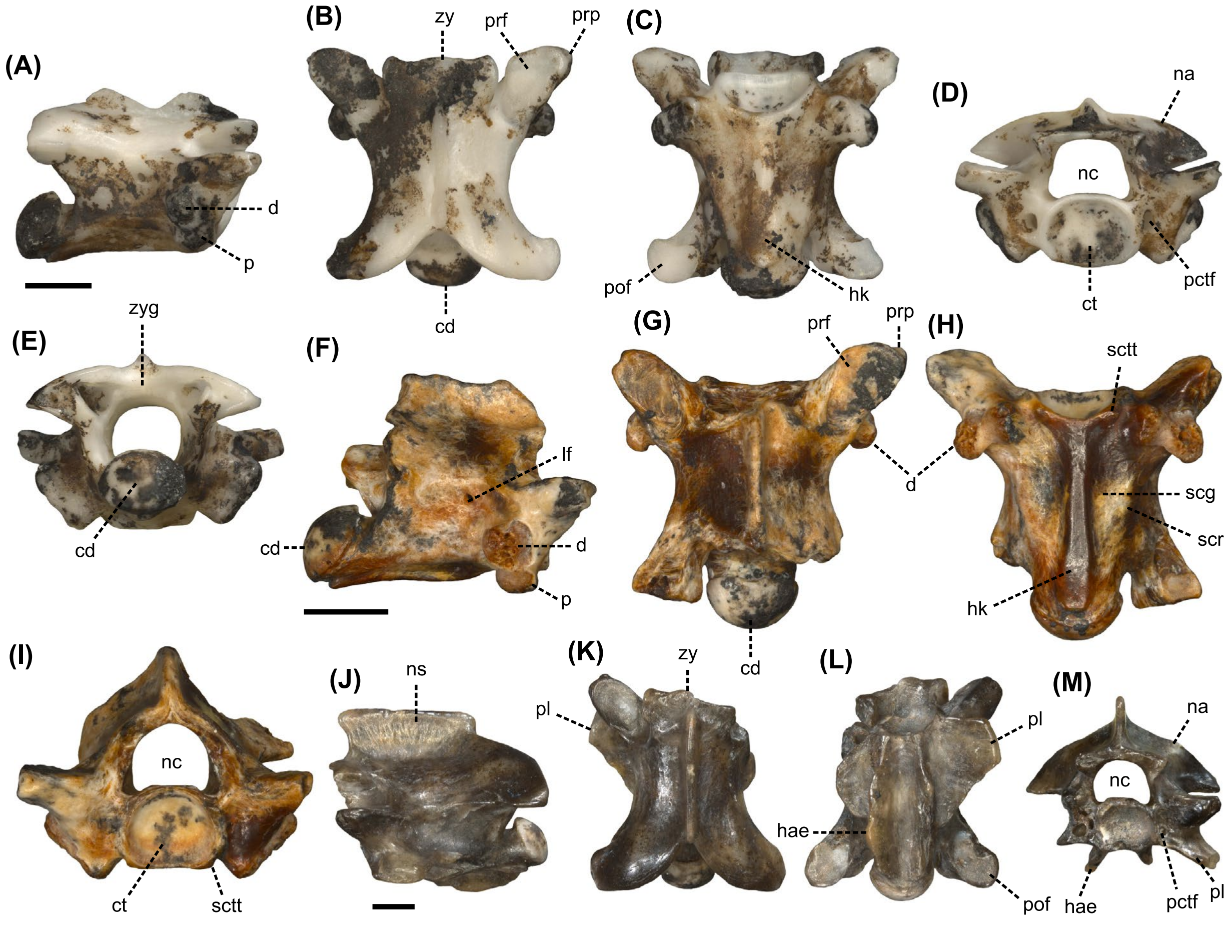

Figure 7. 'Colubrinae', A-E, GIN 950/2001-RE16-57 (Baikadam), cervical vertebra in right lateral (A), dorsal (B), ventral (C), cranial (D) and caudal (E) views. 'Colubrinae' B, F-I, GIN 950/2001-RE16-58 (Baikadam), middle trunk vertebra in right lateral (F), dorsal (G), ventral (H) and cranial (I) views; J-M, GIN 950/2001-RE16-60 (Baikadam), anterior caudal vertebra in left lateral (J), dorsal (K), ventral (L) and cranial (M) views. Abbreviations: cd, condyle; ct, cotyle; d, diapophysis; hae, haemapophysis; hk, haemal keel; lf, lateral foramen; na, neural arch; nc, neural canal; ns, neural spine; p, parapophysis; pctf, paracotylar foramen; pl, pleurapophysis; pof, postzygapophyseal articular facet; prf, prezygapophyseal articular facet; prp, prezygapophyseal process; scr, subcentral ridge; scg, subcentral groove; sctt, subcotylar tubercle; zy, zygosphene; zyg, zygantrum. A-E, J-M, scale equals 1 mm; F-I, scale equals 2 mm.

long but blunt interzygapophyseal ridges. The synapophyses are well-developed with the diapophyses clearly larger than the parapophyses. The parapophyses are short with a rounded base. The dorsally vaulted subcentral ridges are relatively short, reaching to about a half of the vertebral centrum length. The ventral margin of the haemal keel is vaulted slightly dorsally. The condyle occurs on the long neck. In dorsal view, the vertebra is wide with a shallow interzygapophyseal constriction. The prezygapophyseal articular facets are subtriangular in outline. The prezygapophyseal processes are rather small and hardly visible in dorsal view. The zygosphene is crenate with distinct lateral lobes and a wide medial lobe. The postzygapophyses are small without traces of epizygapophyseal spines. The caudal notch of the neural arch reaches the anterior border of the postzygapophyseal articular facets. In ventral view, the subcentral grooves are indistinct with the subcentral foramina situated at the base of a wide haemal keel. The haemal keel becomes slightly wider caudally. The markedly small postzygapophyseal articular facets are subsquare in outline. In cranial view, the neural arch is depressed. The prezygapophyses are tilted dorsally. The prezygapophyseal articular facets occur high above the dorsal margin of the cotylar rim. The neural canal is subsquare in outline with distinctly developed small and narrow lateral sinuses. The cranial margin of the zygosphenal lip is straight. The paracotylar foramina are extremely large and occur on both sides of the dorsoventrally depressed cotyle. The ventral margins of the parapophyses reach the level of the ventral margin of the cotylar rim. In caudal view, the pedicle is massively built. The postzygapophyseal articular facets are tilted dorsally. The zygantral area is gracile. The condyle is depressed dorsoventrally. The measurements of the better preserved vertebra are as follows: cl = 2.85 mm; naw = 2.01 mm; cl/naw = 1.42.

Remarks: The vertebra is lightly built and is longer than it is wide. The shallow subcentral grooves and blunt subcentral ridges indicate that the vertebra comes from the anterior or middle trunk region of the vertebral axis. The small dimensions, the presence of the paracotylar foramina, the well-developed neural spine, as well as the clearly developed haemal keel in the trunk region all indicate that the vertebra belonged to a small-sized 'Colubrinae' snake. The small dimensions, the crenate zygospehenal lip, the depressed neural arch and the wide haemal keel are reminiscent of the genus *Coronella* Laurenti, 1768. However, several characteristics are unusual in small colubrines: 1 – the prezygapophyses are strongly tilted dorsally; 2 – the parapophyses (although slightly damaged) are markedly small; 3 – the paracotylar foramina are extremely large.

'Colubrinae' B
(Figures 7F-M)

Material: Baikadam: two trunk vertebrae (GIN 950/2001-RE16-58 and 59), two caudal vertebrae (GIN 950/2001-RE16-60 and 61); Malyi Kalkaman 2: two trunk vertebrae (GIN 1107/2001-RE03-4 and 5).

Description

Trunk vertebrae. The vertebrae are only partially preserved (Figures 7(F)–(I)). In lateral view, the neural spine was well-developed. The large lateral foramina occur closely below the short interzygapophyseal ridges. The diapophysis was about twice as large as the short parapophysis. The straight subcentral ridges are blunt and rather indistinct. In dorsal view, the prezygapophyseal articular facets are subtriangular in outline. The prezygapophyseal processes are extremely short and hardly visible from the dorsal view. The diapophyses are directed posteriorly rather than posterolaterally. The interzygapophyseal constriction is strongly shifted anteriorly. In ventral view, the haemal keel is wide. Its caudal termination occurs far before the cranial margin of the condyle. The subcentral grooves are wide and rather shallow. The subcentral foramina are very small. The best-preserved vertebra has indistinct subcotylar tubercles. In cranial view, the damaged neural arch is vaulted, and the neural canal is rounded with large lateral sinuses. The cotyle is slightly depressed dorsoventrally. The parapophyses occur clearly below the cotylar rim. The paracotylar foramina occur within depressions on both sides of the cotyle; the cotylar rim is flat. The left paracotylar foramen of one vertebra is doubled. The measurements of the two largest vertebrae are as follows: (1) cl = 5.39 mm; naw = 3.70 mm; cl/naw = 1.46; (2) cl = 4.77 mm; naw = 3.80 mm; cl/naw = 1.26.

Caudal vertebrae. The better preserved anterior caudal vertebra is partially damaged with the pleurapophyses and haemapophyses broken-off close to their bases (Figures 7(J)–(M)). In lateral view, the neural arch is about twice as long as it is high. Its cranial margin is clearly inclined anteriorly with the anterodorsal tip almost reaching the level of the cranial margin of the zygosphenal roof. The caudal margin of the neural spine is vertical. The oval zygosphenal facets are small. The small lateral foramina occur below the well-developed interzygapophyseal ridges. The base of the pleurapophyses is wide. In dorsal view, the only preserved left prezygapophysis has an oval prezygapophyseal facet. The prezygapophyseal process is missing. The zygosphene is crenate with a wide medial lobe. The epizygapophyseal ridges are indistinct. In cranial view, the neural arch is vaulted, and the neural canal is rounded with small lateral sinuses. The zygosphenal lip is vaulted dorsally. The paracotylar foramina are situated within depressions on either side of the cotyle. The left paracotylar foramen is doubled in both vertebrae.

Remarks: The vertebrae are large with a general structure resembling that of 'large-sized colubrines'; however, the extremely short prezygapophyseal processes in the middle trunk vertebrae are rather unusual in these snakes. Poorly-developed prezygapophyseal processes were documented in several North American genera, including the middle Miocene *Nebraskophis* Holman, 1973 ('small-sized colubrine' snake) and extant *Pituophis* Holbrook, 1842 (Holman 1973, 2000; Van Devender and Mead 1978). However, the overall morphology of both above-mentioned genera strongly differs from 'Colubrinae' B. The material from Baikadam and Malyi Kalkaman 2 is limited; therefore, for a more precise comparison, more material is necessary.

Colubridae indet.

Material: Baikadam: one cervical vertebra (GIN 950/2001-RE16-62), 136 trunk vertebrae (GIN 950/2001-RE16-63‑198), 27 caudal vertebrae (GIN 950/2001-RE16-199-225); Malyi Kalkaman 1: seven trunk vertebrae (GIN 1107/1001-RE03-8-14); 1 caudal vertebra (GIN 1107/1001-RE03-15); Malyi Kalkaman 2: one cervical vertebra (GIN 1107/2001-RE03-6), four trunk vertebrae (GIN 1107/2001-RE03-7-10), 1 caudal vertebra (GIN 1107/2001-RE03-11).

Remarks: The overall gracile morphology of the heavily damaged vertebrae, together with the presence of a vaulted neural arch and paracotylar foramina, as well as short parapophyseal processes allow only their identification at the family level. More precise identification based on the available material is impossible.

Viperidae OPPEL, 1811
Viperinae OPPEL, 1811
Vipera LAURENTI, 1768
Vipera ('*Vipera aspis*' complex)
***Vipera* sp.**
(Figures 8A-P)

Material: Baikadam: 11 precaudal vertebrae (GIN 950/2001-RE16-226-236).

Description

Precaudal vertebrae. All vertebrae are fragmentary and preserved with broken neural spines and hypapophyses. In lateral view, the neural spine rises at the level of the posterior half of the zygosphenal roof length. However, the neural spines are broken-off close to their bases with the only exception of one posterior precaudal vertebra, where the complete neural spine is markedly low with vertical cranial and caudal margins (Figures 8(N)–(P)). The oval zygosphenal facets are narrow. The small lateral foramina occur close below the well-developed interzygapophyseal ridges. The subcentral ridges are strongly built and relatively short and straight. The synapophyses are damaged with the diapophyses slightly larger than the parapophyses. The parapophyseal processes are usually strongly damaged; however, the completely preserved right parapophyseal process of the anterior precaudal vertebra (Figure 8(A)) is clearly directed anteroventrally. In dorsal view, the vertebrae possess a wide interzygapophyseal constriction. The prezygapophyseal articular facets are subtriangular in outline and anteriorly enlarged. The prezypapophyseal processes are broken-off close to their bases but a partially damaged right prezygapophyseal process of one vertebra indicates that the prezagapophyseal process was probably more than a half of the prezygapophyseal facet length. In the anterior precaudal vertebrae (Figures 8(A)–(D)), the zygosphenal lip has developed small lateral lobes with a distinct wide medial lobe. However, the medial lobe is underdeveloped in the largest preserved vertebrae and the zygosphene is relatively narrow. The epizygapophyseal spines are absent or moderately developed. In ventral view, the centrum is triangular and elongated craniocaudally. The hypapophysis has a developed triangular anterior keel. Small subcotylar tubercles occur at the base of the cotylar rim. The subcentral grooves are wide and strongly developed in the posterior precaudal vertebrae. The rather small subcentral foramina occur at the base of the hypapophysis. The postzygapophyseal articular facets are subsquare in outline. In cranial view, the neural arch is depressed. The prezygapophyses are slightly tilted dorsally. The zygosphenal lip is straight. The neural canal is rounded with deep lateral sinuses. The paracotylar foramina occur within deep depressions on either side of the circular cotyle. The ventral margin of the cotylar rim is straight. In caudal view, the pedicle is strongly built. The zygantral area is gracile. The condyle is rounded. The measurements are as follows ($n = 4$): cl: or = 4.12–4.72 mm; naw: or = 2.56–3.07 mm; cl/naw: or = 1.54–1.61, mean 1.58 ± 0.03.

Remarks: The presence of the hypapophyses, depressed neural arch, dorsally inclined prezygapophyses and anterolaterally directed parapophyseal processes clearly document that the vertebrae belong to the family Viperidae. The preserved fragmentary hypapophyses document that there was no thickening of their ventral bases, unlike the rather massive hypapophyses of the precaudal vertebrae of the crotaline snakes reported from the same locality (see below). The vertebrae are longer than they are wide and, therefore, coincide with those of the '*Vipera aspis*' complex of the genus *Vipera* (Szyndlar 1991b; Szyndlar and Rage 1999). *Vipera* sp. from Baikadam partially resembles *Vipera antiqua* Szyndlar, 1987 reported from the early Miocene of Central Europe (Szyndlar 1987; Szyndlar and Schleich 1993; Szyndlar and Rage 2002) by its low neural spine (conspicuously low in the posterior precaudal vertebrae) and dorsally moderately inclined prezygapophyses. However, the condylar neck of the precaudal vertebrae of *Vipera* sp. is unusually long.

Crotalinae OPPEL, 1811
Gloydius HOGE & ROMANO-HOGE, 1981
Gloydius (*Gloydius halys* complex)
***Gloydius* sp.**
(Figures 9A-O)

Material: Baikadam: One right maxilla (GIN 950/2001-RE16-237), 16 precaudal vertebrae (GIN 950/2001-RE16-238-253), one cloacal vertebra (GIN 950/2001-RE16-254); Malyi Kalkaman 1: one precaudal vertebra (GIN 1107/1001-RE03-16).

Description

Maxilla. In anterior view, the body of the bone is low and the rather long lingually inclined ascending process is entirely shifted to the lingual border of the bone (Figures 9(A)–(C)). A distinct ridge (r1 – *sensu* Ivanov 1999) extends from the base of the process and diminishes in the middle of the ascending process length. The distal tip of the ascending process forms the distinct labial curvature of the process for maxillary-prefrontal articulation. Another ridge (r2 – *sensu* Ivanov 1999) occurs on the anteromedial border of the ascending process. The base of the fang connected to the labial side of the narrow portion of the bone possesses a partially preserved entrance lumen. In labial view, the base of the ascending process is wide and forms the lingual wall of the thermoreceptive organ. A small foramen occurs on the base of the process. A distinct large orifice of the o1 foramen for the maxillary branch of the trigeminal nerve occurs below the process for maxillary-prefrontal articulation. In posterior view, the o1 + o2 foramina (*sensu* Ivanov 1999) occur within the elongated oval depression bordered by the r2-ridge and a distinct crest situated on the posterior border of the bone. A damaged fossa for the maxillary-ectopterygoid articulation was probably indistinct.

Precaudal vertebrae. All preserved vertebrae are fragmentary usually with broken-off hypapophyses, neural spines and damaged synapophyses (Figures 9(D)–(L)). In lateral view, the neural spine is low with a vertical cranial margin. The neural spine diminishes in the caudal direction. The lateral foramina are small but well visible. They occur close below the relatively sharp

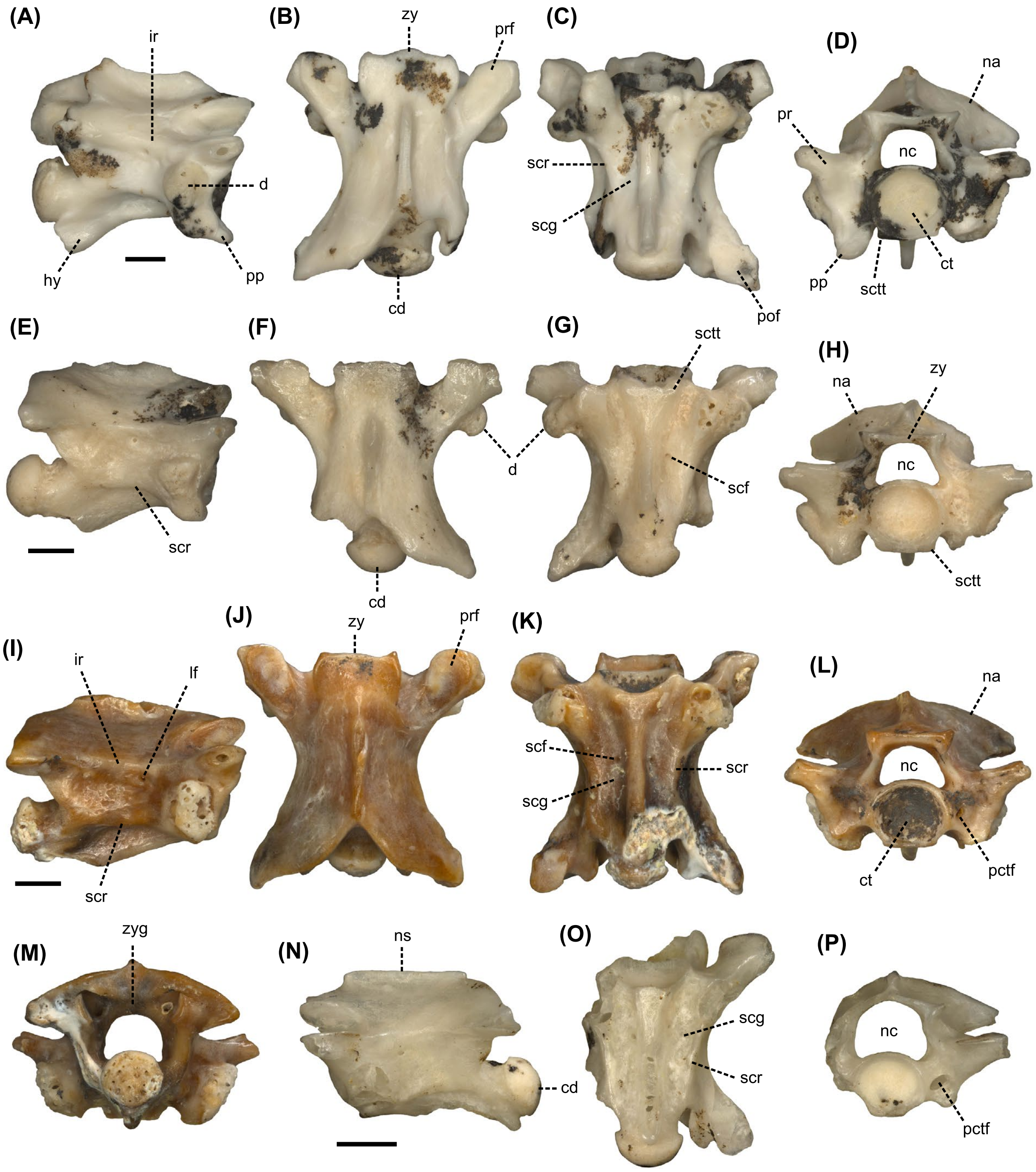

Figure 8. *Vipera* sp. ('*Vipera aspis*' complex). A-D, GIN 950/2001-RE16-226, anterior precaudal vertebra in right lateral (A), dorsal (B), ventral (C) and cranial (D) views; E-H, GIN 950/2001-RE16-227, precaudal vertebra in right lateral (E), dorsal (F), ventral (G) and cranial (H) views; I-M, GIN 950/2001-RE16-230, precaudal vertebra in right lateral (I), dorsal (J), ventral (K), cranial (L) and caudal (M) views; N-P, GIN 950/2001-RE16-232, posterior precaudal vertebra in left lateral (N), ventral (O) and cranial (P) views. Abbreviations: cd, condyle; ct, cotyle; d, diapophysis; hy, hypapophysis; ir, interzygapophyseal ridge; lf, lateral foramen; na, neural arch; nc, neural canal; ns, neural spine; pctf, paracotylar foramen; pof, postzygapophyseal articular facet; pp, parapophyseal proces; pr, prezygapophysis; prf, prezygapophyseal articular facet; scf, subcentral foramen; scg, subcentral groove; scr, subcentral ridge; sctt, subcotylar tubercle; zy, zygosphene; zyg, zygantrum. Scale equals 1 mm.

interzygapophyseal ridges. The synapophyses are well-divided into para- and diapophyses. The diapophysis is larger than the parapophysis. The parapophyseal process with wide base and pointed distal tip is directed anteroventrally. The straight subcentral ridges are distinct and long. They reach the close vicinity of the pedicle caudal margin. The hypapophysis is directed posteroventrally. In dorsal view, the vertebrae are short and wide. The prezygapophyseal articular facets are subtriangular and the prezygapophyseal processes are rather short. If preserved, they reach roughly to one-fourth of the prezygapophyseal articular facets length. The cranial margin of the zygosphenal roof is usually crenate with a distinctly developed medial lobe as well as two lateral lobes. In several specimens, the zygosphene is almost straight; however, this morphology can be the result of poor preservation. The epizygapophyseal ridges are missing. In ventral view, the subcentral ridges are blunt. In the anterior precaudal vertebrae, the subcentral grooves are shallow and well-developed only in the anterior half of the vertebra. In the

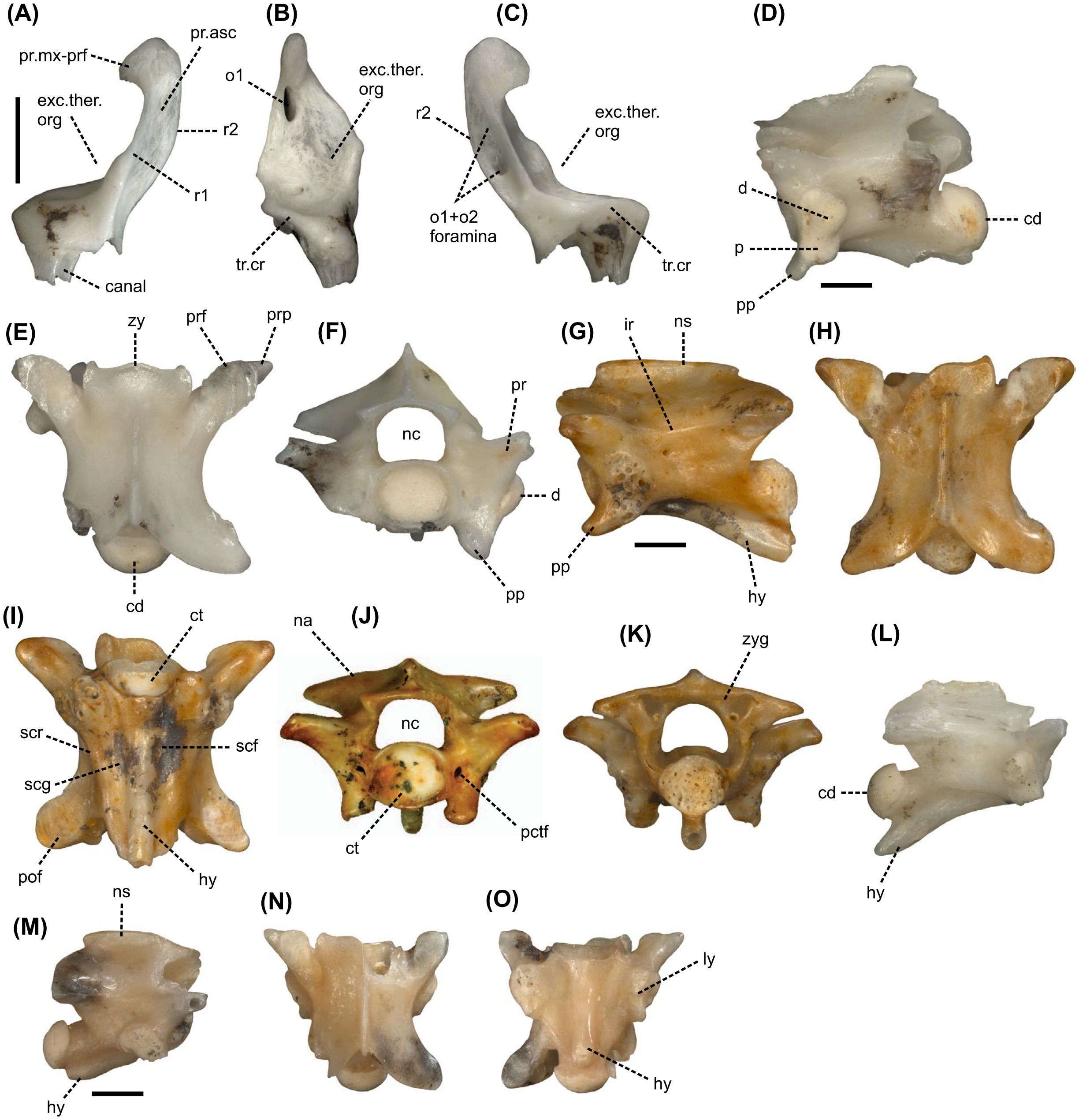

Figure 9. *Gloydius* sp. (*Gloydius halys* complex). A-C, GIN 950/2001-RE16-237, right maxilla in rostral (A), left labial (B) and posterior (C) views; D-F, GIN 950/2001-RE16-240, anterior precaudal vertebra in left lateral (D), dorsal (E) and cranial (F) views; G-K, GIN 950/2001-RE16-241, vertebra from the middle part of precaudal section in left lateral (G), dorsal (H), ventral (I), cranial (J) and caudal (K) views; L, GIN 950/2001-RE16-242, posterior precaudal vertebra from right lateral view; M-O, GIN 950/2001-RE16-254, cloacal vertebra from right lateral (M), dorsal (N) and ventral (O) views. Abbreviations: cd, condyle; ct, cotyle; d, diapophysis; exc.ther.org, excavation for the thermoreceptive organ; hy, hypapophysis; ir, interzygapophyseal ridge; ly, lymphapophysis; na, neural arch; nc, neural canal; ns, neural spine; p, parapophysis; pctf, paracotylar foramen; pof, postzygapophyseal articular facet; pp, parapophyseal proces; pr, prezygapophysis; pr.asc, ascendent proces; prf, prezygapophyseal articular facet; pr.mx-prf, proces for maxillary prefrontal articuation; prp, prezygapophyseal process; r1, r2, r1 and r2-ridge; o1, o2, o1 and o2 foramina; scf, subcentral foramen; scg, subcentral groove; scr, subcentral ridge; tr.cr, transverse crest; zy, zygosphene; zyg, zygantrum. Scale equals 1 mm.

posterior precaudal vertebrae, the subcentral grooves become markedly deeper. The subcentral foramina are rather small and indistinct. They occur at the base of the massively built hypapophysis. The base of the cotylar rim is either smooth, or small subcotylar tubercles can be observed. In cranial view, the neural arch is strongly depressed and the neural canal is rounded with relatively narrow lateral sinuses. The prezygapophyses are tilted dorsally. The cotylar rim is slightly depressed dorsoventrally. The paracotylar foramina are usually rather large. They mostly occur at the medial margin of deep depressions developed on both sides of the cotyle. The measurements are as follows ($n = 6$): cl: or = 3.10–4.64 mm; naw: or = 2.13–2.95 mm; cl/naw: or = 1.27–1.57, mean 1.43 ± 0.10.

Cloacal vertebra. The only preserved vertebra is short and wide (Figures 9(M)–(O)). The neural spine is low with an unpreserved cranial margin. The massively built hypapophysis is rather reduced with the caudal margin situated far from the anterior margin of the condyle. The lymphapophyses are broken-off close to their bases. The zygosphene is crenate. The prezygapophyseal articular facets are subtriangular and the only preserved left prezygapophyseal process is short (less than a half of the prezygapophyseal facet length).

Remarks: The maxillary excavation for the thermoreceptive organ is the most characteristic feature of Crotalinae (Brattstrom 1954, 1964). The ascending process that forms the lingual wall of the excavation is shifted to the lingual margin of the bone, unlike all true vipers (Brattstrom 1954, 1964; Meylan 1982). The direction of the ascending process, which is clearly lingually inclined, differs from the two maxillae reported from the early late Miocene of Grytsiv, Ukraine, where the lingual inclination is less distinct (Ivanov 1999; fig. 2 and 3). The r1-ridge reaches the base of the body of the bone and resembles that of Crotalinae gen. et sp. indet. A from Grytsiv (Ivanov 1999). The morphology of the maxilla from Baikadam closely resembles that of the genus *Gloydius*, which is a common representative of small crotaline snakes (Gloyd and Conant 1990; Wagner et al. 2016). In spite of the high intrageneric diversity (14 species) within the genus *Gloydius* (Uetz and Hošek 2017), the maxilla from Baikadam closely resembles that of the *Gloydius* species from the *Gloydius halys* complex [*Gloydius halys* (Pallas, 1776), *Gloydius intermedius* (Strauch, 1868), *Gloydius rickmersi* (Wagner, Tiutenko, Mazepa, Borkin & Simonov, 2016 – *sensu* Wagner et al. 2016)] and especially *Gloydius halys*.

The middle trunk vertebrae are wide and short with a strongly depressed neural arch. The small dimensions of the vertebrae, together with parapophyses directed anteroventrally, the markedly low neural spine and hypapophysis, which was directed posteroventrally, indicate that the vertebrae belonged to a small representative of Viperidae (Szyndlar and Rage 1999). Although the vertebrae are reminiscent of small viperinae snakes of the '*Vipera aspis*' complex and especially the extinct *Vipera antiqua* reported from the early Miocene of Central Europe (Szyndlar 1987; Szyndlar and Schleich 1993; Szyndlar and Rage 2002), the unusually strongly built hypapophysis, possessing a wide ventral margin as well as the relatively short parapophyseal processes with a wide basis, indicates the presence of Crotalinae (Szyndlar 1991b; Holman 2000; Holman and Tanimoto 2004). The small dimensions of all the precaudal vertebrae coincide with the dimensions of the preserved maxilla; therefore, we presuppose the identification of the fossil material as most probably belonging to the genus *Gloydius*.

Results

Palaeoenvironmental implications

The late middle Miocene vertebrate fauna from the Western Siberian localities Malyi Kalkaman 1 and 2 and Baikadam has provided a relatively rich snake assemblage (Table 1): Boidae: *Albaneryx* cf. *volynicus*, Boinae gen. et sp. indet.; Colubridae: *Coluber* cf. *hungaricus*, *Texasophis bohemiacus*, *Elaphe* aff. *dione*, cf. *Elaphe* sp., 'Colubrinae' A, 'Colubrinae' B, Colubridae indet.; Viperidae: *Vipera* sp. ('*Vipera aspis*' complex) and *Gloydius* sp. (*Gloydius halys* complex).

Among the studied localities, the most diverse snake fauna is provided from Baikadam, whereas the remaining two localities have at least 2–3 taxa each. The fossil snake fauna of Baikadam

Table 1. The amphibian and reptile fauna of the studied localities (Vasilyan et al. 2017), with an update on snake fauna and palaeoprecipitation estimates for those localities.

	Order	Family	Taxon	Malyi Kalkaman 2	Malyi Kalkaman 1	Baikadam	Ecophysiological group
MN				7–8	7–8	7–8	
Age (in Ma)				12.6	12.6	12.1	
Age error				0.8	0.8	0.8	
	Proteoidea	Proteidae	*Mioproteus* sp.	1			aquatic
	Cryptobranchoidea	Hynobiidae	*Salamandrella* sp.		0.3918		peri-aquatic
	Salamandroidea	Salamandridae	*Chelotriton* sp.		0.3918		peri-aquatic
			aff. *Tylototriton* sp.			0.3918	peri-aquatic
	Anura	Bombinatoridae	*Bombina* sp.	0.3918			peri-aquatic
		Bufonidae	*Bufotes viridis*	0	0	0	heliophile
		Ranidae	*Rana temporaria*		0.3918		peri-aquatic
			Rana sp.	0.3918		0.3918	peri-aquatic
			Pelophylax sp.	0.513	0.513		semi-aquatic
	Chelonia	Geoemydidae	*Ocadia* cf. *illiensis*		1		aquatic
		Emydidae	*Chrysemys* cf. *jegalici*		1		aquatic
	Squamata	Lacertidae	*Lacerta* s.l. sp. 1			0	heliophile
			Lacertidae indet.	0	0		heliophile
		Anguidae	*Ophisaurus* sp.			0	heliophile
		Boidae	*Albaneryx* cf. *volynicus*			0.0917	fossorial
			Boinae gen. et sp. indet.			+	N/A
		Colubridae	*Coluber* cf. *hungaricus*			+	N/A
			Texasophis bohemiacus			+	N/A
			cf. *Elaphe* sp.	+	+		N/A
			Elaphe aff. *dione*		+	+	N/A
			'Colubrinae' A	+		+	N/A
			'Colubrinae' B	+		+	N/A
			Colubridae indet.	+	+	+	N/A
		Viperidae	*Gloydius* sp. (*Gloydius halys* complex)		+	+	N/A
			Vipera sp. ('*Vipera aspis*' complex)			+	N/A
			ecophysiological index	0.3828	0.4611	0.1459	
			mean annual precipitation (MAP) (in mm)	883.87	1071.93	314.81	
			recent MAP (in mm)	255	255	255	
			(near) city/town of the value or recent MAP	Pavlodar	Pavlodar	Pavlodar	
			95 % prediction interval - error (in mm)	254.4	258.8	254.9	
			MAP/MAP.recent (in %)	346.62	420.36	123.45	

contains taxa, whose living relatives largely prefer a rather broad range of habitats – from deciduous and coniferous forests to steppe or semi-desertic diverse environments with low vegetation, as well as habitats with slide-rock landscapes and wet sandy soils for the fossorial boids (Ananjeva et al. 2006). Although the localities Malyi Kalkaman 1 and 2 provide significantly less diverse snake fauna than Baikadam, it can be characterised by the comparable environment, with its broad range from deciduous and coniferous forests to steppe or semi-desertic diverse environments as well. The general image of the palaeoenvironment of these localities can also be completed by the amphibian and reptile (non-snake) faunas. The Malyi Kalkaman 1 and 2 localities include forms (Vasilyan et al. 2017) suggesting the presence of aquatic environments (*Mioproteus* sp. for running waters; and *Pelophylax* sp, *Ocadia* sp. and *Chrysemys* sp. for standing water bodies, like ponds or slow flowing rivers); diverse terrestrial environments such as shadowed forests (*Chelotriton* sp., aff. *Tylototriton* sp., *Salamandrella* sp. and *Rana temporaria* Linnaeus, 1758); well-vegetated steppes (*Salamandrella* sp.); open areas near water bodies (*Rana temporaria*, *Rana* sp.); and open areas with slide-rocky landscapes with *Bufotes viridis* (Laurenti, 1768), Lacertidae indet. and Anguinae indet. The fauna of the Baikadam locality (Vasilyan et al. 2017) suggests the predominance of open habitats (*Bufotes viridis*, *Lacerta* sp., *Ophisaurus* sp., Anguinae indet.) with some forms indicating forested areas (aff. *Tylototriton* sp., *Rana* sp.), which is also in good agreement with the snake fauna.

Affinity of Siberian snake fauna with European snake assemblages

The Asian fossil snake fauna is still poorly known. Except for the late middle to early late Miocene Tagay (Togay) site, Ol'khon Island and Baykal Lake (Rage and Danilov 2008), all other Miocene Siberian localities are only known from the Zaisan Basin and nearby areas. The more precisely determined snake taxa from the Zaisan Basin and Central Mongolia (Valley of Lakes; Böhme 2007) belong to extant genera: Erycinae (*Eryx* sp. 1 and 2), indeterminate 'Colubrinae' (Colubrinae 1 and 2 – *sensu* Böhme 2007), Natricinae indet. (Böhme 2007); and Erycinae (*Eryx* sp.) and Viperinae (*Pelias* sp.) (Chkhikvadze 1985). Although the middle Miocene snake fauna reported from the Tagay (Togay) (Rage and Danilov 2008) also provided snakes largely determined only at the familiar or generic levels, it seems interesting that the posterior trunk vertebra of Boinae gen. et sp. indet. and the trunk vertebrae of *Coluber* s.l. '*unnamed species A*' were probably closely related to a species that appeared in Central Europe as early as the early Miocene (Ivanov 2002; Szyndlar 2005, 2012). A fossil snake fauna is also known to have existed in a locality south of Western Siberia, in the Turgai Depression (Shalkar-Teniz locality, Oligocene) (Malakhov 2009).

Boidae

The first possible appearance of the genus *Albaneryx* is known from the middle Miocene of Sansan (Augé and Rage 2000). The western-most occurrence of this genus (*Albaneryx depereti* Hoffstetter & Rage, 1972) was reported from the late middle Miocene of La-Grive-Saint-Alban, France (Hoffstetter and Rage 1972). The coeval occurrence of *Albaneryx* cf. *volynicus* in Baikadam indicates that the genus *Albaneryx* was probably widely distributed in the Eurasiatic region during the late middle Miocene. Although this assumption is supported by the presence of cf. *Albaneryx* sp. from the late middle Miocene of Kleineisenbach, Germany (Böhme and Ilg 2003), this genus is unknown from any other Central European middle Miocene localities. *Albaneryx* from Baikadam closely resembles *Albaneryx volynicus* from the type locality of Grytsiv, Ukraine (Zerova 1989), early late Miocene (11.1 Ma; Kirscher et al. 2016). The possible presence of this species in coeval Felsőtárkány 2, Hungary (*Albaneryx* cf. *volynicus*; Venczel and Hír 2013) indicates that this species persisted in Central and Eastern Europe until the very beginning of the late Miocene. The extinction of *Albaneryx* and decline of other sand boas (of the extant genus *Eryx* Daudin, 1803) from Central and Eastern Europe were probably caused by the climatic changes in the late Miocene when there were rather dry climatic conditions in late Serravallian and late Sarmatian s.s. (around 12 Ma); the mean annual precipitation (MAP) 310‒600 mm was replaced by strongly increased humidity (MAP from 800 up to 1500 mm) during the early Tortonian, early Pannonian (Böhme and Vasilyan 2014). This warm and humid period is known as the first phase of the 'wash-house climate' (Böhme et al. 2008) and most probably was not suitable for erycines, which prefer dry sandy habitats (Darewskij 1993; Tokar and Obst 1993). The small-sized erycines were present in the Zaisan Basin since the early Miocene, but any comparison with this record is impossible since so far they are unfigured and not described (Chkhikvadze 1985). Despite the humid phases in the Zaisan Basin during the Neogene period (Vasilyan et al. 2017), erycines are known reliably from Pliocene and early Pleistocene localities of eastern Kazahkstan: cf. *Eryx* sp. - Pavlodar 3A, early Pliocene, MN 15; *Eryx* sp. [cf. *miliaris* (Pallas, 1773)] – Lebiazhie 1B, early Pleistocene, MN 17 (Ivanov – unpublished) as well as the late Miocene of Mongolia (Böhme 2007).

Snakes of the subfamily Boinae are rare in southern Siberian records; however, indeterminate Boinae reported from the middle Miocene Tagay (Togay) (Rage and Danilov 2008) and Baikadam sites indicate that the subfamily Boinae was largely distributed in regions north of southern Eurasia throughout the middle Miocene. The indeterminate Boinae from Baikadam and Tagay (Togay) are probably closely related to each other and may even represent a single species. However, both preserved specimens differ from the genus *Bavarioboa*, which is the only representative of large Boinae in the European Miocene, with the last occurrence in the early middle Miocene (15 Ma) of Griesbeckerzell 1a, Germany (*Bavarioboa* aff. *hermi*; Ivanov and Böhme 2011). Although the large Boinae disappeared from Europe as a result of the cooling at the end of the Miocene Climatic Optimum (MCO; Böhme 2003), this subfamily persisted in Central and East Eurasia for the next 2–3 million years. The only Boinae genus reported from the Neogene of Eurasia is *Bavarioboa*, with the first occurrences in Western Europe in the late Oligocene (Szyndlar and Rage 2003). The late Oligocene (Rupelian/early Chattian) *Bavarioboa* from the Mendikdere Formation (Turkey) indicates the close terrestrial connections of southwestern Asia with Europe (Szyndlar and Hoşgör 2012). Although *Bavarioboa* temporarily disappeared from Europe at the end of the Oligocene, possibly as a result of aridification, it seems probable that this genus could have survived the Oligocene/Miocene transition in southwestern Asia (Szyndlar and Hoşgör 2012).

Colubridae

Colubrid snakes are the most diverse group in the snake assemblage from Baikadam and Malyi Kalkaman 1 and 2. At least two ‘colubrines’ reported from Baikadam, *Coluber* cf. *hungaricus* and *Texasophis bohemiacus*, are known from European fossil records. *Texasophis bohemiacus* appeared in Central Europe as early as the early Oligocene; the last occurrence is known from the late early Miocene (Szyndlar 1987, 1994, 2012). In Asia, *Texasophis* sp. has been reported from the Tagay locality, Ol’khon Island, middle Miocene. This locality is slightly older than the Malyi Kalkaman 1 and 2 and suggests that the genus *Texasophis* once had wide distribution on the Eurasian continent from Europe to East Asia during the middle Miocene. In total, three fossil genera, *Texasophis* Holman, 1977; *Neonatrix* Holman, 1973 and *Paleoheterodon* Holman, 1964 have long been considered to be possible North American immigrants (Rage and Holman 1984; Szyndlar and Schleich 1993; Ivanov 2001). Although all three genera have been described from North America (Holman 1977, 2000), their New World origin remains questionable. As already suggested, the Asiatic origin of these genera seems possible with subsequent dispersals into both Europe and North America (Szyndlar 1994, 2012). However, Rage and Bailon (2005) admit that the similar vertebral morphologies between the Eurasian and North American representatives of these genera resulted from the convergent evolution of unrelated snake lineages.

The presence of *Coluber* cf. *hungaricus*, which is known from several Central and South European localities from the early middle Miocene up to the early Pliocene (Venczel 1994, 1998; Szyndlar 2009, 2012; Ivanov and Böhme 2011), also supports the assumption (Rage and Danilov 2008) that the middle Miocene snake fauna from Baikadam (like fauna from Tagay) may be regarded as a relict of the formerly homogenous Eurasian fauna (excluding southern Eurasia). Rage and Danilov (2008) describe the colubrines (*Coluber* s.l., *unnamed species A*) from the Tagay locality as closely similar to the European ‘large-sized colubrines’, *‘Coluber’ pouchetii* (de Rochebrune, 1880) and *‘Coluber’ dolnicensis* Szyndlar, 1987. However, the above-mentioned ‘large-sized colubrines’ reported from Central and Western Europe as early as the early Miocene (*‘Coluber’ dolnicensis*, Merkur-North, MN 3a – Ivanov 2002) and early middle Miocene [*‘Coluber’ pouchetii* (de Rochebrune, 1880), Sansan, MN 6 – Augé and Rage 2000;] are absent from the localities of northeastern Kazakhstan. Moreover, the fragmentary preserved vertebrae of ‘Colubrinae’ B with extremely short prezygapophyseal processes differ from all known ‘large-sized colubrines’ and may represent a new genus. The morphotype ‘Colubrinae’ A, described from Baikadam and Malyi Kalkaman 2, also differs by its peculiar morphology from small-sized ‘colubrines’ known from the European Miocene. The vertebral morphology of *Elaphe* aff. *dione* from Baikadam and Malyi Kalkaman 1 resembles that of extant representatives that inhabit large areas of Eurasia, including Kazakhstan (Obst and Ščerbak 1993).

Regarding ‘Natricinae’ snakes, the period from the late early to middle Miocene is considered in Europe to be the ‘Age of »Natricinae«’ with at least nine extinct species assigned to three different genera – extant *Natrix* Laurenti, 1768; extinct *Neonatrix* Holman, 1973 and *Palaeonatrix* Szyndlar, 1982 (Szyndlar in Młynarski et al. 1982; Szyndlar 2012). We presuppose that at least *Natrix* and *Neonatrix* are descendants of the Asiatic ‘natricine’ lineages (Rage and Holman 1984; Szyndlar and Schleich 1993; Rage and Bailon 2005; Szyndlar 2005); therefore, the total absence of ‘natricines’, not only in the studied localities but also in all early and middle Miocene localities in the Zaisan Basin (Chkhikvadze 1985), is astonishing. The absence of ‘natricines’ in Baikadam can be explained as a result of the rather drier climatic conditions in this locality with a MAP of about 300 mm; in Malyi Kalkaman 1 and 2 the climate was more humid and the MAP varied from about 880 to 1100 mm (Table 1; Vasilyan et al. 2017). We do not expect that the absence of ‘natricines’ in the middle Miocene of Siberia is an artefact (e.g. caused by a limited number of preserved snake remains).

Viperidae

True vipers assigned to ‘*Vipera aspis*’ complex are reported only from the Baikadam site. The remains of the early and middle Miocene vipers reported by Chkhikvadze (1985) from the Zaisan Basin do not have distinct taxonomic assignation (Szyndlar and Rage 2002) and need to be revised. Regarding the ‘Oriental vipers’, the only fragmentary vertebra from the Miocene of Siberia comes from the middle Miocene Tagay site (Rage and Danilov 2008).

The subfamily Crotalinae is reported by the presence of *Gloydius* sp. from the late middle Miocene localities of Baikadam and Malyi Kalkaman 1. Apart from a single trunk vertebra of possible *Trimeresurus* Lacépède, 1804 (cf. *Trimeresurus* sp. indet.) from the late early Miocene of Mizunami, Japan (Holman and Tanimoto 2004) and the indeterminate maxillaries of Crotalinae gen. et sp. indet. A and B from the early late Miocene of Grytsiv, Ukraine (Ivanov 1999), the new record of *Gloydius* sp. represents the third distinct occurrence of the crotaline snakes in the Old World. The small dimensions and morphology of the only preserved maxilla coincide with those of the extant genus *Gloydius*, which inhabits Siberia in the present time (Gloyd and Conant 1990; Gumprecht et al. 2004). The discovery of *Gloydius* sp. in the late middle Miocene of Kazakhstan (13–12 Ma; Vasilyan et al. 2017), as well as occurrences of indeterminate crotalines (different from those of Kazakhstan) in the early late Miocene of Ukraine (Grytsiv, 11.1 Ma; Ivanov 1999) indicate that snakes of the subfamily Crotalinae were probably widely distributed in the Eurasian region since the middle Miocene, and diversified in the late Miocene. This assumption is supported by molecular studies which revealed the monophyletic *Gloydius* lineage (Fenwick 2012; Pyron et al. 2013), formed probably in the early middle Miocene at 15 Ma, and the species differentiation which could begin in the late Miocene about 10 Ma (Xu et al. 2012). It seems probable that the crotalines never entered Central Europe (Ivanov 1999).

Conclusions

The fossil snakes from the late middle Miocene of northeastern Kazakhstan represent so far the best-documented Miocene snake assemblage in Central Asia. Previous studies, which were based on rather limited material from several localities (Figure 1), admitted that snake fauna could be homogeneous over a large part of Eurasia (excluding South Asia) during the Miocene with the late middle (or early late) Miocene assemblages being similar to snake assemblages which inhabited Europe in the late early and early middle Miocene (MN 3 to MN 5) (Rage and Danilov 2008; Szyndlar 2012). This assumption is partially supported by the presence of *Texasophis bohemiacus* and *Coluber* cf. *hungaricus*, as well as small vipers of the '*V. aspis*' complex in the Baikadam site. However, the presence of taxa which are probably not related to European representatives ('Colubrinae' A and B), as well as taxa which never occurred in Central and Western Europe and which are closely related to species recently inhabiting southern Siberia (*Elaphe* aff. *dione*, *Gloydius* sp.), indicates that the faunal dissimilarity was relatively high within Eurasia during the late middle Miocene. This assumption is in accordance with Maridet et al. (2007), who reported decreasing homogenity of the European mammal assemblages during the middle Miocene.

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References

Ananjeva NB, Orlov NL, Khalikov RG, Darevsky I, Ryaboc SA, Barabanov AV. 2006. The reptiles of Northern Eurasia: Taxonomic diversity, distribution, conservation status. Sofia: Pensoft; p. 245.

Augé M, Rage J-C. 2000. Les Squamates (Reptilia) du Miocéne moyen de Sansan (Gers, France). Mém Mus Natl Hist Nat. 183:263–313.

Blain H-A. 2016. Amphibians and Squamate Reptiles from Azokh 1. In: Fernández-Jalvo Y, King T, Yepiskoposyan L, Andrews P, editors. Azokh Cave and the Transcaucasian Corridor. Springer; p. 191–210.

Böhme M. 2003. The Miocene climatic optimum: evidence from the ectothermic vertebrates of Central Europe. Palaeogeogr Palaeoclimatol Palaeoecol. 195:389–401.

Böhme M. 2007. Herpetofauna (Anura, Squamata) and palaeoclimatic implications: preliminary results. In: Daxner-Höck G, editor. Oligocene-Miocene Vertebrates from the Valley of Lakes (Central Mongolia): Morphology, phylogenetic and stratigraphic implications. Vol. 108A. Ann Nat hist Mus Wien; p. 43-52.

Böhme M, Ilg A. 2003. FosFARbase. [accessed 2017 April 24]. www.wahre-staerke.com/.

Böhme M, Ilg A, Winklhofer M. 2008. Lace Miocene 'washhouse' climate in Europe. Earth Planet Sci Lett. 275:393–401.

Böhme M, Vasilyan D. 2014. Ectothermic vertebrates from the late Middle Miocene of Gratkorn (Austria, Styria). Palaeobio Palaeoenv. 94:21–40.

Bolkay St J. 1913. Additions to the fossil herpetology of Hungary from the Pannonian and Praeglacial periode. Mitteilungen aus dem Jahrbuch der koeniglichen ungarischen Geologischen Reichsanstalt. 21:217–230.

Bonaparte CL. 1831. Saggio di una distribuzione metodica degli animali vertebrati. Rome: Antonio Boulzaler; p. 144.

Borisov BA. 1963. Stratigraphy of upper Cretaceous and Paleogene-Neogene of Zaisan basin. Trans Pansov Sci Res Geol Instit. New Ser. 94:11–75.

Brattstrom BH. 1954. The fossil pit-vipers (Reptilia: Crotalidae) of North America. Trans San Diego Soc Nat Hist. 12:31–46.

Brattstrom BH. 1964. Evolution of the pit vipers. Trans San Diego Soc Nat Hist. 13(11):31–46.

Chkhikvadze VM. 1984. Survey of the fossil urodelan and anuran amphibians from the USSR. Izvest Akad Nauk Gruz SSR, Ser Biol. 10(1):5–13 (in Russian).

Chkhikvadze VM. 1985. Preliminary results of studies on tertiary amphibians and squamate reptiles of the Zaisan Basin. In: Darevsky I, editor. Questions of herpetology, The sixth all-union herpetological conference. Tashkent: Nauka; p. 234–235 (in Russian).

Chkhikvadze VM. 1989. Neogene turtles of USSR. Tbilisi: Metsniereba (in Russian).

Darewskij IS. 1993. *Eryx miliaris* (Pallas, 1773) – Östliche Sandboa. In: Böhme W, editor. Handbuch der Reptilien und Amphibien Europeas. Wiesbaden: AULA – Verlag; p. 55-66 (in German).

Daudin FM. 1803. Histoire Naturelle Generale et Particuliere des Reptiles. Vol. 6. Paris: F. Dufart; p. 108.

Daxner-Höck G, Böhme M, Kossler A. 2013. New data on Miocene biostratigraphy and paleoclimatology of Olkhon Iland (Lake Baikal, Siberia). In: Wang X, Flynn LJ, Fortelius M, editors. Fossil mammals of Asia: Neogene biostratigraphy and chronology. New York (NY): Columbia University Press; p. 508–517.

Fahlbusch V, Mayr H. 1975. Microtoide Cricetiden (Mammalia, Rodentia) aus der Oberen Süßwasser-Molasse Bayerns. Paläontologische Zeitschrift. 49:78–93.

Fenwick A. 2012. Beyond building a tree: Phylogeny of pitvipers and exploration of evolutionary patterns. Electronic Theses and Dissertations Paper 2333, University of Central Florida.

Fitzinger LJ. 1833. *Elaphe parreyssii* – Parreyss's *Elaphe*. In: Wagler J, editor. Descriptiones et icones Amphibiorum (3). München: JG Cotta'sche Buchhandlung; p. 3–4.

Gloyd HK, Conant R. 1990. Snakes of the *Agkistrodon* complex – A monographic review. Oxford (Ohio): Society for the study of Amphibians and Reptiles; p. 614.

Gnibidenko ZN. 2006. Late Cenozoic paleomagnetism of the West Siberian Plate. Russian Geol Geophys. 48(4):337–348.

Gray JE. 1825. A synopsis of the genera of Reptilia and Amphibia. Ann Philos, N S. 10:193–217.

Gumprecht A, Tillack F, Orlov NL, Captain A. 2004. Asian Pitvipers. Berlin: Geitje Books.

Head J. 2005. Snakes of the Siwalik Group (Miocene of Pakistan): Systematics and relationships to environmental change. Palaeontol Electron. 8:1–33.

van den Hoek Ostende LW, Gardner JD, van Bennekon L, Alçiçeket C, Murray A, Wesselingh FP, Alçiçek H, Tesakov A. 2015. Ericek, a new Pliocene vertebrate locality in the Çameli Basin (southwestern Anatolia, Turkey). Palaeobio Palaeoenv. DOI:10.1007/s12549-015-0202-3.

Hoffstetter R, Gasc J-P. 1969. Vertebrae and Ribs of Modern Reptiles. In: Gans C, Bellairs Ad'A, Parsons TS, editors. Biology of the Reptilia. Vol. 1. London: Morphology A. Academic Press; p. 200-310.

Hoffstetter R, Rage J-C. 1972. Les Erycinae fossiles de France (Serpentes, Boidae). Compréhension et histoire de la sous-famille. Annls Paléont (Vert) 58(1):81–124.

Hoge AR, Romano-Hoge SA. 1981. Poisonous snakes of the World. I. Checklist of the Pitvipers: Viperoidea, Viperidae, Crotalinae. Mem Inst Butantan. 42/43:179-309.

Holbrook JE. 1842. North American Herpetology; or, A Description of the Reptiles Inhabiting the United States. Vol. IV. Philadelphia, PA: J. Dobson; p. 138.

Holman JA. 1964. Fossil snakes from the Valentine Formation of Nebraska. Copeia. 1964:631–637.

Holman JA. 1973. Reptiles of the Egelhoff local fauna (Upper Miocene) of Nebraska. Contrib Mus Paleontol. 24:125–134.

Holman JA. 1977. Amphibians and reptiles from the Gulf Coast Miocene of Texas. Herpetologica. 33:391–403.

Holman JA. 1984. *Texasophis* (Reptilia: Serpentes), an Addition to the Miocene (Clarendonian) of North America. Copeia. 1984(3):660–661.

Holman JA. 2000. Fossil snakes of North America origin, evolution, distribution, paleoecology. Bloomington: Indiana University Press; p. 357.

Holman JA, Tanimoto M. 2004. Cf. *Trimeresurus* Lacépède (Reptilia: Squamata: Viperidae: Crotalinae) from the Early Miocene of Japan. Acta zool cracov. 47(1):1-7.

Ivanov M. 1999. The first European pit viper from the Miocene of Ukraine. Acta Palaeontol Pol. 44(3):327–334.

Ivanov M. 2001. Changes in the composition of the European snake fauna during the Early Miocene and at the Early/Middle Miocene transition. Paläont Z. 74(4):563–573.

Ivanov M. 2002. The oldest known Miocene snake fauna from Central Europe: Merkur-North locality, Czech Republic. Acta Palaeontol Pol. 47(3):513–534.

Ivanov M, Böhme M. 2011. Snakes from Griesbeckerzell (Langhian, Early Badenian), North Alpine Foreland Basin (Germany), with comments on the evolution of snake fauna in Central Europe during the Miocene Climatic Optimum. Geodiversitas. 33(3):411–449.

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

Lacépède BGEL. 1804. Mémoire sur plusieurs animaux de la Nouvelle-Hollande dont la description n'a pas encore été publiée. Annls Mus Hist nat Paris. 4:184–211.

Laurenti JN. 1768. Austriaci Viennensis specimen medicum, exhibens synopsin reptilium emendatam cum experimentis ca Venena et antidota reptilium Austriacorum quod authoritate et consensu., Wien: J. Thomae, Caes. Reg. Aulae Typogographi; p. 217.

Linnaeus C. 1758. Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Holmiæ: Tomus I. Editio decima, reformata, Laurentii Salvii; p. 824.

Lucas SG, Bray ES, Emry RJ, Hirsch KF. 2012. Dinosaur eggshell and the Cretaceous-Paleogene boundary in the Zaysan Basin, Eastern Kazakstan. J Stratigr. 36(2):417–435.

Lychev GF. 1963. Neogene mammals of Malyi Kalkaman site. In: Materials on the history of fauna and flora of Kazakhstan. Vol. 10. Alma-Ata; p. 12-21 (in Russian).

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

Malakhov DV. 2009. Fossil amphibians and reptiles from Cenozoic of Kazakhstan: state of art and new materials. Trans Instit Zool MES RK. 50:25–34.

Maridet O, Escarguel G, Costeur L, Mein P, Hugueney M, Legendre S. 2007. Small mammals (rodents and lagomorphs) European biogeography from the Late Oligocene to the mid Pliocene. Glob Ecol Biogeogr. 16:529–544.

Meylan PA. 1982. The Squamate Reptiles of the Inglis IA Fauna (Irvingtonian: Citrus County, Florida). Bull Florida State Mus, Biol Sci. 27(3):1-85.

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

Nopcsa F. 1923. Die Familien der Reptilien. Fortschr Geol Paläontol. 2:1–210.

Obst FJ, Ščerbak NN. 1993. *Elaphe dione* (Palaas, 1773) – Steppennatter. In: Böhme W, editor. Handbuch der Reptilien und Amphibien Europeas. Wiesbaden: AULA – Verlag; p. 295–315.

Oppel M. 1811. Die Ordnungen, Familien und Gattungen der Reptilien als Prodrom einer Naturgeschichte derselben. München: Joseph Lindauer; p. 86.

Paicheler JC, de Broin F, Gaudant J, Mourer-Chauviré C, Rage J-C, Vergnaud–Grazzini C. 1978. Le bassin lacustre miocène de Bes-Konak (Anatolie–Turquie): Géologie et introduction à la paléontologie des Vertébrés. Geobios. 11:43–65.

Pallas PS. 1773. Reise durch verschiedene Provinzen des Russischen Reiches. Vol. 2. St. Petersburg: Kaiserl Akad Wiss.; p. 744.

Pallas PS. 1776. Reise durch verschiedene Provinzen des russischen Reichs. Vol. 3. St. Petersburg: Kais Akad Wiss.; p. 703.

Pyron RA, Burbrink FT, Wiens JJ. 2013. A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. BMC Evol Biol. 13(1):93. DOI:10.1186/1471-2148-13-93.

Rage J-C. 1984. Serpentes. In: Wellnhofer P, editor. Handbuch der Paläoherpetologie (Encyclopedia of Paleoherpetology). Vol. 11. Stuttgart: Gustav Fischer Verlag; p. 80.

Rage J-C, Bailon S. 2005. Amphibians and squamate reptiles from the late early Miocene (MN 4) of Béon 1 (Montréal-du-Gers, southwestern France). Geodiversitas. 27(3):413–441.

Rage J-C, Danilov IG. 2008. A new Miocene fauna of snakes from eastern Siberia, Russia. Was the snake fauna largely homogenous in Eurasia during the Miocene? C R Palevol. 7:383–390.

Rage J-C, Ginsburg L. 1997. Amphibians and squamates from the Early Miocene of Li Mae Long, Thailand: the richest and most diverse herpetofauna from the Cainozoic of Asia. In: Roček Z, Hart S, editors. Herpetology. Vol. 97. Prague; p. 167–168.

Rage J-C, Gupta SS, Prasad GVR. 2001. Amphibians and squamates from the Neogene Siwalik beds of Jammu and Kashmir, India. Paläont Z. 75:197–205.

Rage J-C, Holman JA. 1984. Des Serpents (Reptilia, Squamata) de type Nord-Américain dans le Miocéne francais. Evolution paralléle ou dispersion? Géobios. 17:89–104.

Rage J-C, Sen S. 1976. Les amphibiens et les reptiles du Pliocéne supérieur de Çalta (Turquie). Géol Médit. 3(2):127–134.

Ratnikov VJ. 2002. Pozdnekainozoiskie zemnovodnye i češujčatye presmykajuščiesja vostočno-evropejskoj ravniny [Late Cenozoic amphibians and reptiles of the East-European Platform]. Trudy Voronežskyj gosudarstvennyj universitet, Naučno-issledovatelskij institut geologii, Voronež. 10:1–138 (in Russian).

Ratnikov VJ. 2004. Identification of some Eurasian species of *Elaphe* (Colubridae, Serpentes) on the basis of vertebrae. Russ J Herpetol. 11(2):91–98.

de Rochebrune AT. 1880. Révision des ophidiens fossiles du Muséum d'Histoire naturelle. Nouv Arch Mus Hist Nat Paris. 2(3):271–296.

Schaub S. 1930. Fossile Sicistinae. Schweiz Paleont Ges, Eclogae geol Helvetiae. 23(2):616–636.

Schlosser M. 1924. Tertiary vertebrates from Mongolia. Palaeont Sinica, ser C. 1:1-119.

Schneider JG. 1801. Historiae Amphibiorum naturalis et literariae Fasciculus secundus continens Crocodilos, Scincos, Chamaesauras, Boas Pseudoboas, Elapes, Angues Amphisbaenas et Caecilias. Jena: Frommanni; p. 374.

Strauch A. 1868. Concerning poisonous snakes distributed in Russia. Trudy Perv Siezda Russ Yestestv Zool 1(294) (also cited as Trans First Conf Russ Nat., St.Petersburg) 1:271–297 (in Russian).

Sun A. 1961. Notes on fossil snakes from Shanwang, Shangtung. Vertebrat Palasiatic. 4:310–312.

Swinton WE. 1926. *Daunophis langi*, gen et sp. n. (Pliocene, Burma). Ann Mag nat Hist. 17:342–348.

Szyndlar Z. 1984. Fossil snakes from Poland. Acta zool cracov. 28(1):3–156.

Szyndlar Z. 1987. Snakes from the lower Miocene locality of Dolnice (Czechoslovakia). J Vert Paleontol. 7:55–71.

Szyndlar Z. 1991a. A review of neogene and quaternary snakes of Central and Eastern Europe. Part I: Scolecophidia, Boidae, Colubridae. Estud geol. 47:103–126.

Szyndlar Z. 1991b. A review of neogene and quaternary snakes of Central and Eastern Europe. Part II: Natricinae, Elapidae, Viperidae. Estud geol. 47:237–266.

Szyndlar Z. 1994. Oligocene snakes of the Southern Germany. J Vert Paleontol. 14(1):24–37.

Szyndlar Z. 2005. Snake fauna from the Late Miocene of Rudabánya. Palaeontogr ital. 90(2003):31–52.

Szyndlar Z. 2009. Snake fauna (Reptilia: Serpentes) from the Early/Middle Miocene of Sandelzhausen and Rothenstein 13 (Germany). Paläontol Z. 83:55–66.

Szyndlar Z. 2012. Early Oligocene to Pliocene Colubridae of Europe: a review. Bull Soc Géol Fr. 183(6):661–681.

Szyndlar Z, Hoşgör I. 2012. *Bavarioboa* sp. (Serpentes, Boidae) from the Oligocene/Miocene of eastern Turkey with comments on connections between European and Asiatic snake faunas. Acta Palaeont Pol. 57(3):667-671.

Szyndlar Z, Rage J-C. 1999. Oldest fossil vipers (Serpentes: Viperidae) from the Old World. Kaupia. 8:9–20.

Szyndlar Z, Rage J-C. 2002. Fossil record of the true vipers. In: Schuett GW, Höggren M, Douglas ME, Greene HW, editors. Biology of the vipers. Eagle Mountain: Eagle Mountain Publishing; p. 419–444.

Szyndlar Z, Rage J-C. 2003. Non-erycine Booidea from the Oligocene and Miocene of Europe. Kraków: Institute of Systematics and Evolution of Animals, Polish Academy of Sciences; p. 109.

Szyndlar Z, Schleich HH. 1993. Description of Miocene snakes from Petersbuch 2 with comments on the Lower and Middle Miocene ophidian faunas of Southern Germany. Stuttgarter Beitr Naturk B. 192:1–47.

Szyndlar Z, Schleich HH. 1994. Two species of the genus *Eryx* (Serpentes; Boidae; Erycinae) from the Spanish Neogene with comments on the past distribution of the genus in Europe. Amphibia-Reptilia. 15:233–248.

Thomas H, Sen S, Khan M, Battail B, Ligabue G, editors. 1982: The Lower Miocene fauna of Al Sarrar (Eastern Province, Saudi Arabia). Atlal. 5:109–136.

Tleuberdina PA. 1988. Main sites of *Hipparion* fauna of Kazakhstan and their biostratigraphical correlation. In: Materials on the history of fauna and flora of Kazakhstan Interregional comparison of Mesozoic-Cenozoic fauna and flora of Kazakhstan. Vol. 10. Alma-Ata; p. 38-73 (in Russian).

Tleuberdina PA. 1989. On the age of vertebrate fauna from gray-green clays of Pavlodar Priirtyshye. In: Proceedings of the Institute of Geology and Geophysics of the Siberian Branch of the USSR Academy of Science. Vol. 668. Novosibirsk: Cenozoic of Siberia and the North-East of USSR; p. 59-86 (in Russian).

Tleuberdina PA, Volkova VS, Lushczaeva TT, Lychev GF, Pita OM, Tjutkova LA, Chkhikvadze VM. 1993. Vertebrate fauna of Kalkaman (Pavlodar Priirtyshe). In: Tleuberdina PA, editor. Faunistic and Floristic Complexes of Mesozoic and Cenozoic of Kazakhstan. Vol. 12. Baspager: Almaty; p. 132–157.

Tokar AA, Obst FJ. 1993. *Eryx jaculus* (Linnaeus, 1758) – Westliche Sandboa. In: Böhme W, editor. Handbuch der Reptilien und Amphibien Europeas. Wiesbaden: AULA – Verlag; p. 35-53 (in German).

Uetz P, Hošek J, editors. 2017. The Reptile Database. [accessed 2017 April 16]. http://www.reptile-database.org.

Van Devender TR, Mead JI. 1978. Early Holocene and Late Pleistocene amphibians and reptiles in Sonoran Desert packrat middens. Copeia. 1978(3):464–475.

Vasilyan D, Böhme M, Klembara J. 2016. First record of fossil *Ophisaurus* (Anguimorpha, Anguidae) from Asia. J Vert Pal. 36(6):e1219739.

Vasilyan D, Zazhigin VS, Böhme M. 2017. Neogene amphibians and reptiles (Caudata, Anura, Gekkota, Lacertilia, and Testudines) from the south of Western Siberia, Russia, and Northeastern Kazakhstan. PeerJ. 5:e3025; DOI 10.7717/peerj.3025.

Venczel M. 1994. Late Miocene snakes from Polgárdi (Hungary). Acta zool cracov. 37(1):1–29.

Venczel M. 1998. Late Miocene snakes (Reptilia: Serpentes) from Polgárdi (Hungary): a second contribution. Acta zool cracov. 41(1):1–22.

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

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

Venczel M, Ştiucă E. 2008. Late middle Miocene amphibians and squamate reptiles from Tauţ, Romania. Geodiversitas. 30(4):731–763.

Wagner P, Tiutenko A, Mazepa G, Borkin LJ, Simonov E. 2016. Alai! Alai! – a new species of the *Gloydius halys* (Pallas, 1776) complex (Viperidae, Crotalinae), including a brief review of the complex. Amphibia-Reptilia. 37(1):15–31.

Xu Y, Liu Q, Myers EA, Wang L, Huang S, He Y, Peng P, Guo P. 2012. Molecular phylogeny of the genus *Gloydius* (Serpentes: Crotalinae). Asian Herpetol Res. 3(2):127–132.

Zerova GA. 1989. The first find of a fossil Sand Boa of the genus *Albaneryx* (Serpentes, Boidae) in the USSR. Vestnik Zool. 1989(5):30–35 (in Russian).

Zerova GA, Chkhikvadze VM. 1984. Review of Cenozoic lizards and snakes of the USSR. Izvest Akad Nauk Georg Acad Sci. 10(5):319–326 (in Russian with English abstract).

Zykin VS. 1979. Stratigraphy and Unionids of the Pliocene of Southern Part of Western Siberian plain. Novosibirsk: Nauka; p. 135.

Zykin VS. 2012. Stratigraphy and evolution of environments and climate during late Cenozoic in the Southern West Siberia. Novosibirsk: Geo; p. 487.

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