

Systematic Palaeontology (Vertebrate Palaeontology)

A new Miocene fauna of snakes from eastern Siberia, Russia. Was the snake fauna largely homogenous in Eurasia during the Miocene?

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Received 30 January 2008; accepted after revision 20 May 2008
Available online 3 July 2008

Presented by Philippe Taquet

Abstract

Togay, a locality from Ol'khon Island, Baykal Lake, Russia, has yielded a fauna of snakes of Late Middle or early Late Miocene age. It is located in a broad area from which no Neogene snake has been reported; therefore, it represents an important landmark. The fauna includes a non-erycine boid, two or three colubrids, a viperid of the 'oriental complex' of *Vipera*, and perhaps another viperid. This assemblage is astonishingly reminiscent of the snake faunas from the late Early and early Middle Miocene from western and central Europe, it being understood that Miocene faunas are practically unknown in the geographically intermediary area. It may be entertained whether a homogenous snake fauna inhabited Eurasia (except the southern part of the continent) during the Miocene.

To cite this article: J.-C. Rage, I.G. Danilov, C. R. Palevol 7 (2008).

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Résumé

Une nouvelle faune de serpents miocènes en Sibérie orientale, Russie. La faune de serpents eurasiatique était-elle largement homogène au Miocène ? Togay, gisement de l'île d'Ol'khon (lac Baïkal, Russie), a produit des serpents du Miocène moyen tardif ou supérieur précoce. Il se situe au sein d'une très vaste zone qui n'avait pas fourni de serpents néogènes ; il s'agit donc d'un repère important. La faune comprend un Boidae non Erycinae, deux ou trois Colubridae, un Viperidae du groupe des 'vipères orientales' et, peut-être, un autre Viperidae. De façon étonnante, cette faune rappelle celles du Miocène inférieur tardif et moyen précoce d'Europe occidentale et centrale, étant entendu que les faunes miocènes sont pratiquement inconnues dans la zone géographiquement intermédiaire. Ce gisement suggère donc qu'une faune peut-être homogène occupait l'Eurasie, sauf sa partie méridionale, pendant le Miocène. **Pour citer cet article :** J.-C. Rage, I.G. Danilov, C. R. Palevol 7 (2008).

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Keywords: Snakes; Miocene; Boidae; Colubridae; Viperidae; Eastern Russia; Palaeobiogeography

Mots clés : Serpents ; Miocène ; Boidae ; Colubridae ; Viperidae ; Russie orientale ; Paléobiogéographie

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1. Introduction

In Eurasia, fossil snakes from the Neogene are well documented from western and central Europe, but they are very poorly known from more eastern regions. East of westernmost Russia, and aside from Ol'khon Island, central Mongolia, northeastern China and few localities in the Zaisan Basin (see below), Neogene snakes were reported only from southern Eurasia: Anatolia [13,20,31], Saudi Arabia [34], Siwalik beds of Pakistan and India [5,18], Burma [24], Thailand [17], and Japan [6].

This paper reports on a snake fauna from the Miocene of the Togay locality, Ol'khon Island, Baykal Lake, Russia. Ivanjev and Khosatzky [7] briefly listed fossils from the locality and assigned, without any comments, all snake remains to *Coluber*. However, our study shows that this fauna includes several taxa of snakes and represents a small but significant assemblage from the late Middle or early Late Miocene. Togay is located in the middle of a broad area from which no Neogene snake has been studied. Consequently, it is an important landmark. The closest locality from which Neogene snakes were reported is Builstyn Khudang (Late Miocene, central Mongolia) (Fig. 1), which yielded two erycines, two colubrids and one natricine [3]. Two other Neogene localities of the area are more distant: Zaisan Basin (Kazakhstan) and Ertemte (Inner Mongolia, northeastern China). Chkhikvadze [4] listed, but did not describe snakes from the Zaisan Basin (see below), whereas Schlosser [23] only reported an inde-



Fig. 1. Neogene localities bearing snakes in Eurasia (M: Miocene, P: Pliocene). Grey area: part of Europe from which Neogene snakes are well-documented.

Gisements d'Eurasie ayant fourni des serpents néogènes (M : Miocène, P : Pliocène). Zone grisée : partie de l'Europe où les serpents néogènes sont fréquents.

terminate snake from the latest Miocene (MN 13) of Ertemte.

2. The locality

Togay is situated in the Togay Bay of Ol'khon Island, Baykal Lake, Russia (Fig. 1 in [7]). Snakes come from the lower part of the Khalagai Formation, whose age is estimated as late Middle or early Late Miocene [10,11].

3. Systematic account

The fauna is not rich, but it comprises four, perhaps six species that belong to the Boidae, Colubridae s.l., and Viperidae. The material was collected by N.A. Logachev in 1958 and it is preserved in the Zoological Institute of the Russian Academy of Sciences, palaeoherpetological collection (ZIN PH), Saint Petersburg, Russia.

3.1. Boidae

Boinae

Indeterminate genus and species (Fig. 2)

Material. One trunk vertebra (ZIN PH 1/101).

Description

Only one trunk vertebra is referred to the Boidae. It displays the characteristic vertebral morphology of the family: vertebra short, wide and massive; prezygapophyseal processes small, not projecting laterally; hypapophysis replaced by a haemal keel in the non-anterior part of the vertebral column. The presence of well-marked subcentral grooves suggests that the vertebra likely comes from the posterior trunk region. Other noticeable characters are the relatively vaulted neural arch, clearly inclined zygapophyses, well-developed neural spine, slightly thickened dorsal border of the neural spine, and the presence of two paracotylar foramina on either side of the cotyle.

Discussion

The Boidae are generally subdivided into three groups: Boinae, Erycinae and Pythoninae; however, the pythonines are sometimes regarded as a family distantly related to the boine-erycine assemblage [35,37]. Irrespective of the precise relationships between these three groups, it should be noted that the overall vertebral morphology of the three taxa is very homogenous. Erycinae are distinguished from the two other groups on the basis of the peculiar morphology of their caudal vertebrae; however, their trunk vertebrae may be useful here because their neural arch is never vaulted. The latter feature shows that the vertebra from Togay cannot be

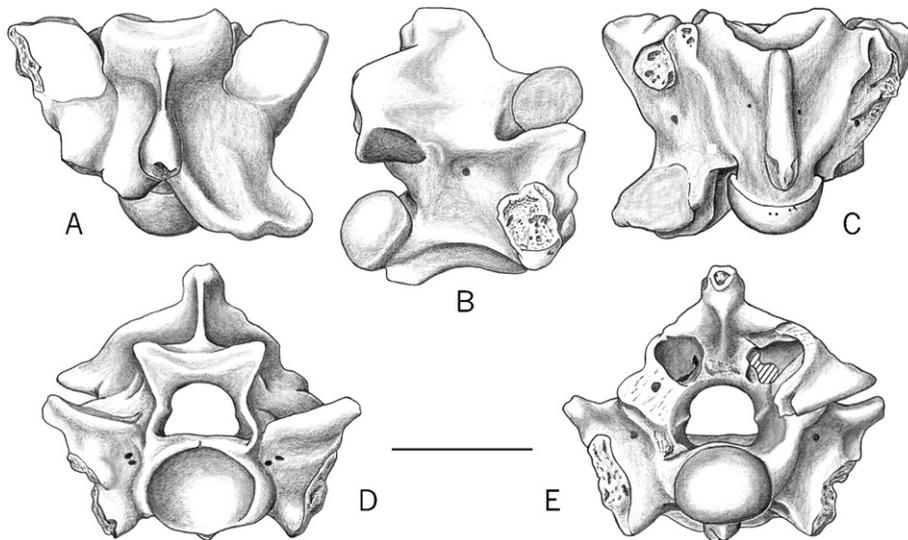


Fig. 2. Boidae, indeterminate genus and species, posterior trunk vertebra (ZIN PH 1/101) in (A) dorsal, (B) lateral, (C) ventral, (D) anterior, and (E) posterior views. Scale bar: 5 mm.

Boidae, genre et espèce indéterminés, vertèbre dorsale postérieure (ZIN PH 1/101) en vues dorsale (A), latérale (B), ventrale (C), antérieure (D) et postérieure (E). Échelle: 5 mm.

referred to the Erycinae. The distinction between boines and pythonines is difficult [22,32]. However, the presence of paracotylar foramina clearly argues against an assignment to pythonines [32,33]. In addition, the lack of a vertical ridge on the anterior face of the zygosphenes and the clearly inclined zygapophyses are consistent with the boine morphology [22].

Extant Boinae occur in tropical Americas, Madagascar and islands of the West Pacific. Extinct Boinae were reported from the Tertiary of Europe and the Americas [14,32]. The specimen from Togay differs from all American boines from the Tertiary [14]; they are not considered here. It clearly differs from the European Palaeogene boines *Palaeopython* and *Paleryx* in having paracotylar foramina, zygapophyses clearly inclined on the horizontal, and the neural spine shorter anteroposteriorly. The overall morphology of the vertebra does not markedly differ from that of *Bavarioboa* (Oligocene and Miocene of Europe); more specifically, the presence of two paracotylar foramina on each side and the thickened dorsal border of the neural spine are somewhat reminiscent of *Bavarioboa hermi* from the Early Miocene of Europe [32]. However, the boine from Togay is distinguished from *Bavarioboa* by its anteroposteriorly shorter neural spine and by the concave anterior border of the zygosphenes. Finally, although not markedly different from *Bavarioboa*, the boine from Togay cannot be referred to one of the known Boinae, but it cannot be described as a new taxon because it is represented by a single vertebra.

3.2. Colubridae s.l.

The Colubridae, as they have been long understood, make up an enormous, non-monophyletic assemblage. Despite this phylogenetic structure, morphological features are homogenous and the systematics of colubrids based on such characters has been so far unsuccessful. Many attempts at a subdivision of the traditional Colubridae into several monophyletic families have been made, the most recent ones being based on molecular data [38]. However, palaeontology is at a loss to distinguish such subgroups. In view of these difficulties, and for convenience, palaeontologists retain the traditional understanding of this assemblage that is here referred to as 'Colubridae s.l.' On the basis of vertebrae, it is only possible to clearly distinguish two morphological groups, the 'colubrines' and the 'natricines', that is an artificial subdivision. In 'colubrines', mid- and posterior trunk vertebrae lack hypapophyses, whereas in 'natricines', hypapophyses are present in the entire trunk region. Togay has yielded only 'colubrines'; two or three species are present. It is worth mentioning that among the extant colubrids, present in the area around the Baykal Lake and potentially on Ol'khon Island, are two species [1]: *Elaphe dione* (a 'colubrine') and *Natrix natrix* (a 'natricine').

3.2.1. Coluber s.l.

As used in palaeontology, the genus name *Coluber* does not correspond to the genus in its present taxo-

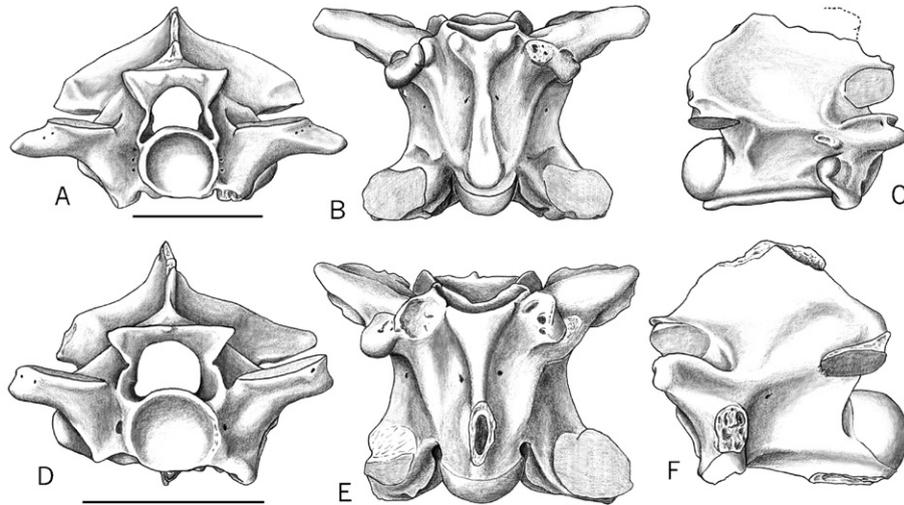


Fig. 3. (A–C) Colubridae s.l., unnamed species A, mid-trunk vertebra (ZIN PH 2/101), anterior border of neural spine reconstructed from ZIN PH 3/101. (D–F) Viperidae, ? *Vipera* ('oriental complex'), mid-trunk vertebra (ZIN PH 34/101) (A, D: anterior views; B, E: ventral views; C, F: lateral views). Each scale bar: 5 mm.

(A–C) Colubridae s.l., espèce A non nommée, vertèbre dorsale moyenne (ZIN PH 2/101), bord antérieur de la neurépine basé sur ZIN PH 3/101. (D–F) Viperidae, ? *Vipera* « groupe des vipères orientales », vertèbre dorsale moyenne (ZIN PH 34/101) (A, D: faces antérieures; B, E: faces ventrales; C, F: faces latérales). Échelles: 5 mm.

nomic meaning. Vertebrae of several living and extinct colubrids show a homogenous morphology that renders identification difficult or impossible at the genus level. More specifically, in several living genera, the vertebral morphology is similar to that of *Coluber*. Consequently, extinct species belonging to this assemblage have been referred symbolically to the genus *Coluber* s.l., it being understood that the relationships between these snakes remain unknown within this complex.

3.2.1.1. Unnamed species A (Fig. 3A–C).

Material. 25 trunk vertebrae (ZIN PH 2/101 to 26/101).

Description

This snake is a large colubrine; the length of the centrum ranges from above 7 to 4.9 mm. The vertebrae are comparatively high and short. The neural arch is moderately vaulted; moreover, in posterior view, the posterior borders of the neural arch are nearly straight to weakly convex. Epizygapophyseal spines are present on most vertebrae; apparently, their presence does not depend on the size of the vertebrae. The neural spine is often incomplete, but some remnants show that it was relatively high. The anterior border of the zygosphenes is approximately straight between the two lateral lobes; however, in several vertebrae, a weakly convex median lobe is present, the lobe being indented by a median notch (which results in the presence of two lobes between the lateral lobes: Fig. 3B). In most vertebrae, the cotyle and condyle are slightly compressed laterally, which is a

somewhat unusual feature. The prezygapophyseal processes are well developed, strong, but short. Paracotylar foramina are present. Astonishingly, the presence of two foramina on each side represents the most frequent condition; moreover, foramina may be as numerous as four on one side and three on the other side. The ventral face of the centrum is triangular and longer than wide. It bears a well-defined haemal keel that is spatulate, except in two vertebrae in which it is gladiate. The para- and diapophyseal areas are distinct from each other. The diapophysis is clearly shifted posteriorly with regard to the parapophysis. Two other features are worth noting. A sinuous, blunt and vertical ridge occurs on either side, below the postzygapophyseal facet; the smaller vertebrae lack it. A marked, uneven tuberosity is present on each side of most vertebrae, close to the lateral foramen and dorsal to the paradiapophysis. Its size and shape are variable and its presence does not appear to be connected to the size of the vertebrae. Only six vertebrae lack it.

Discussion

This snake clearly belongs to the so-called 'large-sized colubrines' [27,29]. This informal group includes extinct species referred to the genera *Coluber*, *Elaphe*, and *Malpolon* which are still extant. Among these large species, the vertebral morphology of species A from Togay most approaches that of *Coluber pouchetii*, *C. dolnicensis* and *C. caspioides*. *C. pouchetii* was reported from the Early (MN 4) and Middle (MN 6) Miocene of France [16] and perhaps from the Late Miocene (MN

9) of Hungary [29]. *C. dolnicensis* is known only from the Early Miocene (MN 3 and 4) of the Czech Republic [9,25]. *C. caspioides* was recovered from the Early Miocene of the Czech Republic (MN 3 [9]), Germany (MN 4 [33]) and Austria (MN 4 [29]), and from the Middle Miocene (MN7+8) of France [29]. In addition, a younger colubrine from the Pliocene of the Balearic Islands belongs to this assemblage, but it cannot be identified at the species level [2]. Aside from the large size, four characters are common to *C. pouchetii*, *C. dolnicensis*, *C. caspioides*, and species A from Togay: (1) neural arch weakly depressed to moderately vaulted, (2) posterior borders of the neural arch nearly straight to weakly convex in posterior view, (3) neural spine not low, (4) anterior border of the zygosphenes generally indented by a median notch, the border being otherwise straight, weakly convex or weakly concave between the lateral lobes.

Within this assemblage, species A compares more favourably with *Coluber pouchetii* and *C. dolnicensis*. In these three snakes, the diapophysis is shifted posteriorly and the cotyle and condyle of various vertebrae are slightly compressed laterally. However, aside from the presence of lateral tuberosities whose significance is unknown, two characters distinguish species A from *C. pouchetii* and *C. dolnicensis*. In at least a part of the vertebral column of the latter two species, the haemal keel forms a step in the anterior portion of the centrum, while species A lacks such a step. Moreover, both *C. pouchetii* and *C. dolnicensis* have a single paracotylar foramen on either side of the cotyle, which is the condition in nearly all colubrids. Most vertebrae of species A have at least two foramina on each side, and four foramina are even present on one side in two vertebrae; to our knowledge, so numerous paracotylar foramina were not reported previously in snakes (except in the Cretaceous–Eocene Palaeophiidae). Finally, species A from Togay appears to be related to the ‘large-sized colubrine’ assemblage previously reported from the Neogene of Europe, but it probably represents a distinct, new species. The description of this new taxon is not our present objective.

3.2.1.2. ? *Unnamed species B*.

Material. Five trunk vertebrae (ZIN PH 27/101 to 31/101).

Description

The vertebrae are somewhat similar to those of species A, but they are smaller (length of centrum: 5.1 to 4.2 mm). Aside from its size, this snake differs from species A in having more vaulted neural arches and convex posterior borders of neural arches in posterior view. Moreover, the cotyles and condyles are not com-

pressed laterally. In addition, ‘colubrine B’ lacks the lateral tuberosities and the subvertical ridges located below the postzygapophyses. Epizygapophyseal spines may be present or absent. At least two paracotylar foramina are present on each side, but three foramina can occur.

Discussion

Several of the characters that distinguish specimens allocated to ‘colubrine B’ from those referred to species A are perhaps not significant. The absence of lateral compression of the cotyles and condyles also occurs in various vertebrae of species A and the small number of specimens belonging to ‘colubrine B’ precludes any conclusion. The absence of tuberosities and posterior subvertical ridges may be size related, although the tuberosities are lacking in some large vertebrae, but are present in some small vertebrae of species A. On the other hand, the more vaulted neural arches and more convex posterior borders of the neural arches do not appear to result from the smaller size. On the contrary, the posterior borders of the neural arches tend to be more convex in large individuals than in small ones. From this, it might be inferred that ‘colubrine B’ is distinct from species A. However, the presence of at least two paracotylar foramina on each side – a very peculiar character – is common to these two snakes and argues for the referral of ‘colubrine B’ to species A. Unfortunately, the limited sample does not permit us to establish whether ‘colubrine B’ is distinct from species A.

3.2.1.3. *Indeterminate genus and species*.

Material. Two trunk vertebrae (ZIN PH 32/101 and 33/101).

Description and discussion

Two vertebrae of a small colubrine display a morphology clearly distinct from that of the *Coluber* assemblage. The centrum length of the largest vertebra is 3.9 mm. The vertebrae are elongate and depressed. The neural arch is strongly depressed and the neural spine is low and long. The zygosphenes are wide (wider than the slightly depressed cotyle), thin and provided with a wide median lobe. One paracotylar foramen opens on either side of the cotyle. The paradiapophyses are comparatively massive and they lack a constriction between the para- and diapophyseal areas.

These vertebrae are reminiscent of the extant Eurasian genus *Coronella*, the earliest species of which is reported from the Latest Miocene (MN 13) of Europe [36]. However, the vertebrae from Togay differ from those of *Coronella* in being more elongate and in having centra growing narrower posteriorly. On the other hand, small colubrids are so numerous and their osteology is so poorly known that it cannot be excluded (? it is proba-

ble) that the vertebral morphology of the fossil occurs among unstudied living forms.

3.3. Viperidae

? Viperinae.

3.3.1. ? *Vipera* ('oriental complex')

Indeterminate species (Fig. 3D–F).

Material. One trunk vertebra (ZIN PH 34/101).

Description. This relatively large vertebra (centrum length: 5.2 mm) shows a combination of characters that is typical of viperids: vertebra depressed, short and wide; neural arch depressed; hypapophysis present. Other features that are worth mentioning are the marked slanting of the prezygapophyseal facets, the small size of the prezygapophyseal processes that do not strongly project laterally, and the probable presence of epizygapophyseal spines. Unfortunately, the hypapophysis, neural spine and parapophyseal processes are broken away.

Discussion

The marked shortness of the vertebra, the strongly depressed condition of the neural arch, and the relatively large size point to the 'oriental complex' of species of *Vipera*. This informal assemblage includes living and extinct species, whose precise relationships are debated, but whose osteology is homogenous [30,31].

However, the vertebrae of the extant viperine *Daboia* [30] and crotaline *Protobothrops* (formerly *Trimeresurus*) *flavoviridis* [28] are somewhat similar to those of the 'oriental vipers'. Unfortunately, the main difference between the 'oriental vipers' and *Daboia* is the markedly higher neural spine of the latter. This character cannot be used, since the neural spine is broken off in the fossil. On the other hand, the vertebrae of *Daboia* appear to be higher and narrower than that from Togay; consequently, assignment of the fossil to this genus seems unlikely. *P. flavoviridis* may be discarded on the basis of its clearly larger cotyle and condyle, markedly more extended zygapophyseal facets, and perhaps (as far as may be inferred from the fossil) less anteriorly directed parapophyses. Nevertheless, taking into account the fact that the 'oriental vipers' assemblage is not well defined, and that the feature that clearly distinguishes this assemblage from *Daboia* is not preserved, the referral of the fossil from Togay to the 'oriental complex' of *Vipera* cannot be accepted definitely.

Today, 'oriental vipers' inhabit southwestern Asia, the Middle East, southeasternmost Europe, and northernmost Africa. The group was present in the southern

half of Europe from the late Early Miocene (MN 4) to the Latest Pliocene (MN 16) and in southwesternmost Asia (Anatolia) during the Late Miocene [31]. In Africa, it perhaps reached the South of the continent during the Early Miocene [15]. *Daboia* occurs in south Asia and it was reported from the Early Pliocene [26] and perhaps the Early Miocene [30] of western Europe and southern Africa [15]. *Protobothrops flavoviridis* is restricted to Ryukyu Islands (Japan). An Early Miocene fossil from Honshu Island (Japan) would be close to this species [6].

3.3.2. Indeterminate Viperidae.

Material. One trunk vertebra (ZIN PH 35/101).

Description and discussion

This specimen is only poorly mineralized or not mineralized at all. It is probably not a fossil, but this cannot be demonstrated. It displays the morphology of the species belonging to the 'berus complex' of *Vipera* [30,31], but the osteology of the small Asian crotalines (*Gloydius*) being practically unknown, this specimen is regarded a viperid indeterminate. It should be noted that the living *Vipera berus* and *Gloydius halys* occur in the area of Baykal Lake and that their presence on Ol'khon Island seems very probable [1].

4. Palaeobiogeographical relationships

Although neither rich nor very diverse, this fauna provides palaeobiogeographic information.

4.1. Faunal affinities with Europe

Astonishingly, the overall composition of the fauna from Togay recalls that of the late Early Miocene and early Middle Miocene (MN 3–MN 5) of Europe: presence of a rather large non-erycine boid, of colubrids including a large colubrine, and of a large viperid (the latter lacking from MN 3). In Europe, the boid may be either the pythonine *Python* or the boine *Bavarioboa*. The European colubrids are diverse, but they always include at least one large colubrine that may belong to *Coluber* or *Elaphe*. The large viperid from the MN 4–MN 5 period in Europe belongs to the 'oriental complex' of *Vipera* or to *Daboia*. Before MN 3, the Miocene of Europe lacks non-erycine large boids and large vipers [8,21,32]. After MN5, non-erycine boids were definitely ousted from Europe by colubroids.

4.2. The Asian faunas

In Asia, only six localities, or complexes of localities, previously produced faunas (i.e. more than one

species) of Neogene snakes: the Siwalik beds (Pakistan and India), Builstyn Khudang (Mongolia), Li Mae Long (Thailand), Zaisan Basin (Kazakhstan), Al Sarrar (Saudi Arabia), all Miocene in age, and Çalta (Anatolia), which is Pliocene. The Siwalik beds [5,18] and Li Mae Long [17] correspond to aquatic environments and they cannot be significantly compared to Togay and to the European sites.

The terrestrial snakes from the Miocene of Al Sarrar and Zaisan Basin are poorly known. The overall composition of the fauna from Al Sarrar (late Early Miocene [34]) is similar to that of Europe and Togay, but the boids, colubrids and viperids are small, which may result from taphonomic conditions. As the fauna from Togay, the Late Miocene of Builstyn Khudang includes large colubrids, but it differs from it by the presence of two erylacines and a natricine and in lacking non-erylacine boids [3]. The localities of the Zaisan Basin collectively yielded poor faunas that extend from the Early to the Late Miocene [4]. Only the presence of a large viperid is reminiscent of Europe and Togay. The fauna of Çalta is the only assemblage of snakes described from the Pliocene of Asia [20]; it mainly differs from Togay in lacking non-erylacine boids and viperids and in having an elapid.

4.3. Was the Eurasian fauna homogenous during the Miocene?

Maridet et al. [12] showed that the European fauna of mammals was homogenous during the Miocene up to zone MN 4. During the interval MN 5–MN 7 + 8, the homogeneity decreased and it reached its lowest level during MN 11 (middle Late Miocene) (Fig. 9 in [12]). In addition, faunal dissimilarity mainly corresponds to a north–south gradient. Unfortunately, this study was not extended to Asia. As far as snakes are concerned, the similarity between the faunas from Togay and Europe raises the question of a possible faunal homogeneity over a large part of Eurasia (southern Eurasia excluded) during the Miocene. Obviously, the earliest possible age of Togay appears to be late Middle Miocene, while the ‘similar’ period in Europe ends by the early Middle Miocene, but the fauna from Togay may be regarded as a relict of a formerly homogenous Eurasian fauna. The only intervening faunas (Zaisan Basin) neither go against nor support this possibility. The hypothesis of the faunal homogeneity in Eurasia during the Neogene is indirectly supported by the fact that various snakes (and mammals) from the Miocene of Europe and North America are related, Asia appearing as the intervening area for dispersals [19].

Acknowledgements

This study was made possible by the financial support of a grant of the President of the Russian Federation to the Leading Scientific Schools (NSh-119.2008.4) and a grant of the Russian Foundation for Basic Research (08-04-00041-A). F. de Lapparent (MNHN, Paris) and M. Venczel (Muzeul Tarii Crisurilor, Oradea) provided useful comments.

References

- [1] N.B. Ananjeva, N.L. Orlov, R.G. Khalikov, I.S. Darevsky, S.A. Ryabov, A.V. Barabanov, *The Reptiles of northern Eurasia*, Pensoft, Sofia, 2006 (245 p.).
- [2] S. Bailon, J. Quintana, J. Garcia Porta, Primer registro fósil de las familias Gekkonidae (Lacertilia) y Colubridae (Serpentes) en el Plioceno de Punta Nati (Menorca, Islas Baleares), *Monogr. Soc. Hist. Nat. Balears* 12 (2005) 27–32.
- [3] M. Böhme, Herpetofauna (Anura, Squamata) and palaeoclimatic implications: preliminary results, *Ann. Naturhist. Mus. Wien* 108 A (2007) 43–52.
- [4] V.M. Chkhikvadze, Preliminary results of studies on Tertiary amphibians and squamate reptiles of the Zaisan Basin, in: 6th All-Union Herpetol. Conference, Tashkent, 1985, pp. 234–235 (in Russian).
- [5] J. Head, Snakes of the Siwalik Group (Miocene of Pakistan): Systematics and relationships to environmental change, *Palaeontol. Electron.* 8 (2005) 1–33.
- [6] J.A. Holman, M. Tanimoto, cf. *Trimeresurus* Lacépède (Reptilia: Viperidae: Crotalinae) from the late Early Miocene of Japan, *Acta Zool. Cracov.* 47 (2004) 1–7.
- [7] L.I. Ivanjev, L.I. Khosatzky, Remains of Neogene reptiles and amphibians of the Ol’khon Island of Baykal Lake, *Izvest. Vost.-Sibir. Otd. Geograf. Obshch. SSSR* 67 (1970) 153–158 (in Russian).
- [8] M. Ivanov, Changes in the composition of the European snake fauna during the Early Miocene and at the Early/Middle Miocene transition, *Palaeontol. Z.* 74 (2001) 563–573.
- [9] M. Ivanov, The oldest known Miocene snake fauna from Central Europe: Merkur-North locality, Czech Republic, *Acta Palaeontol. Pol.* 47 (2002) 513–534.
- [10] L.I. Khosatzky, V.M. Chkhikvadze, New data on Miocene turtles of the genus *Baicalemys*, *Bull. Acad. Sci. Georgia* 148 (1993) 155–160 (in Russian).
- [11] N.A. Logachev, T.K. Lomonosova, V.M. Klimanova, *Cenozoic Deposits of Irkutsk Amphitheatre*, Nauka, Moscow, 1964 (195 p., in Russian).
- [12] O. Maridet, G. Escarguel, L. Costeur, P. Mein, M. Huguency, S. Legendre, Small mammal (rodents and lagomorphs) European biogeography from the Late Oligocene to the mid Pliocene, *Global Ecol. Biogeogr.* 16 (2007) 529–544.
- [13] J.-C. Paicheler, F. de Broin, J. Gaudant, C. Mourer-Chauviré, J.-C. Rage, C. Vergnaud-Grazzini, Le bassin lacustre miocène de Bes-Konak (Anatolie, Turquie). Géologie et introduction à la paléontologie des vertébrés, *Geobios* 11 (1978) 43–56.
- [14] J.-C. Rage, Fossil snakes from the Palaeocene of São José de Itaboraí, Brazil. Part II. Boidae, *Palaeovertebrata* 30 (2001) 111–150.
- [15] J.-C. Rage, Squamate reptiles from the Early Miocene of Arrisdrift (Namibia), in: M. Pickford, B. Senut (Eds), *Geology and*

- Palaeobiology of the Central and Southern Namib, 2: Palaeontology of the Orange River Valley, Namibia, Mem. Geol. Surv. Namibia 19 (2003) 43–50.
- [16] J.-C. Rage, S. Bailon, Amphibians and squamate reptiles from the late Early Miocene (MN 4) of Béon 1 (Montréal-du-Gers, southwestern France), Geodiversitas 27 (2005) 413–441.
- [17] J.-C. Rage, L. Ginsburg, Amphibians and squamates from the Early Miocene of Li Mae Long, Thailand: the richest and most diverse herpetofauna from the Cainozoic of Asia, in: Z. Roček, S. Hart (Eds), Herpetology'97, Prague, 1997, pp. 167–168.
- [18] J.-C. Rage, S.S. Gupta, G.V.R. Prasad, Amphibians and squamates from the Neogene Siwalik beds of Jammu and Kashmir, India, Palaeontol. Z. 75 (2001) 197–205.
- [19] J.-C. Rage, J.A. Holman, Des serpents (Reptilia, Squamata) de type nord-américain dans le Miocène français. Évolution parallèle ou dispersion? Geobios 17 (1984) 89–104.
- [20] J.-C. Rage, S. Sen, Les amphibiens et les reptiles du Pliocène supérieur de Çalta (Turquie), Geol. Mediterr. 3 (1976) 127–134.
- [21] J.-C. Rage, Z. Szyndlar, Latest Oligocene–Early Miocene in Europe: Dark period for booid snakes, C. R. Palevol 4 (2005) 428–435.
- [22] J.D. Scanlon, B.S. Mackness, A new giant python from the Pliocene Bluff Downs local fauna of northeastern Queensland, Alcheringa 25 (2002) 425–437.
- [23] M. Schlosser, Tertiary vertebrates from Mongolia, Palaeont. Sin. C 1 (1924) 1–119.
- [24] W.E. Swinton, *Daunophis langi*, gen. et sp. n. (Pliocene, Burma), Ann. Mag. Nat. Hist. 17 (1926) 342–348.
- [25] Z. Szyndlar, Snakes from the Lower Miocene locality of Dolnice (Czechoslovakia), J. Vertebr. Paleontol. 7 (1987) 55–71.
- [26] Z. Szyndlar, Two extinct species of the genera *Malpolon* and *Vipera* (Reptilia, Serpentes) from the Pliocene of Layna (Spain), Acta Zool. Cracov. 31 (1988) 687–706.
- [27] Z. Szyndlar, A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part I: Scolecophidia, Boidae, Colubridae, Estud. Geol. 47 (1991) 103–126.
- [28] Z. Szyndlar, A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part II: Natricinae, Elapidae, Viperidae, Estud. Geol. 47 (1991) 237–266.
- [29] Z. Szyndlar, Snake fauna from the Late Miocene of Rudabánya, Palaeontogr. Ital. 90 (2005) 31–52.
- [30] Z. Szyndlar, J.-C. Rage, Oldest fossil vipers (Serpentes: Viperidae) from the Old World, Kaupia 8 (1999) 9–20.
- [31] Z. Szyndlar, J.-C. Rage, Fossil record of the true vipers, in: G.W. Schuett, M. Höggren, M.E. Douglas, H.W. Greene (Eds.), Biology of the vipers, Eagle Mountain Publ, Eagle Mountain, UT, USA, 2002, pp. 419–444.
- [32] Z. Szyndlar, J.-C. Rage, Non-erycine Booidea from the Oligocene and Miocene of Europe, Inst. Syst. Evol. Anim., Cracow (2003) 109.
- [33] Z. Szyndlar, H.H. Schleich, Description of Miocene snakes from Petersbuch 2 with comments on the Lower and Middle Miocene ophidian faunas of southern Germany, Stuttg. Beitr. Naturkd., Ser. B 192 (1993) 1–47.
- [34] H. Thomas, S. Sen, M. Khan, B. Battail, G. Ligabue (Eds), The Lower Miocene fauna of Al Sarrar (Eastern Province, Saudi Arabia), Atlat J. Saudi Arab. Archaeol. 5 (1982) 109–136.
- [35] G. Underwood, A systematic analysis of boid snakes, Linn. Soc. Symp. Ser. 3 (1976) 151–175.
- [36] M. Venczel, Late Miocene snakes (Reptilia: Serpentes) from Polgárdi (Hungary): a second contribution, Acta Zool. Cracov. 41 (1998) 1–22.
- [37] N. Vidal, A.S. Delmas, S.B. Hedges, The higher-level relationships of alethinophidian snakes inferred from seven nuclear and mitochondrial genes, in: R.W. Henderson, R. Powell (Eds.), Biology of the Boas and Pythons, Eagle Mountain Publ, Eagle Mountain, UT, 2007, pp. 27–33.
- [38] N. Vidal, A.S. Delmas, P. David, C. Cruaud, A. Couloux, S.B. Hedges, The phylogeny and classification of caenophidian snakes inferred from seven nuclear protein-coding genes, C. R. Biologies 330 (2007) 182–187.