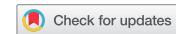


ARTICLE



## The first record of amphisbaenian and anguimorph lizards (Reptilia, Squamata) from the upper Miocene Solnechnodolsk locality in Russia

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### ABSTRACT

The amphisbaenian and anguimorph fossil lizards from the late Miocene (MN 13) Solnechnodolsk locality (southern European Russia) are described. Amphisbaenians are represented only by isolated vertebrae of which more precise allocation is difficult. The anguine material shows the presence of at least two taxa which are described from this area for the first time: *Anguis cf. rarus* and *Ophisaurus cf. spinari*. The *A. rarus* was previously known only from the early Miocene of Germany. *Ophisaurus spinari* has a broad stratigraphic range – from the early and middle Miocene of Central Europe, with the last occurrence documented from the late Pliocene of Italy. However, no record was known from the late Miocene, which would show an important part of the story. The parietal of *A. cf. rarus* forms the first evidence of its survival to the end of the Miocene by its shifting to south areas of Eastern Europe, together with *O. spinari*. The Solnechnodolsk material is evidence of a broad spatial and/or temporal distribution of both these anguine taxa and the parietal of *Anguis* unambiguously documents the presence of this taxon in Russia already in the late Miocene. The thermophilic forms in Solnechnodolsk are represented by monitor lizards (*Varanus*).

### ARTICLE HISTORY

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## Introduction

The clade Squamata consists of lizards, snakes and amphisbaenians. It is a highly successful group of terrestrial reptiles with an extended range of habitats and lifestyles, forming the largest and by far the most diverse group of non-avian reptiles currently living on Earth (e.g., Evans 2003). The fossil history of this clade, which today consists of more than 10,000 extant species (Uetz et al. 2018), is extensively studied. Although fossil records of lizards are well documented in western and central Europe, many aspects of the eastern European record still remain unknown. This represents a significant knowledge gap in our understanding of the evolutionary history of these reptiles in Europe. However, this area can be crucial for our understanding of their biogeography and evolution (see e.g. Rage 2013; Georgalis et al. 2017a) as well as the climate changes during Neogene. In general, reptiles represent a group of ectothermic animals and thus, their distribution, richness and diversity are highly dependent on temperature and climatic condition (see e.g. Haller-Probst 1997; Markwick 1998). For these reasons, the dramatic climate changes during the Cenozoic had a marked impact on squamate history (Rage 2013). During the MN 13, the climate remained warm, although the temperature dropped if compared to the Miocene Climatic Optimum (Böhme 2003; Rage 2013). However, the amplitude of the temperature drop varies geographically (Bruch et al. 2004; Montuire et al. 2006) and a more distinct climatic zonation on the European continent has lead to a survival of the thermophilic ectothermic animals only in southern regions (Böhme 2003).

Unfortunately, the study of lizards from this interval has been largely neglected and many aspects remain unknown (see Rage 2013; in the last years, several squamate assemblages have been reported from the late Miocene of Italy (Colombero et al. 2014; 2017) and Greece (Georgalis et al. 2017b)). Necessarily, this brings several principal problems. According to Rage (2013), regionalisation of squamate assemblages during the following period, the Pliocene, was affected by local extinctions of lineages that occurred earlier in northern than in southern areas, which resulted in withdrawals of thermophilic taxa towards southern areas. Therefore taxa which were still present in western and southern Europe during the Pliocene, were already absent in Central Europe. However as was already noted by Rage (2013), regionalisation cannot be entirely resolved because the Pliocene (and terminal Miocene) of eastern Europe are practically unknown. We here describe a part of the lizard fauna (Amphisbaenia and Anguimorpha) from a site at Solnechnodolsk in southern European Russia (Figure 1; the Pontic-Caspian steppe region). The Solnechnodolsk locality (45° 18' N, 41° 33' E) is situated in the Northern Caucasus, 40 km NW of the city of Stavropol. In paleogeographical terms, it is located at the southern shore of the Pontian marine basin. The vertebrate fossils occurred as disassociated bones coming from fluvial and lacustrine beds incised in the Middle Sarmatian (Bessarabian) limestones. Only preliminary accounts of the fauna have been so far published (Tesakov et al. 2010, 2013; Titov and Tesakov 2013). The data obtained from small mammals indicates the

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**Figure 1.** The location of the locality Solnechnodolsk.

correlation of the Solnechnodolsk fauna with the late Turolian, MN 13 of the European Neogene Mammal biochronological system (Steininger 1999). The locality yielded one of the most abundant and diverse vertebrate faunas of the late Miocene in Russia. Among them, the only fossil herpetofauna to have been described are remains of *Pelobates* (Syromyatnikova 2017) and a preliminary list of the herpetofauna can be found in Syromyatnikova et al. (2015). The end of the Miocene in Europe is also affected by one of the greatest evaporitic event of Earth's history, the Messinian salinity crisis (MSC) of the Mediterranean (Krijgsman et al. 1999; Rouchy and Caruso 2006).

The aims of this paper are as follows: (1) to describe disarticulated materials of amphisbaenian, anguine and varanid lizards from the late Miocene locality Solnechnodolsk in Russia; (2) taxonomic allocation of these finds; (3) studying the spatial and temporal distribution of the present taxa in Europe during the Miocene, with a special reference to the terminal Miocene.

## Material and methods

The lizard specimens described here are housed in the Geological Institute of the Russian Academy of Sciences, Moscow, Russia, prefixed under individual GIN numbers. Since the site discovery in 2009, the material was sampled in 2009, 2010, 2014, and 2017 by the expedition of the Russian Academy of Sciences. Fossils were extracted from sediments by screen washing method with mesh size 0.5, 0.7, and 1 mm. The excavated vertebrate material includes fishes, amphibians, reptiles, birds, small and large mammals.

The specimens were photographed under a scanning electron microscope (Cambridge CamScan-4) at the Paleontological Institute of the Russian Academy of Sciences in Moscow (Russia) and under a MC-100 binocular microscope with mounted Nikon Digital Camera 7200 (using focus stacking technique and combined with Helicon Focus software version 7.0.1). The standard anatomical orientation system is used throughout this paper – the terminology of individual structures of the bones

are mostly from Fejérváry-Lángh (1923), Oelrich (1956), Hoffstetter and Gasc (1969) and Evans (2008). The image processing program ImageJ (Schneider et al. 2012) was used for measurements. For comparison, the specimen of *Anguis colchica* (voucher no. 4308 deposited in the collection of the Department of Zoology, Comenius University in Bratislava) was scanned using the micro-computed tomography (CT) facility at the Slovak Academy of Sciences in Banská Bystrica, using a Phoenix mikro-CTv|tome|x L240. The CT data sets were analyzed using Avizo 8.1 on a high-end computer workstation at the Department of Ecology (Comenius University in Bratislava).

## Systematic palaeontology

**Squamata** Oppel, 1811  
**Amphisbaenia** Gray, 1844

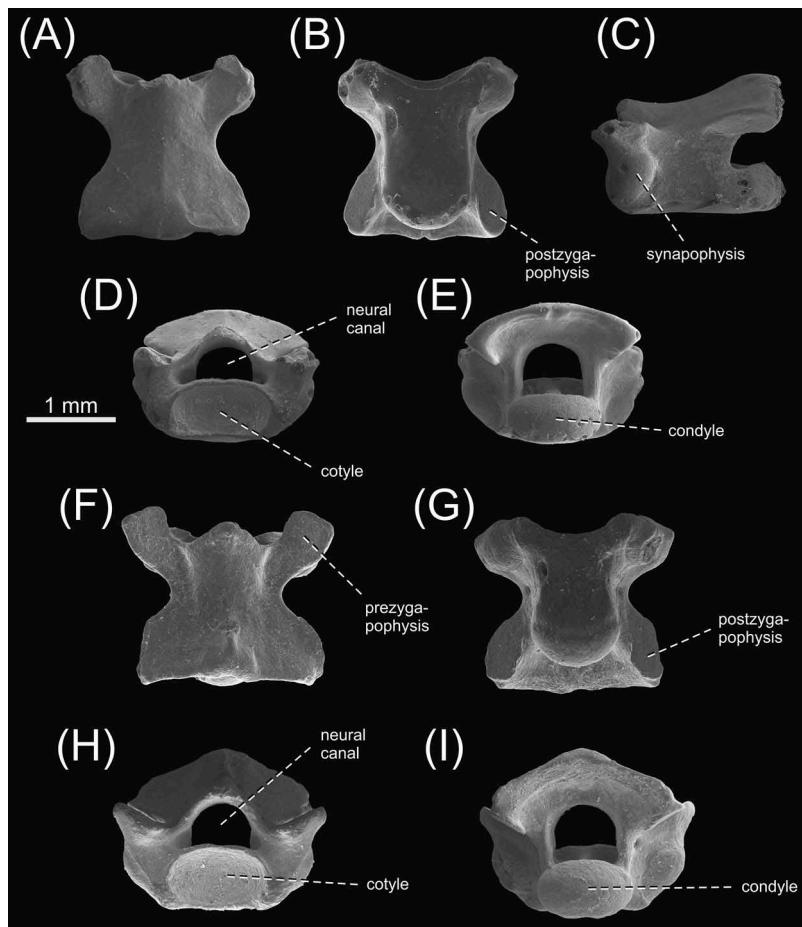
**Amphisbaenia** indet.  
Figure 2

*Material* -two isolated dorsal vertebrae GIN 1145/260–261.

## Description

### Dorsal vertebra

Two dorsal vertebrae are preserved (Figure 2). They are small in size. The whole centrum is depressed, as well as condyle and cotyle – thus they are elliptical. The ventral side of the centrum is flat, pierced by a pair of subcentral foramina in the anterior 1/3 of the anteroposterior length. The lateral margins (subcentral ridges) are roughly parallel in ventral aspect. The neural canal is tunnel-like, pentagonal, and its dorsoventral height is lower than the dorsoventral height of the cotyle. The synapophyses are rounded and robust. The neural spine is absent, the dorsal portion of the neural arch forms a median edge. The posterior portion of the neural arch is fused with the postzygapophyses, forming the dorsal roof (or lamina) between the left and right postzygapophysis. In lateral view, the neural arch has a sinusoid



**Figure 2.** Amphisbaenia indet. from the late Miocene of the locality Solnechnodolsk. Vertebrae GIN 1145/260 and GIN 1145/261 in dorsal (A, F); ventral (B, G); lateral (C) aspects; anterior (D, H); and posterior (E, I) aspects.

shape, rising gradually with a gentle curve towards the posterior end.

**Remarks.** The vertebrae described here can be placed to Amphisbaenia based on the following combination of features (see Estes 1983): (1) depressed centrum with a flat ventral surface; (2) roughly parallel lateral margins in ventral aspect; (3) massive synapophyses; (4) absence of zygosphene; and (5) and a sinusoidal neural arch lacking a neural spine.

#### Anguimorpha Fürbringer, 1900

Anguidae Gray, 1825

Anguinae Gray, 1825

*Anguis* Linnaeus, 1758

#### *Anguis cf. rarus* Klembara and Rummel 2018

Figure 3(A, B)

Material -parietal GIN 1145/262.

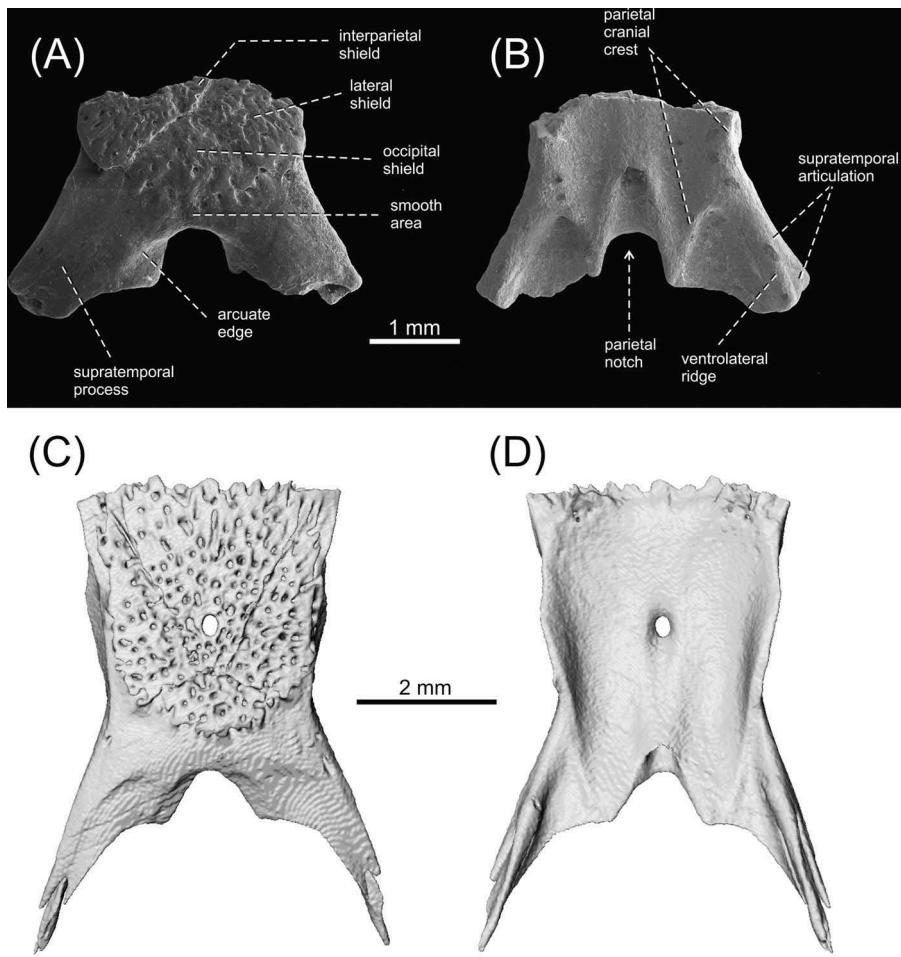
#### Description

##### Parietal

The specimen GIN 1145/262 represents a posterior half of the parietal, but only the bases of the supratemporal processes are

preserved (Figure 3(A, B)). The preserved portion of the parietal table is covered by several osteodermal shields. These shields bear ornamentation which consists of low tubercles and pits and short grooves. The parietal (lateral sensu Klembara and Rummel 2018) shields are only partly preserved on both sides, completely covering here the lateral margins of the parietal table. The central shield is the interparietal shield, but is incomplete. Posteriorly, there is the large occipital shield. It is triangular in shape with a posteriorly convex posterior margin. The anteroposterior length of the occipital shield is almost three times longer than the smooth area of the parietal table which is located immediately posterior to this shield (measured in the median plane). A fine arcuate border is exposed posteriorly to the smooth area. Between the supratemporal processes, the distinct parietal notch is present. The supratemporal processes have broad bases which are well diverged laterally.

In ventral aspect, the parietal fossa is located in the posterior mid-region of the parietal table. Its ventral lamina that anteriorly borders the parietal fossa is partly damaged. The facet for the supratemporal is located at the lateral edge of the supratemporal process. This facet is long and reaches anteriorly to the level of the parietal table. The muscular surface is absent, the parietal cranial edge forms the lateral border of the parietal.



**Figure 3.** *Anguis* cf. *rarus* from the late Miocene of the locality Solnechnodolsk. Parietal GIN 1145/262 in dorsal (A); and ventral (B) aspects. Comparison with the extant taxon *A. colchica*, parietal in dorsal (C); and ventral (D) aspects.

### Remarks

Although the parietal is incompletely preserved, it can be allocated to *Anguis* based on the following combination of diagnostic features: (1) the occipital shield is distinctly longer than the posteriorly located smooth area (see Klembara 2015; Klembara and Rummel 2018); (2) distinct parietal notch is present; (3) absence of the muscular surface. The presence of the muscular surface is typical for members of the genus *Pseudopus* (see e.g., Klembara et al. 2017a), although in some cases it can be observed in large adult individuals of other taxa, e.g. *Ophisaurus holeci* Klembara et al. 2017b). The preserved portion of the parietal from Solnechnodolsk shares two character states with the early Miocene (MN 3) taxon *Anguis rarus* described by Klembara and Rummel (2018): (1) the bases of the supratemporal processes are well diverging laterally [this is not present to such a degree in *A. fragilis*, see Klembara and Rummel (2018) nor in *A. colchica*: Figure 3(C, D)]; and (2) the facet for the supratemporal reaches anteriorly to the level of the parietal table. For these reasons, the Solnechnodolsk parietal most likely represents the species *A. rarus*. However, interpretations of the incomplete fossil elements always need to be met with caution and we decided to allocate this material as *A. cf. rarus*.

### *Ophisaurus* Daudin, 1803

#### *Ophisaurus* cf. *spinari* Klembara, 1979

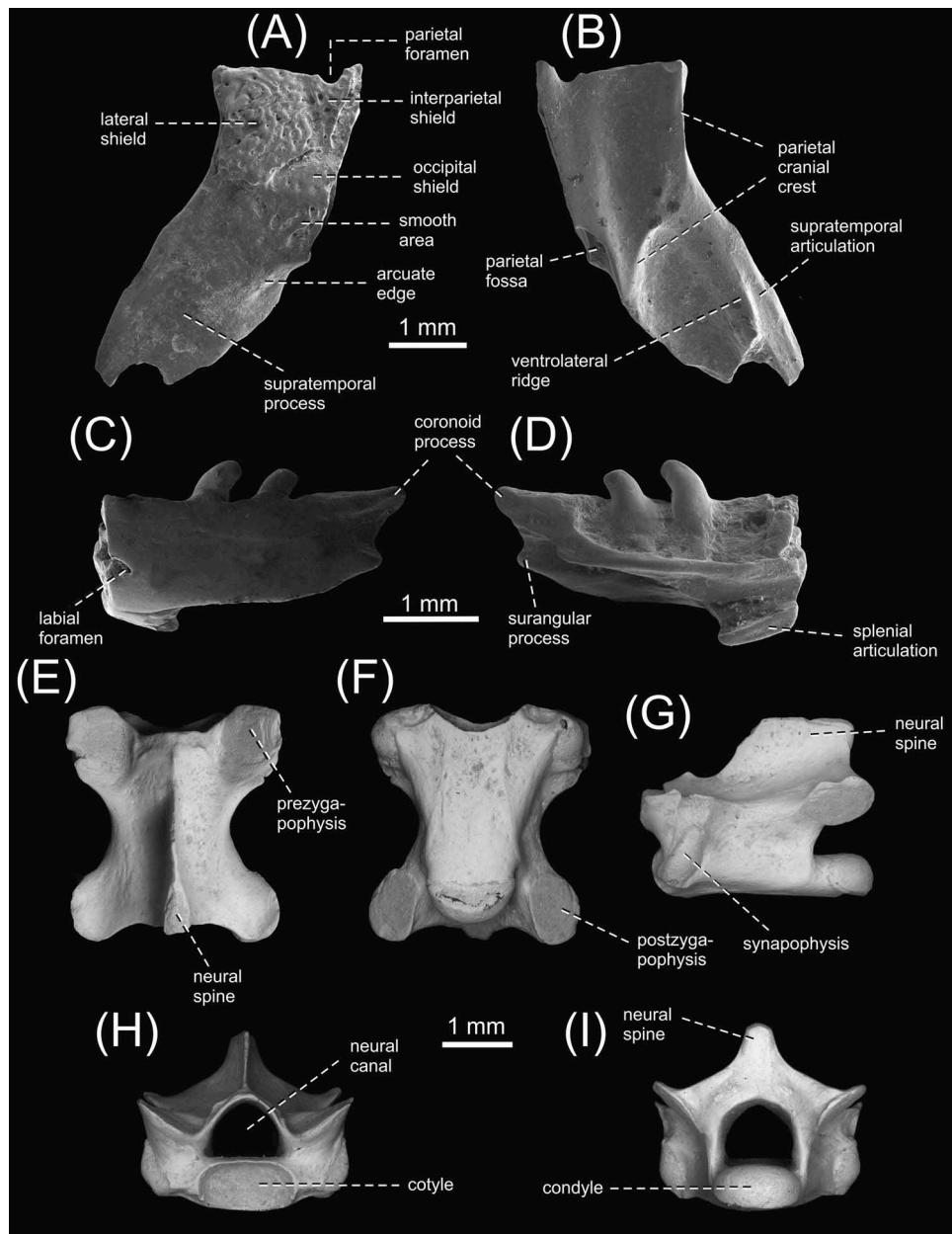
Figure 4(A, B)

Material -parietal GIN 1145/263.

### Description

#### Parietal

The specimen GIN 1145/263 is damaged, mainly the left portion of the parietal is preserved, together with portion of the central region and large portion of the left supratemporal process (Figure 4(A, B)). The parietal table is mostly covered by osteodermal shields. The shields are ornamented and this ornamentation is densely arranged. It consists of the pits, elongated grooves and ridges. In the central region, the posterior portion of the interparietal shield is present where the posterior half of the parietal foramen is visible. Laterally to this shield, the large parietal shield is present, but its anterior portion is broken off. The occipital shield is partly preserved and small. The left half of its posterior margin is well preserved here. Posteriorly to this shield, a smooth area is present which is slightly anteroposteriorly longer than the anteroposterior mid-length of



**Figure 4.** *Ophisaurus* from the late Miocene of the locality Solnechnodolsk. Parietal GIN 1145/263 of *Ophisaurus* cf. *spinari* in dorsal (A); and ventral (B) aspects. Dentary GIN 1145/264 of *Ophisaurus* sp. in lateral (C); and medial (D) aspects. Dorsal vertebra GIN 1145/265 of *Ophisaurus* sp. in dorsal (E); ventral (F); lateral (G); anterior (H); and posterior (I) aspects.

the occipital shield. This area possesses several grooves that gives it a wrinkled appearance. It is most likely made by the postoccipital osteoderms that have detached. A fine arcuate border is exposed posteriorly to the smooth area. The left supratemporal process is preserved, but its posterior portion is broken off. The process is mediolaterally broad. A parietal notch was most likely present, as it can be estimated from the preserved portion.

In ventral view, the parietal fossa reaches slightly posteriorly to the level of the ventrolateral ridge – parietal cranial crest contact. The course of the posterior section of the parietal cranial crest is not straight, but curves posteromedially. The muscular surface is absent. The facet for the supratemporal is located at the lateral

edge of the supratemporal process and reaches anteriorly to the level of the posterior margin of the parietal table.

### Remarks

This specimen differs from the parietal described here as *Anguis* cf. *rarus* in several features: (1) the type of ornamentation; (2) the ratio of the mid-length of the occipital shield and the smooth area; (3) the lateral divergence of the supratemporal processes is not so pronounced. This shows the presence of at least two anguine taxa in Solnechnodolsk. The specimen GIN 1145/263 can be allocated as *Ophisaurus* cf. *spinari* on the base of the following

features: (1) the densely arranged ornamentation; and (2) the course of the posterior section of the parietal cranial crest is not straight, but typically curves posteromedially (see Klembara 1979; Klembara and Rummel 2018).

### *Ophisaurus* sp.

Figure 4C–I

*Material* -left dentary GIN 1145/264, vertebra GIN 1145/265.

## Description

### Dentary

Only the posterior region of the left dentary is preserved (Figure 4 (C, D)). It bears four tooth positions (two teeth are still attached). The subdental shelf is thin. It forms a dorsal roof of the open Meckel's groove. The posterior region possesses a blunt coronoid process and a triangular and shorter surangular process located below. Only the base of angular process is preserved. Here, the ventral margin bears a facet for the splenial. The lateral side of the dentary is smooth, having only partly preserved labial foramen in the anterior region of the preserved portion.

**Dentition.** The implantation is pleurodont. The preserved two posterior teeth are recurved. The anterior cutting edges are well developed. The tooth apices of the preserved teeth are blunt (however, this can be caused by wearing or due to taphonomic reasons).

### Vertebra

Only one isolated complete vertebra is preserved (Figure 4(E–I)). Its maximum anteroposterior length is higher than the maximum dorsoventral height. In lateral aspect, the neural spine is low, trapezoidal in shape. Its dorsal margin is almost straight and the neural spine does not exceed the condyle posteriorly. In dorsal aspect, it has a narrower appearance – it gradually widens only slightly posteriorly. Anteriorly, a low medial ridge runs to the end of the neural arch, where it forms a small spike. The pre- and postzygapophyses are well expanded, with a deep interzygapophyseal constriction. The articulation area on the prezygapophysis is rounded, whereas it is ovoid on the postzygapophysis. The synapophysis is well developed, laterally expanded, located in the anterior region. The neural canal is a large, tunnel-like structure. The cotyle and condyle are markedly depressed. The dorsoventral height of the cotyle is smaller than the height of the neural canal. In ventral view, lateral margins of the centrum (= subcentral ridges) gradually become closer anteroposteriorly. They have more or less straight courses in the anterior 2/3, but further posteriorly become slightly concave. The ventral region of the centrum is flat, although it has two visible edges which run from the level of the cotyle and end slightly before the level of the condyle. These edges slightly diverge posteriorly.

### Remarks

The straight course of the lateral margins of the centrum might resembles the vertebrae of *Pseudopus* (see Klembara

1981; Čerňanský et al. *Forthcoming*). However in this vertebra from Solnechnodolsk, some concavity is present in the posterior section. Moreover, one of the character states of *Pseudopus* vertebrae is that the dorsoventral height of the cotyle is higher than the height of the neural canal (Čerňanský et al. *Forthcoming*). This is the opposite of the condition in both *Ophisaurus* and the Solnechnodolsk vertebra.

### *Anguinae* indet.

Figure 5

*Material* -two isolated osteoderms GIN 1145/266 and 1145/269.

## Description

### Osteoderms

The osteoderms are of two morphotypes. The first morphotype (Figure 5(A, B)) is represented by a slender, flat, rectangular osteoderm. It possesses a low medial ridge running along their entire central region, although being most distinctive in the sculptured region. The ornamentation is formed by short grooves, tubercles, pits and ridges diverging from the central region. The sculptured region forms approximately 3/4 of the entire length of the osteoderm. The rest is formed by the anterior smooth overlap surface. The lateral bevel is highest close to the overlap surface. The central part of the internal surface is pierced by three foramina, whereas shallow grooves are located on the periphery of the internal surface.

The second morphotype (Figure 5(C, D)) is roughly square in shape, slightly narrowing posteriorly. The medial ridge is absent. This osteoderm also differs from the first morphotype by its sculpture. It is formed by radially divergent long grooves and pits. The smooth overlap surface is large. The internal surface is pierced by three foramina, however, they are located anteriorly.

### Varanidae Gray, 1827 (sensu Estes et al., 1988)

*Varanus* Merrem, 1820

### *Varanus* sp.

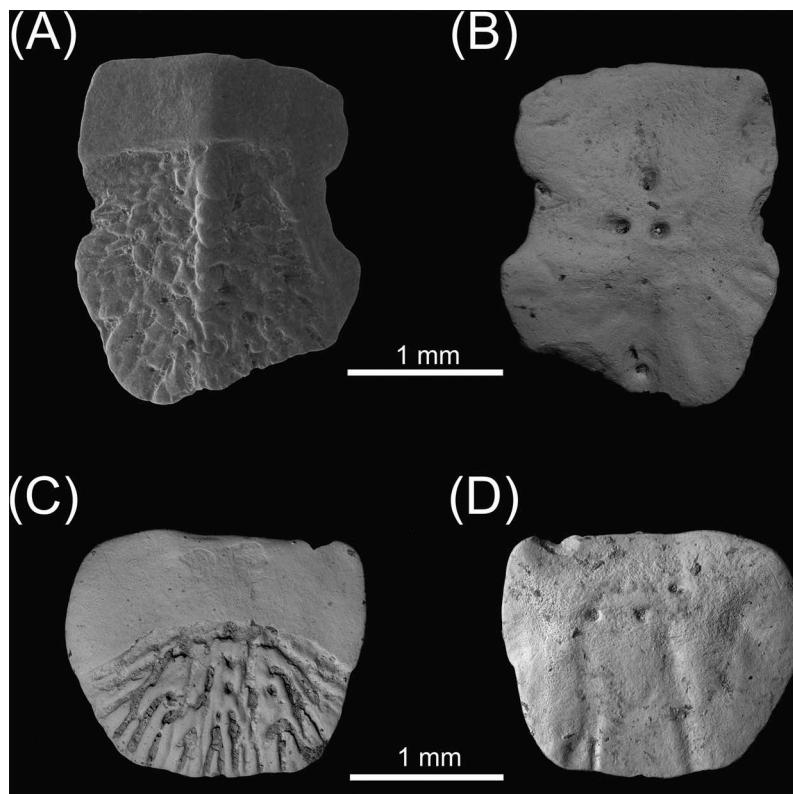
Figure 6

*Material* – one sacral vertebra GIN 1145/267, one caudal vertebra GIN 1145/268.

## Description

### Sacral vertebra

The vertebra is robustly built (Figure 6(A–E)). The neural arch is unfortunately damaged and the posterior portion with the neural spine as well as postzygapophyses are lacking. The prezygapophyses are well dorsally inclined at an angle of 45°. They are strongly elliptical in dorsal view and anteriorly overhang the cotyle. The transverse processes are broken off, only their bases are preserved. The preserved portion



**Figure 5.** Anguinae indet. from the late Miocene of the locality Solnechnodolsk. Isolated osteoderms, the morphotype 1. GIN 145/266 and the morphotype 2. GIN 145/269 in external (A, C); and (B, D) internal aspects.

appears narrow distally in dorsal or ventral aspects. The neural canal is tunnel-like (roughly pentagonal) and small if compared to cotyle. The cotyle and condyle are large and depressed. The articular surface of the condyle is exposed mainly dorsally, whereas the cotyle is exposed ventrally. The condyle is kidney-shaped in posterior aspect. In ventral aspect, its lateral margins are slightly laterally expanded, thus overreaches anteriorly located portion of the centrum. The centrum is short and its ventral margin is concave in lateral aspect.

#### Caudal vertebra

The centrum of this caudal vertebra (Figure 6 (F–J)) is narrow and distinctly anteroposteriorly elongated if compared to the centrum of sacral vertebra. The neural spine starts to rise dorsally approximately in the mid-length of the neural arch. The neural spine is high, but its dorsalmost portion is broken off. In lateral aspect, it is trapezoidal in shape. In anterior and/or posterior aspects, the neural spine is robust rather than thin. The pre- and postzygapophyses are small, markedly inclined dorsally. The prezygapophyses overhang the cotyle anteriorly, but the postzygapophyses do not reach the level of the posterior end of the condyle (the condyle extends beyond the level of the postzygapophyses). The cotyle and condyle are large and depressed, whereas the tunnel-like neural canal is small. Only the bases of the transverse processes are preserved, located in the anterior region of the vertebra. They are expanded laterally, slightly inclined ventrally. Only the pedestals (sensu Augé and Guével 2018),

which form the support of the chevron bones, are preserved. They are located in the posterior region of the ventrolateral section of the centrum. They continue anteriorly as two parallel ridges (or keels) running to the cotyle, but gradually become less distinct. An autotomy septum is lacking.

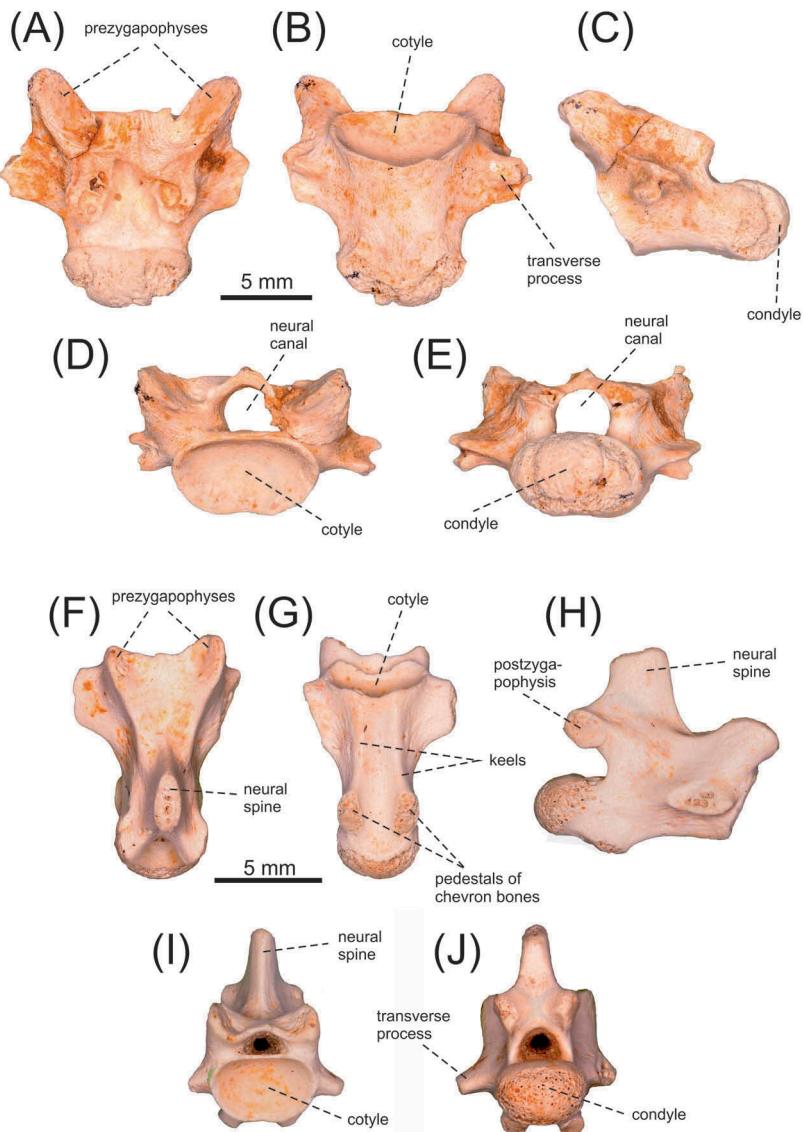
#### Remarks

The vertebrae possess two varanid synapomorphies: (1) articular surface of the condyle exposed dorsally with the cotyle exposed ventrally (e.g. Camp 1923; Bailon and Rage 1994; Venczel 2006; Holmes et al. 2010); and (2) the presence of two parallel keels running along the ventral surface of the centrum of caudal vertebra (see Augé and Guével 2018).

#### Discussion

The late Miocene Solnechnodolsk paleoherpetofauna is quite diverse, showing a very interesting composition of lizards in this part of Russia during this geological period. Besides lacertids and skinks (to be published elsewhere), three other clades are present here: Amphisbaenia, Anguidae and Varanidae.

The amphisbaenian material is represented only by two isolated vertebrae. This makes a solid allocation at the family level very difficult, because of lack of clear diagnostic features for identification of amphisbaenian isolated vertebrae (Estes 1983; Augé 2005, 2012; Georgalis et al. 2016, 2017a). We can exclude rhineurids, because all members of this clade (extant and fossil) have a denticulate vertebral posterior margin. The same is true for



**Figure 6.** *Varanus* sp. from the late Miocene of the locality Solnechnodolsk. Sacral GIN 1145/267 (A-E) and caudal GIN 1145/268 (F-J) vertebrae in dorsal (A, B); ventral (B, G); lateral (C, H); anterior (D, I) and posterior (E, J) aspects.

trogonophiids. This state is variably present in Amphisbaenidae: for example, the posterior margin of *Amphisbaena alba* vertebrae is smooth, whereas it is indented in the African amphisbaenid *Monopeltis* and in many other Amphisbaenidae (Kearney 2003; Augé 2012; Čerňanský et al. 2015a). According to geographical position of the locality and age of the sediments, these vertebrae most likely represent a blanid taxon. Today, the *Blanus strauchi* complex occurs in Anatolia and parts of the Middle East, but is also present in certain islands in the southern Aegean Sea (Sindaco et al. 2014). The vertebrae of this clade are described from MN 7 + 8 from other side of the Black Sea, from western Romania by Venczel and Štiučă (2008). The Miocene record of the clade Amphisbaenia is reported from most of Europe (MN 9 yielded the last amphisbaenian from central Europe, see Böhme and Ilg 2003), whereas since the Pliocene, their spatial distribution appears to be restricted to the region of Mediterranean countries (Delfino 1997).

The Solnechnodolsk anguine material shows the presence of at least two taxa which are described from this area for the

first time: *Anguis* cf. *rarus* and *Ophisaurus* cf. *spinari*. The fossil Miocene record of *Anguis* is very sparse. Only one single parietal was previously documented (Klembara and Rummel 2018) and the parietal described here represents only the second known parietal bone of the Miocene *Anguis*. *Anguis rarus* was described from the early Miocene (MN 3) of the Petersbuch 62 locality in Germany (Klembara and Rummel 2018). The Solnechnodolsk parietal of *Ophisaurus* can be allocated to *O. cf. spinari*. The taxon *O. spinari* was previously known from several early and middle Miocene (MN 2 – MN 5) localities, all in Central Europe: the Czech Republic, Germany, and Austria (Klembara 1979; Roček 1984; Čerňanský et al. 2015b; Čerňanský 2016; Klembara and Rummel 2018; it should be noted that the material described as *O. spinari* by Böhme and Vasilyan 2014; from the late middle Miocene of Austria is not regarded as belonging to this taxon by Klembara and Rummel 2018). The youngest record of this species is known, astonishingly, from the late Pliocene of Italy (formerly allocated as *Dopasia*

sp. in Delfino et al. 2011; but later placed to *O. spinari* by Klembara and Rummel 2018). However, no record was known from the late Miocene or early Pliocene, which would shed more light on the history of this taxon during this particularly relevant time. The Solnechnodolsk anguine material brings crucial data. The material of *A. cf. rarus* forms the first evidence of the survival of this *Anguis* species to the end of the Miocene by its shifting to south areas of Eastern Europe prior the Pliocene. The same is true for *O. spinari*. This probably reflects the middle Miocene cooling (see Böhme 2003; although this hypothesis deserves a comment here. In the early Miocene, *Anguis rarus* is known only from its type locality in Germany. Therefore, a shifting of the range during the Miocene cooling is certainly possible. But the real distribution of this taxon in the early Miocene is unknown – it could be restricted to the area of Central Europe only, but it could have had a wider range including southern portions of Europe too. Thus, a shrinking cannot be excluded based on our current knowledge). One of the last records of *Ophisaurus* species from Central Europe come from MN 7–8 (*O. robustus* from Hungary, see Hír et al. 2001; Venczel and Hír 2013; Klembara and Rummel 2018), and MN 9–10 respectively – the taxon *O. acuminatus* was described by Jörg (1965) from the Heweneg/Hegau locality (near city Öhningen, Germany). Although members of *Ophisaurus* are absent in modern ecosystems of Europe, the youngest record on this continent comes from the Early Pleistocene (south of the Iberian Peninsula; Bailon and Blain 2007). Nowadays, the clade Anguinae (Anguimorpha, Anguidae) comprises legless lizards and includes three extant taxa (see e.g. Estes 1983): *Pseudopus* (Southeast Europe to Central Asia), *Anguis* (Europe, Western Asia) and *Ophisaurus* (North America, Northern Africa [= *Hyalosaurus*] and Southeast Asia [= *Dopasia*]). Two of five species of *Anguis* are distributed in the current territory of Russia as a result of fast postglacial recolonization of Europe and western Asia: *A. fragilis* in the Kaliningrad Region (northward along the coast of the Baltics) and the other areas are occupied by *A. colchica* (see e.g. Gvoždík et al. 2010; Jablonski et al. 2017). The Solnechnodolsk parietal GIN 1145/262 unambiguously documents that *Anguis* was already present in Russia in the late Miocene, the same age as that of the basal radiation of extant forms of *Anguis* (Gvoždík et al. 2010). This is evidence that the genus *Anguis* is very old with a wide former distribution. It should be noted that Chkhikvadze (1985) listed *Anguis* and/or *Ophisaurus* from the early Miocene deposits of eastern Kazakhstan. However, his interpretations are in need of revision (moreover, the original material is most likely lost; see Vasilyan et al. 2017).

The same age as the Solnechnodolsk locality (MN 13) is represented by a northern Greek locality Ano Metochi (see Georgalis et al. 2017b) and the preserved portion of the Solnechnodolsk *Ophisaurus* dentary resembles the dentary of *Ophisaurus* from Greece (Georgalis et al. 2017b: Figure 4(B, C)). From the same age as Solnechnodolsk (MN 13), *Anguis* sp. and *Ophisaurus* sp. are also described from the Süleymanlı locality in Turkey (see Čerňanský et al. 2017). The morphology of the *Ophisaurus* vertebra from this Turkish locality is similar to that of the *Ophisaurus* vertebra from Solnechnodolsk and also from Ano Metochi (e.g. in having distinct edges, limiting

the flat ventral portion of the centrum and small level of the subcentral ridges concavity; see Čerňanský et al. 2017: Figure 2J; Georgalis et al. 2017b: Figure 4K). Moreover, the morphology of the Solnechnodolsk vertebra mainly resembles the dorsal vertebrae of the Asiatic lineages such as *O. harti* (see Čerňanský et al. Forthcoming).

The thermophilic reptiles in Solnechnodolsk are represented by the monitor lizard. Only the genus *Varanus* is currently reported from European Neogene and Quaternary localities. Its stratigraphic distribution spans from the early Miocene to the Middle Pleistocene (Delfino et al. 2013; Ivanov et al. 2018), with the last European record known from the middle Pleistocene of Greece (Georgalis et al. 2017c). This genus includes a clade of mid-sized to large, mostly carnivorous (some frugivorous) lizards widely distributed in tropical and subtropical regions (Bauer 1998; Pianka et al. 2004).

In conclusion, the Solnechnodolsk lizard fauna supports in general the previous drawn from other squamate lineages (see e.g. Böhme 2003; Delfino et al. 2008; Rage 2013). Many taxa, which were present in the paratropical ecosystems of Central Europe during the early Miocene, gradually disappeared from this region because of the climatic cooling (Böhme 2003). However, some of those lineages were still present at Solnechnodolsk during the late Miocene. Based on paleobotanical data, major vegetation changes occurred in the late Miocene in southeastern areas of Europe. Ivanov et al. (2011) reported slight cooling and some drying at the beginning of the late Miocene, followed by cycling changes of humid/dryer and warmer/cooler conditions. The occurrence of *Varanus* sp. in Solnechnodolsk suggests a mean annual temperature not less than around 15 °C (see Böhme 2003). The presence of *Ophisaurus* cf. *spinari* fits well with the previous paleoenvironmental interpretations of the locality (see Introduction). Böhme (2002) suggested that this taxon is found especially in fluviatile basin sediments, although it should be noted that this taxon occurs across wider environmental conditions than e.g. *O. fejvari* (see Čerňanský 2016). The very rare presence of *Anguis* cf. *rarus* sheds new light on the evolution of this lineage in Europe during the late Miocene.

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