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SHORT COMMUNICATION

FIRST RECORD OF FOSSIL *OPHISAURUS* (ANGUIMORPHA, ANGUIDAE) FROM ASIA

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The family of glass lizards Anguidae consists of four subfamilies. Two of them, Gerrhonotinae and Diploglossinae, are restricted to the New World. The third subfamily, Glyptosaurinae, is known exclusively from the fossil record from Late Cretaceous to late Oligocene localities in North America, Europe, and Asia (Sullivan, 1979; Estes, 1983; Böhme, 2007). The extant members of the fourth subfamily, Anguinae, occur in Eurasia, North Africa, and North America. In Eurasia, fossils of *Ophisaurus* have previously been found only in localities west of the Ural Mountains (Klembara, 1981, and references therein; e.g., Estes, 1983; Augé, 2005; Klembara, 2012, 2015). Although fossil *Ophisaurus* remains from Asia have been mentioned (Chkhikvadze, 1985), the material has never been described or figured. Because it has been hypothesized that *Ophisaurus* originated in Europe, dispersed to North Africa and Southeast Asia, and finally reached North America via the Bering Strait (Klembara, 1981; Macey et al., 1999), fossils of *Ophisaurus* are expected to be found in Asia.

Western Siberia is an area of Russia and northern Kazakhstan bordered on the west by the Urals, on the east by the Central Siberian Plateau, and to the south by the Kazakh Plain and Altay Mountains. On the north it borders the Arctic Ocean, where the major Siberian rivers Irtysh and Ob drain into the ocean. In the southern part of the territory, Neogene and Quaternary sediments are widely distributed, extensively cropping out along the river banks of the Ob and Irtysh rivers. Over many decades mollusks and small mammals from these deposits have been intensively studied for stratigraphic correlation, paleoclimatological reconstructions, and paleoenvironmental interpretations of the Neogene and Quaternary of the region (e.g., Zykin, 1979, 2012; Zykin and Zazhigin, 2008). Besides the small mammals, some of the localities have yielded amphibian and reptile fossil remains that will be published in a separate paper.

As for Anguinae, there is only one paper indicating the presence of *Anguis* and *Ophisaurus* in Miocene localities of Kazakhstan (Chkhikvadze, 1985). Without indication about the nature of the skeletal elements, Chkhikvadze (1985) mentioned from the Zaisan Basin: (1) "*Aguis*" [sic] in the Akzhar Svita deposits of early Miocene age; (2) "*Anguis* sp." from the middle Miocene Sarybulak Svita; an assignment to a specific horizon/locality is lacking; and (3) vertebrae of "small *Ophisaurus* (or big *Anguis*?)" from the late Miocene Kalmakpai Svita deposits (Fig. 1). Unfortunately, Chkhikvadze (1985) only mentions the presence of these anguins in the above-mentioned Miocene deposits. No data are given about the institution where these specimens are deposited. A visit by two of the authors (D.V. and M.B.) to the Institute of Paleobiology in Tbilisi, where the material was expected to be deposited, did not locate the material; thus, we were not able to study the specimens mentioned by Chkhikvadze (1985).

The aim of this short communication is (1) to describe the skeletal elements of *Ophisaurus* from Miocene to latest Pliocene–earliest Pleistocene deposits of western Siberia that represent the only evidence for fossil *Ophisaurus* in Asia, and (2) to demonstrate the significance of the morphology of these skeletal elements for the evolution and paleobiogeography of *Ophisaurus*.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York, New York, U.S.A.; **BSPG**, Bayerische Staatssammlung für Paläontologie, Munich, Germany; **CM**, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A.; **DE**, Department of Ecology, Comenius University in Bratislava, Faculty of Natural Sciences, Bratislava, Slovakia; **GIN**, the Geological Institute of the Russian Academy of Sciences, Moscow, Russia; **UF**, University of Florida, Gainesville, Florida, U.S.A.

MATERIALS AND METHODS

The skeletal remains described herein, the maxilla, the dentaries, and the vertebrae, have been recovered from two middle Miocene (Baikadam, Malyi Kalkaman 1), one late Miocene (Selety 1A), and one earliest Pleistocene (Podpusk 1) locality in Kazakhstan (Fig. 1). The fossil material is stored in the paleontological collection of the Geological Institute of the Russian Academy of Sciences. Stratigraphic assignment of the fossil localities is based on local lithostratigraphy in addition to biochronology of several small mammal lineages, e.g., *Microtocricetus molassicus* at Baikadam and Malyi Kalkaman 1; *Lophocricetus vinogradovi, Rhinocerodon seletyensis*, and *Plioscirtopoda antiqua* at Selety 1A; and *Mimomys pliocaenicus* at Podpusk 1 (Zykin et al., 2007, 2008). For the identification of fossil bones, the following skeletons of Recent anguins were used: *Anguis fragilis* (DE 14–21, 24, 25, 45–48); *Ophisaurus ventralis* (AMNH 73057; CM 1411; DE 34, 35, 38; UF 52539); *Ophisaurus attenuatus* (DE 32, 33, 43, 44); *Ophisaurus compressus* (DE 50); *Ophisaurus mimicus* (DE 49); *Ophisaurus koellikeri* (DE 30, 41); *Ophisaurus harti* (AMNH 34956; DE 36, 37, 56, 57, 86); *Ophisaurus. gracilis* (DE 42); and *Pseudopus apodus* (BSPG 1982X2383; DE 1, 3–13, 22, 23, 29, 52–54, 58, 59).

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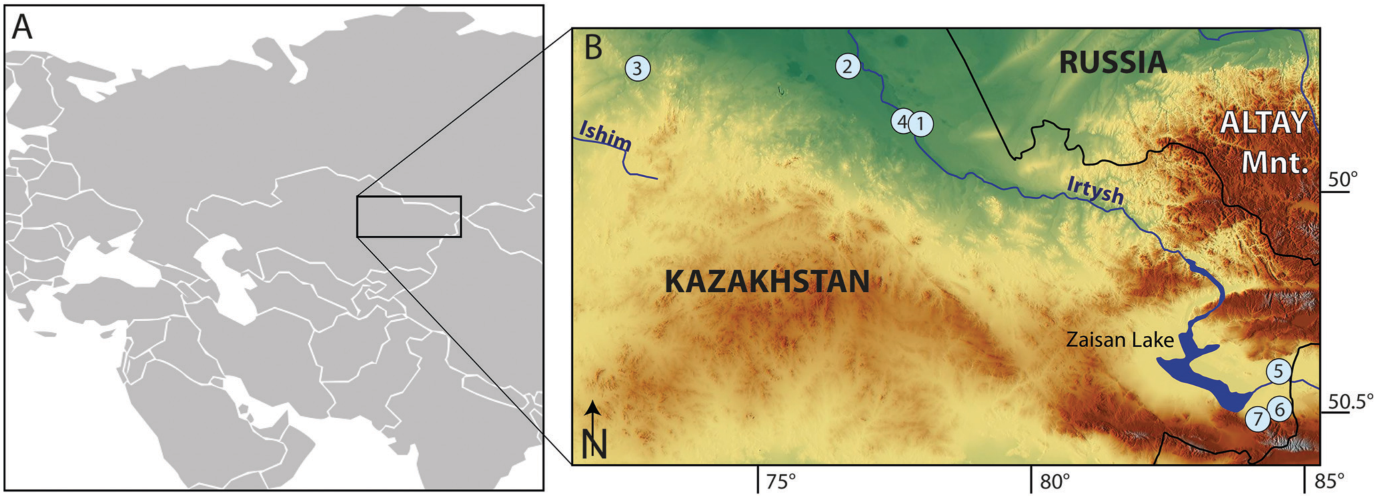

FIGURE 1. **A**, geographic location of the studied region (black rectangle); **B**, topographic map of northeastern Kazakhstan with position of the fossil localities. **1**, Baikadam; **2**, Malyi Kalkaman 1; **3**, Selety 1A; **4**, Podpusk 1; **5**, Zmei Gorynych; **6**, Sarybulak Svita; **7**, Kalmakpai Svita.

Specimens were imaged using both digital stereomicroscopy (Leica DVM5000; Tübingen, Germany) and scanning electron microscopy (Inspect S50; Madrid, Spain).

SYSTEMATIC PALAEONTOLOGY

SQUAMATA Oppel, 1811
ANGUIMORPHA Fürbinger, 1900
ANGUIDAE Gray, 1825
ANGUINAE Gray, 1825
OPHISAURUS Daudin, 1803

OPHISAURUS sp.
(Figs. 2, 3)

Referred Specimens—GIN 950/2001-RE01, a right maxilla; GIN 950/2001-RE02, a left dentary; GIN 950/2001-RE03–RE05, numerous vertebrae; all from Baikadam, Kalkaman Svita (late middle Miocene, early Serravallian). GIN 951/1001-RE01 and GIN 951/1001-RE02, two trunk vertebrae, from Selety 1A, Kedey Svita (late Miocene, early Messinian). GIN 950/5001-RE01 and GIN 950/5001-RE02, two trunk vertebrae, from Podpusk 1, Irtysh Svita (earliest Pleistocene).

Description—A middle portion of the right maxilla with three well-preserved teeth is present (Fig. 2A, B). Only the ventral portion of the nasal process is preserved. At the level of its posterior margin, a well-preserved palatine process extends medially. The superior alveolar foramen lies between the palatine and nasal processes. Immediately laterally to the palatine process, a distinct groove indicates the ventral process of the prefrontal articulation.

A fragment of the middle portion of the left dentary is also preserved (Fig. 2C, D). The external surface of the dentary displays three mental foramina. It bears three perfectly preserved teeth. At the level of the teeth, the dental crest is flexed ventrally.

The teeth are pleurodont and conical in shape (Fig. 2). The tip is curved posteriorly and slightly lingually. The apex bears distinct mesial and distal cutting edges. The lingual surface of the apex is striated, and striae extend to the surface of the cutting edges. Whereas the bases of teeth are only slightly mesiodistally broadened, their lingual portions are distinctly bulged (Fig. 2C, D).

The procoelous vertebrae show flattened and elongate centra, with the cotyle positioned ventrally at the level of the condyle (Fig. 3). The margins of the posteroventral surface of centra run parallel to each other and anteriorly diverge laterally (Fig. 3B, G). Two small subcentral foramina are usually present in the anteroventral portion of the centrum. The prezygapophyses are directed anterolaterally and inclined dorsally. The postzygapophyses project slightly laterally. The neural spine is well developed and high; it reaches the anterodorsal margin of the neural arch. In dorsal and lateral views, a distinct interzygapophyseal constriction is observable. In posterior view, the neural arch is high, whereas its anterior portion is low and broad. The neural canal is higher than the height of the cotyle (Fig. 3D, I).

Comparison—Although the skeletal elements described above are mostly fragmentary, the teeth on the two tooth-bearing bones exhibit distinguishing features of *Ophisaurus*. The teeth of all living species of *Ophisaurus* are conical in shape, have similarly developed mesial and distal cutting edges, and the lingual surface of the tooth apex is striated (Klembara et al., 2014). In contrast to the teeth of the species living in North America, the tooth crowns of the species living in North Africa and Southeast Asia have more distinctly developed mesial and distal cutting edges, with bases that are mesiodistally broader and that do not exhibit a bulge on the lingual surface (Klembara et al., 2014). Previously, the bases of teeth of the species living exclusively in North America were thought to be mesiodistally compressed and lingually bulged (Klembara and Green, 2010; Klembara et al., 2014). However, our new finds clearly document that teeth with bulged lingual portions at the base, previously identified only in the Recent North American species of *Ophisaurus*, were already present by the middle Miocene of Asia (Fig. 2C, D).

As for the dorsal vertebrae, the anatomy corresponds to that of *Ophisaurus*. Contrary to the condition in both *Anguis* and *Pseudopus*, the height of the neural canal is greater than the height of the cotyle (more distinctly developed in larger, adult specimens) in *Ophisaurus* (Fig. 3D, I). In *Anguis*, the posterior section of the lateral walls of the centrum is distinctly constricted. Regarding the shape in *Pseudopus*, the lateral margins of the centrum are straight (Klembara, 1981). In *Ophisaurus*, the lateral margins of the centrum are slightly constricted at about mid-length, as is the case of the vertebrae described herein. The smaller of the figured dorsal vertebrae (Fig. 3A–E) corresponds morphologically to the vertebrae of *O. gracilis*. In contrast, the

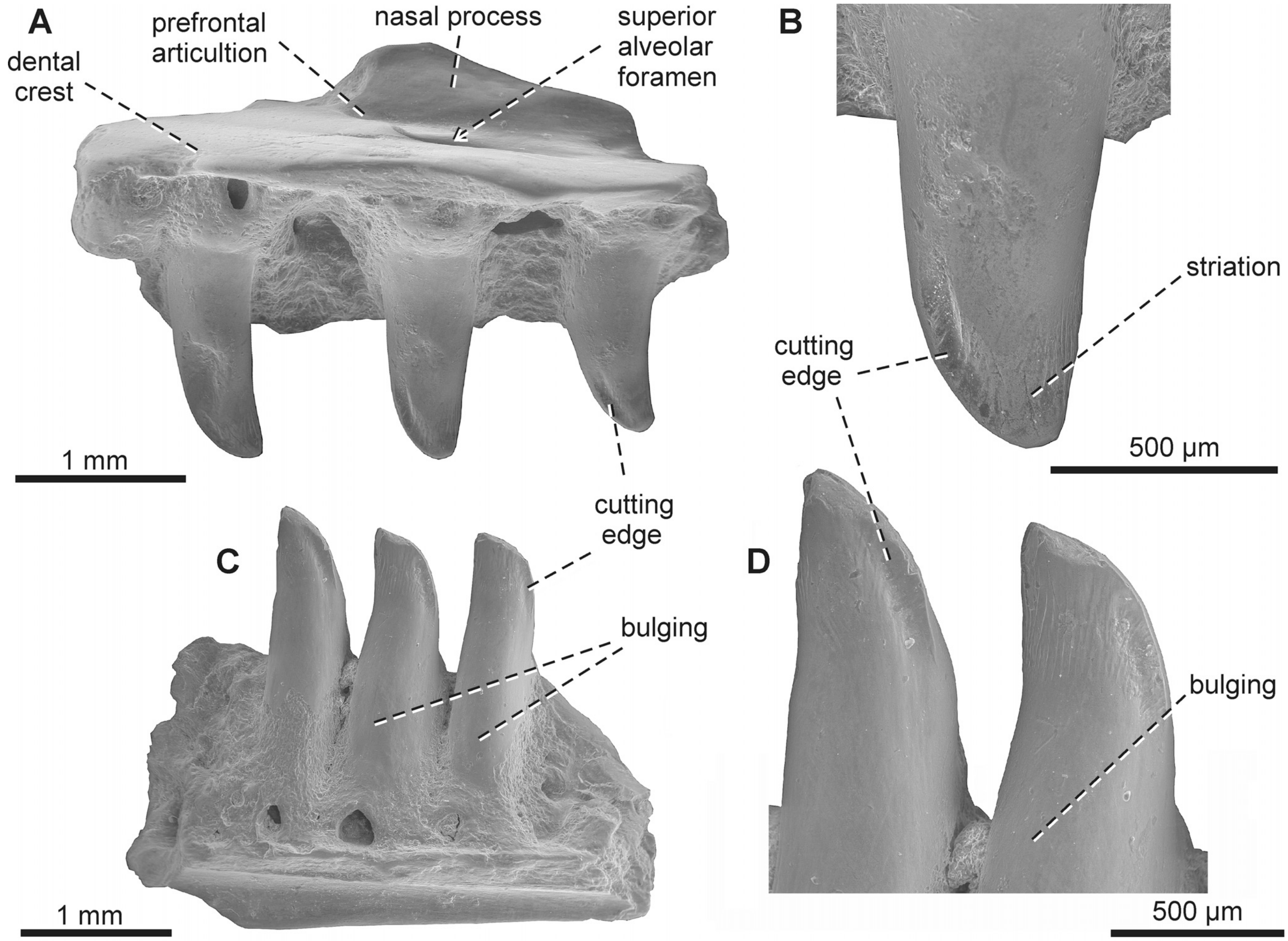

FIGURE 2. *Ophisaurus* sp. from the locality Baikadam. **A**, GIN 950/2001-RE01, right maxilla, in medial view; **B**, close up of the middle tooth of the same specimen in lingual view. **C**, GIN 950/2001-RE02, left dentary, in medial view; **D**, close up of two teeth of the same specimen in medial view.

larger vertebra (Fig. 3F–J) corresponds morphologically to the mid-trunk vertebrae of North American species such as *O. ventralis* and *O. attenuatus* in having a large, anteroposteriorly elongated neural spine.

ANGUINAE indet.
(Fig. 4)

Referred Specimens—GIN 950/2001-RE05 and GIN 950/2001-RE06, right and left dentaries, respectively, from Baikadam, Kalkaman Svita; GIN 1107/2001-RE01, a right dentary, from Malyi Kalkaman 1, Kalkaman Svita, early middle Miocene.

Description—On the basis of tooth morphology, all these fragmentary dentaries may be associated with a single taxon (Fig. 4). The symphysial region is oval in shape and the dental crest is curved ventrally (Fig. 4D). The teeth are slender, conical, and slightly curved posteriorly. The apex bears weakly developed mesial and distal cutting edges. The crown surface is smooth, and the lingual surface of the apex bears no striations. The basal portion of the teeth does not bulge lingually.

Comparison—The morphology of the teeth of GIN 950/2001-RE05 and GIN 950/2001-RE06 (Fig. 4) differs from extant *Ophisaurus*; however, it is very similar to that of Anguine morphotype 2 from the early Miocene of the Czech Republic (Klembara, 2015). In both taxa, the teeth are slender, slightly curved posteriorly, the mesial and distal cutting edges are only weakly developed, the lingual surfaces of their apices are not striated, and their bases do not bulge lingually.

DISCUSSION AND CONCLUSIONS

The anguine record from the studied localities in Kazakhstan reveals two taxa: *Ophisaurus* sp. and Anguinae indet. As already indicated above, it has been supposed that *Ophisaurus* originated in Europe in the early Cenozoic and spread into North Africa (*O. koellikeri* living in Morocco and Libya), Southeast Asia (e.g., *O. harti, O. gracilis*), and North America via the Bering Strait (Klembara, 1981; contra Sullivan, 1987; Macey et al., 1999). Sullivan (1987) concluded that the North American species of *Ophisaurus* have an independent origin from the *Anguis-Pseudopus* group living in Eurasia. Sullivan (1987) considered *Parophisaurus pawneensis* from the early Oligocene of North America a potential representative of the ancestral lineage for North American *Ophisaurus*. However, it was later shown that *P. pawneensis* is a gerrhonotine (Conrad and Norell, 2008; Conrad et al., 2011). The earliest record of *Ophisaurus* in Europe is a parietal of *Ophisaurus* sp. from the late Eocene Newton Bone Bed (Osborne Member, ca. 35 Ma) of the Hampshire Basin in

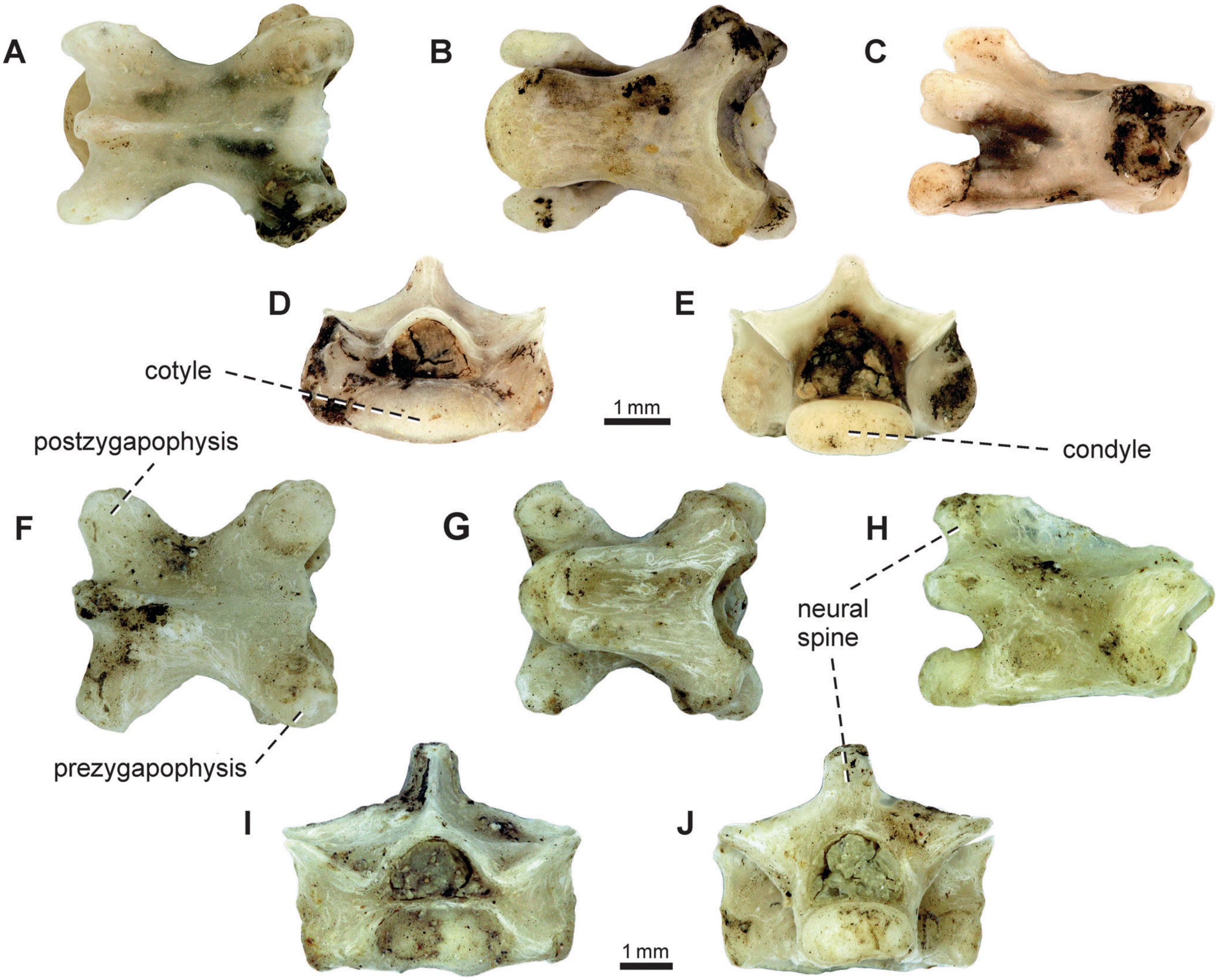

FIGURE 3. Dorsal vertebrae of *Ophisaurus* sp., locality Baikadam, from anterior (**A**–**E**; GIN 950/2001-RE04) and posterior (**F**–**J**; GIN 950/2001-RE03) regions of the vertebral column. **A**, **F**, dorsal view; **B**, **G**, ventral view; **C**, **H**, right lateral view; **D**, **I**, anterior view; **E**, **J**, posterior view.

southern England (Klembara and Green, 2010), although the presence of this genus in earlier deposits is not excluded (Augé, 1990; Rage and Augé, 1993). The earliest definitive record of *Ophisaurus* in North America is *O. canadensis* described from late Miocene deposits in Canada (Holman, 1970).

Thus far, the easternmost record of *Ophisaurus* from Eurasia comes from the locality of Gritsev, Ukraine, 11–12 Ma (Böhme and Ilg, 2003; Bailon and Blain, 2007; Vasilyan et al., 2013), west of the Ural Mountains. Heretofore, fossil remains of *Ophisaurus* east of the Ural Mountains were absent. In the context outlined above, the material described here is very important from two points of view.

First, we document the presence of the anguine genus *Ophisaurus* in the middle Miocene deposits east of the Turgai Strait. This is the first record of fossil *Ophisaurus* in Asia, supporting the original hypothesis regarding the origin of *Ophisaurus* in Europe and its spread via Asia into North America (Klembara, 1981; see also Macey et al., 1999). Taking into account data from the literature (Chkhikvadze, 1985) mentioning *Anguis* and/or *Ophisaurus* from the Zaisan Basin (Akzhar, Sarybulak, and Kalmapkai Svitas), eastern Kazakhstan, the presence of anguines since the early Miocene in Asia can be assumed. However, the interpretations of Chkhikvadze (1985) are in need of revision.

Second, the morphology of the teeth of the dentary (GIN 950/2001-RE02) and maxilla (GIN 950/2001-RE01) from Baikadam (Fig. 2) exhibits a combination of features typical for the species of *Ophisaurus* living in North Africa and Southeast Asia on one hand and North America on the other. The tooth base in GIN 950/2001-RE02 (Fig. 2D) is mesiodistally compressed with a lingually developed bulge. To date, this has been recorded only in Recent species of *Ophisaurus* from North America (Klembara et al., 2014). Further, among the extant North American species of *Ophisaurus, O. ventralis* has the most distinctly developed mesial and distal cutting edges and striations that extend over the lingual surfaces of the teeth (Klembara et al., 2014). These features are also typical for specimens GIN 950/2001-RE01 and GIN 950/2001-RE02 described here (Fig. 2). Such a pattern of striations is also present in *O. koellikeri* and *O. harti*, but these species have mesiodistally broad bases and lack the lingual bulge (Klembara et al., 2014). In summary, the specimens of

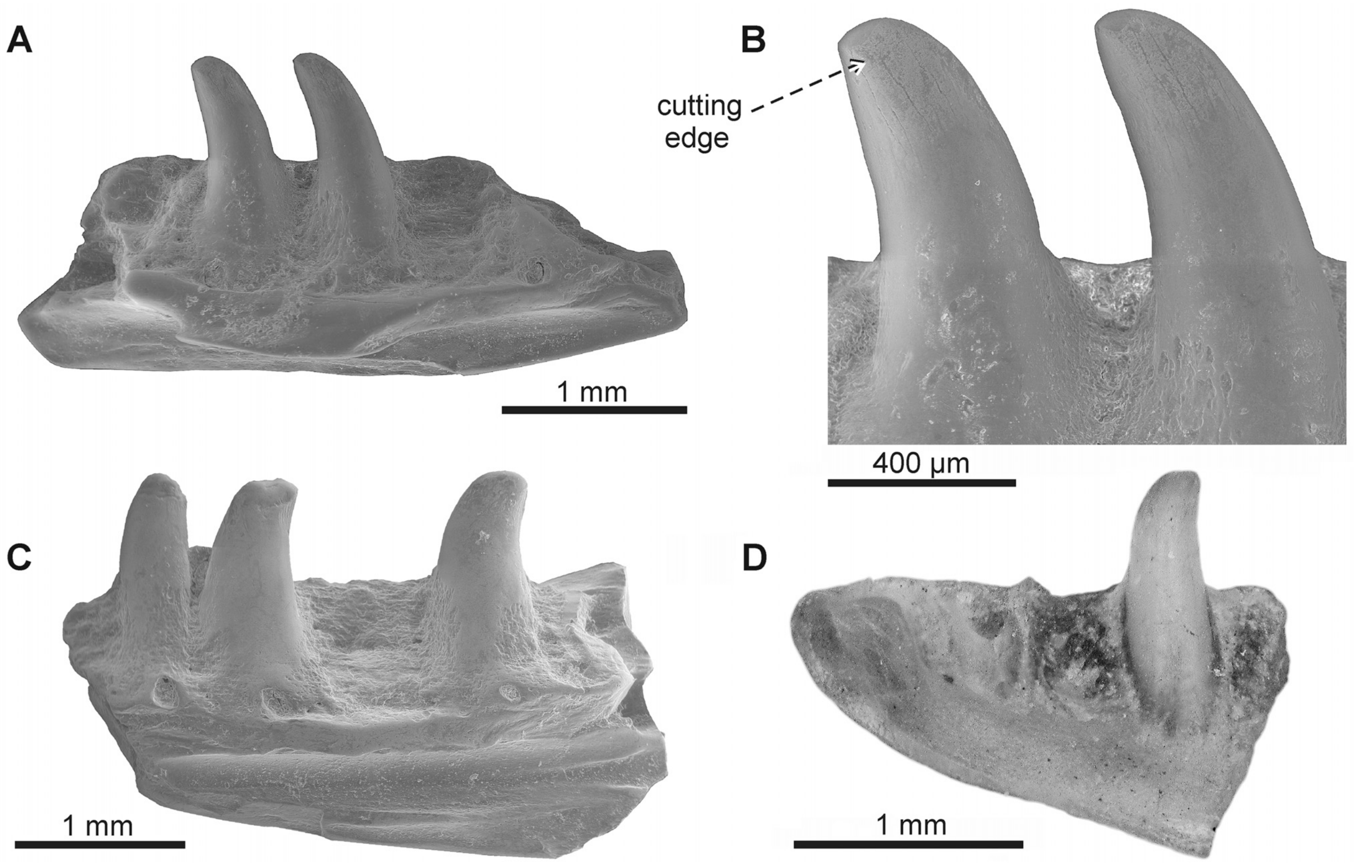

FIGURE 4. Anguinae indet. from Baikadam (**A**–**C**) and Malyi Kalkaman 1 (**D**) localities. **A**, GIN 950/2001-RE06, left dentary, in medial view; **B**, close up of two teeth of the same specimen in medial view. **C**, GIN 950/2001-RE05, right dentary, in medial view; **D**, GIN 1107/1001-RE02, right dentary, in medial view.

Ophisaurus sp. GIN 950/2001-RE01 and GIN 950/2001-RE02 exhibit features (1) typical for North American *O. ventralis* (Klembara et al., 2014:fig. 12B–E, G), and (2) recorded in extinct and extant species of *Ophisaurus* in Eurasia. This presents solid evidence that the tooth morphology exhibited in living species of North American *Ophisaurus* originated in Eurasia, thereby supporting the hypothesis of a European origin for *Ophisaurus* with dispersal via Asia to North America (Klembara, 1981). This interpretation is also supported by Macey et al. (1999) on the basis of genetic data.

Augé (2005) assigned all extinct and extant species from Southeast Asia and North Africa, previously assigned to *Ophisaurus*, to the genus *Dopasia* (originally used by Gray, 1853, for the extant *D. gracilis* from Southeast Asia). The phylogenetic analysis presented by Klembara et al. (2014) showed *Ophisaurus* to be monophyletic. Besides this, Klembara et al. (2014) concluded that it is more prudent, based on our present state of knowledge of Anguinae, to use one generic name, *Ophisaurus*, for all species living today in North America, North Africa, and Southeast Asia. The present study supports these conclusions (Klembara et al., 2014), in that the tooth morphology of *Ophisaurus* (the taxon first used for the species living in North America) is not limited to the species of North America, but is present also in the specimens from Asia, specifically from Kazakhstan. Based on the available evidence, it seems most probable that in addition to *Ophisaurus* described above, a further anguine (Anguinae indet., from Baikadam and Malyi Kalkaman 1) similar to that of Anguine morphotype 2 from the early Miocene of the Czech Republic (Klembara, 2015), has dispersed into Central Asia at least by the early middle Miocene.

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