Lizards of the Families Dorsetisauridae and Xenosauridae (Anguimorpha) from the Aptian–Albian of Mongolia

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Abstract—This paper describes two new species of lizards of the infraorder Anguimorpha from the Aptian-Albian of Mongolia. One of these, *Paradorsetisaurus postumus* gen. et sp. nov., is the youngest in the family Dorsetisauridae, while the other, *Xenostius futilus* gen. et sp. nov. is the earliest fossil find within the family Xenosauridae s. str. The paper also includes remarks on the importance of the fossil finds from Mongolia for the reconstruction of lizard diversity in Central Asia up to the beginning of the late Cretaceous.

INTRODUCTION

The Khoobur (Hobur, Höövör, Khovboor, Guchin Us) terrestrial vertebrate locality is located in Central Mongolia (Guchin basin, Övörkhangai aimag). It is composed of Aptian-Albian fluvial and fluvial-lacustrine sandstones and shales. Tetrapod fossils from Khoobur (mammals, dinosaurs, pterosaurs, crocodiles, turtles, lizards) in the collections of the A.A. Borissiak Paleontological Institute (PIN) mainly come from screen-washed fossil-bearing layers.

Fieldwork was carried out by several missions of the Soviet-Mongolian Expedition, mostly between 1969 and 1972. Most of the fossils within the collection are lizards.

Lizards from Khoobur are represented by numerous (hundreds of specimens) isolated skeletal, cranial, mandibular elements, which are difficult to identify. However, already the first and largely preliminary identifications (Alifanov 1993, 2000a, 2000b) showed a large number of lizard families (Fig. 1), making Khoobur the richest assemblage between the Middle Jurassic and late Early Cretaceous. The assemblage also has key importance for the elucidation of the details of early diversification within the studied group.

Some lizards from Khoobur have been studied in more detail. Within Gekkonidae s.l. (Gekkota), we have described the earliest representative, *Hoburogekko suchanovi* (Alifanov, 1989, Daza et al., 2012). The family Hodzhakuliidae Alifanov, 1993 (Scincomorpha) is represented by *Hodzhakulia magna* Nessov, 1985, previously described from the Late Albian of Uzbekistan, as well as by new species: *Car-*

noscincus eublepharus, *Bagaluus primigenius* and *Platynotoides altidentatus* (Alifanov, 2016). We have also published descriptions of material attributed to the Temuijiniidae family (Temuijiniidae gen. indet., Alifanov, 2018) belonging to the microorder Iguanomorpha (Iguania).

This article continues our research on the diversity of lizards from Khoobur. This time it is focused on fossils from the infraorder Anguimorpha, in particular the families Dorsetisauridae and Xenosauridae. The systematic description is preceded by a summary of the history of views regarding their classification, phylogeny, and geographic distribution. In the closing section of the article we discuss details of the formation of lizard diversity in Central Asia during the Jurassic and Early Cretaceous.

CURRENT ISSUES IN THE RESEARCH OF DORSETISAURIDAE AND XENOSAURIDAE

The family Dorsetisauridae was established by P. Hoffstetter (1967) for *Dorsetisaurus purbeckensis* that he described from cranial and mandibular fragments from the Purbeck Formation (Tithonian–Neocomian) of England. The species has osteodermal sculpture on skull roof bones in the form of mid-sized scutes, is characterized by pineal opening located within the parietal, and the small number of teeth with a high and lancet-shaped apical part (Figs. 2a–2c). Later, representatives of the family were found in the Late Jurassic of the United States (Prothero and Estes, 1980) and Portugal (Seiffert, 1973, Broschinski,

Alifanov, 1993	Alifanov, 2000	This paper	Zoogeographic classification
†Paramacellodidae	†Paramacellodidae	†Paramacellodidae	Jurassic endemics of Afrolaurasia
†Macrocephalosauridae s.l.	†Mongolochamopidae		
†Dorsetisauridae	†Dorsetisauridae	†Dorsetisauridae	
		†Ardeosauridae	
	†Globauridae	†Globauridae	
Gekkonidae s.l.	Gekkonidae s.l.	Gekkonidae s.l.	Aptian−Albian endemics of Central Asia
Xenosauridae	Xenosauridae	Xenosauridae	
Xantusiidae	†Eoxantidae	†Eoxantidae	
†Slavoiidae	†Slavoiidae		
†Hodzakuliidae	†Hodzakuliidae	†Hodzakuliidae	
†Necrosauridae			
†Priscagamidae	†Pleurodontagamidae	†Temujiniidae	

Fig. 1. Family composition (compiled from several sources) and faunistic structure of the lizard assemblage from the Khoobur locality (Mongolia, Övörkhangai aimag; early Cretaceous, Upper Aptian−Lower Albian, Hühteeg Horizon).

2000), as well as in the Early Cretaceous of Mongolia (Alifanov, 1993, 2000a, 2000b).

Originally, Dorsetisauridae were either placed in the Anguoidea (Hoffstetter, 1967), or between the modern Xenosauridae s.l. and the Anguidae (Estes, 1983). The type species was seen as a basal anguimorph (Evans et al., 2006) or as a basal platynotan (Conrad, 2008). However, its affiliation with the Anguimorpha has not been proven so far because of fragmentary material available, which makes any hypotheses regarding its relationships tentative. It is as a tentative suggestion that we previously thought possible a close phylogenetic link between dorsetisaurids and Xenosauridae s.l. (Alifanov, 2000a, 2012).

The discovery of *Kuwajimalla kagaensis* Evans et Manabe, 2008 from the Early Cretaceous of Japan (Ishikawa) sheds new light on Dorsetisauridae. This species, described from fragments of the skull and of the mandible with teeth having a lancet-shaped apex was placed, in the original description, within the cladistic taxon Borioteiioidea Nydam et al., 2007. This taxon aggregates what we previously had described (Alifanov, 2000a, 2012) as the Late Cretaceous microorders Polyglyphanodontia (Agamognatha) and Macrocephalosauria (Chameleomorpha). It is worth pointing out that none of their representatives have been found in Central Asia. Besides that, *K. kagaensis* does not have subpleurodont mandibular teeth which are typical for Polyglyphanodontia and Macrocephalosauria. All of this makes this original reconstruction of phylogenetic affinity doubtful. It is also difficult to agree with the interpretation, given in the original description, of serrate-dentate edges of tooth apices as multiple cusps. On the other hand, lancet-shaped teeth, eupleurodonty (transitional condition between subpleurodonty and hyperpleurodonty) and the presence of sockets for tooth bases (Figs. 2d, 2e) admit an interpretation of affinity of *K. kagaensis* with Dorsetisauridae.

In discussing Dorsetisauridae, it is interesting to look at the data on *Chometokadmon fitzingeri* Costa, 1864 (Fig. 2f). The structure of the frontal and the parietal in *Ch. fitzingeri* is identical to *Dorsetisaurus purbeckensis* Hoffstetter, 1967. In addition, *C. fitzingeri* has free osteoderms in the head region, similar to Xenosauridae s.l. (Bever et al., 2005). However, S. Evans et al. (2006) noted the generalization of *Ch. fitzingeri*, relating it, besides *D. purbeckensis*, to *Parviraptor* Evans, 1994 from the Late Jurassic and Neocomian of the United States and Great Britain. It is remarkable that this latter taxon, known from isolated skeletal fragments, has been interpreted quite differently, e.g., as related to snakes (Caldwell et al., 2015). We consider *Parviraptor* as representative of the Mosasauria, which are characterized by sharp teeth as well as by a zygosphenic-zyganthral vertebral articulation.

Judging from the details of skull structure, the mandible, and the tooth system, the embryos from the Early Cretaceous of Thailand found in hard shell (unusual for lizards) can also be attributed to the Dorsetisauridae, rather than the Platynota (varanoid lizards are not known in the Early Cretaceous), as was suggested in the original description (Fernandez et al.,
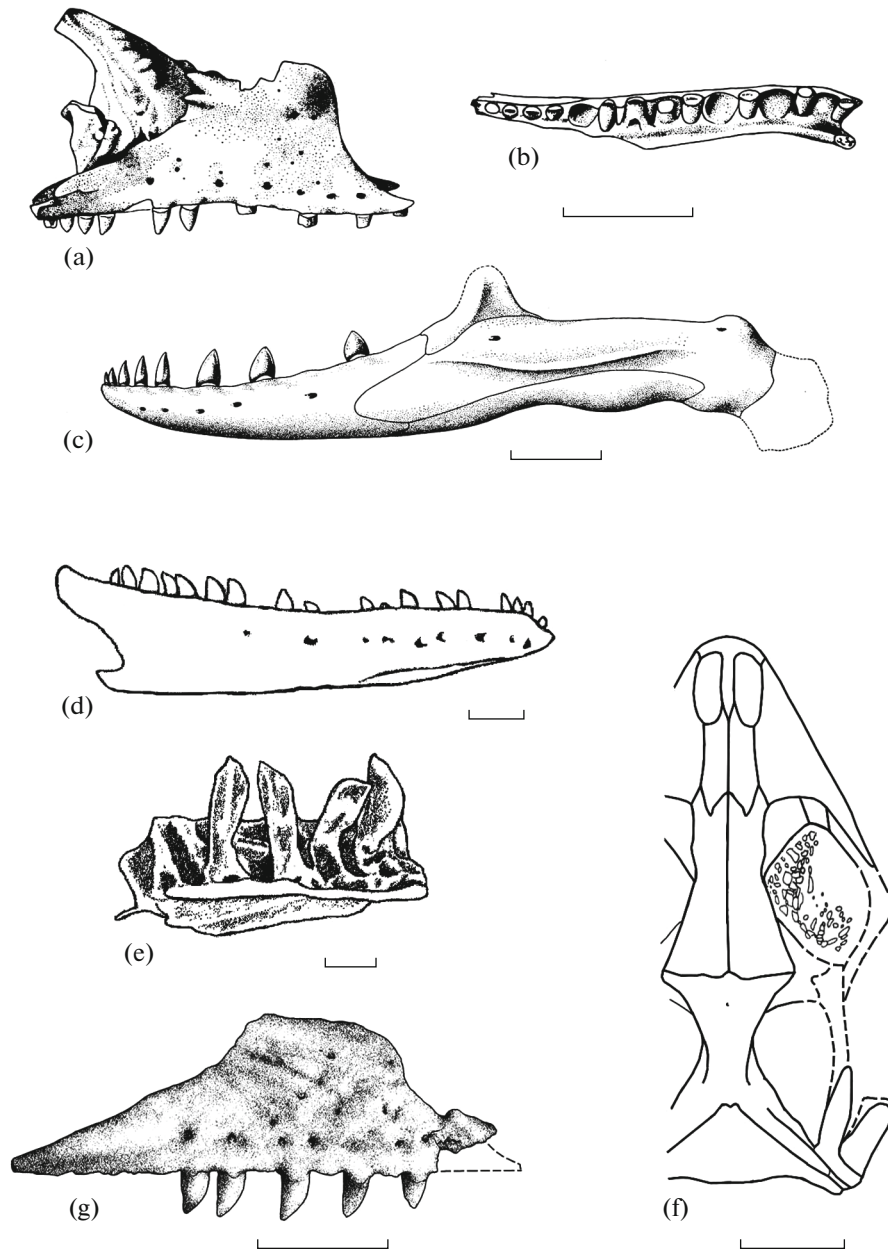
Fig. 2. Lizards of the family Dorsetisauridae (Anguimorpha): (a–c) *Dorsetisaurus purbeckensis* Hoffstetter, 1967 (Hoffstetter, 1967, text-figs. 10A, 11C): (a, b) right maxilla articulated with the prefrontal and lacrymal in labial (a) and ventral view (b); BMNH R8248, (c) reconstructed left ramus of the dentary in labial view; UK, Tithonian–lower Neocomian; (d, e) *Kuwajimalla kagaensis* Evans et Manabe, 2008 (from Evans and Manabe, 2008, text-figs. 4B, 5A), right dentary (d) in labial view (SBEI 1538) and dentary teeth (e) in lingual view (SBEI 557); Japan, Barremian–Aptian; (f) *Chometokadmon fitzingeri* Costa, 1864; holotype MPN 539 (from Evans et al., 2006, text-fig. 2B), reconstructed skull in dorsal view; Italy, early Cretaceous; (g) *Paradorsetisaurus postumus* gen. et sp. nov.; holotype PIN 3334/517, right maxilla in labial view; Mongolia, Övörkhangai aimag, Khoobur locality; early Cretaceous, Upper Aptian–Lower Albian, Hühteeg Horizon. Scale 5 mm for (a–c), (f), and (g); 1 mm for (d) and (e).

2015). Our attribution takes into account the skull reconstruction in the cited paper, which shows the maxillary participating in the suborbital fenestra border (not found in varanoids), the structure of frontals (wide, paired and sculptured), the presence of a rostral process of the coronoid, a deep notch of the posterior margin of the generally short dentaries and flattened apices of the tooth crown.

On the other hand, the attribution of *Changetisaurus estesi* Nessov, 1992 from the Middle Jurassic of Kyrgyzstan to dorsetisaurids is questionable because of a well-developed angular process and rectangular osteoderms. This condition is typical both for the fossil Paramacellodidae (Cordyloidea, Scincomorpha), e.g., *Sharovisaurus karatauensis* Hecht et Hecht, 1984 from the Middle Jurassic of Kazakhstan, and for *Par-*
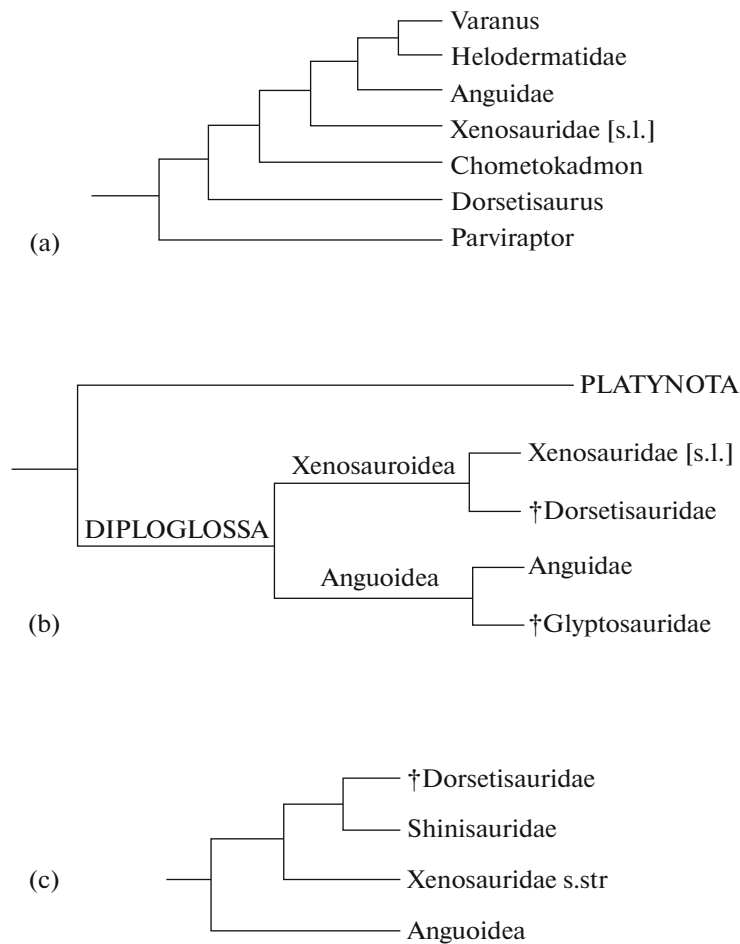
Fig. 3. Proposed phylogenetic relationships of the families Dorsetisauridae and Xenosauridae (Anguimorpha) according to different authors: (a) S. Evans et al., 2006, (b) V.R. Alifanov, 2012, (c) this study.

meosaurus scutatus Gao et Hou, 2000 from the late Cretaceous of Mongolia.

Unlike the dorsetisaurids, Xenosauridae s.l., represented by the modern genera *Xenosaurus* (Mexico) and *Shinisaurus* (China), undoubtedly belong to the Anguimorpha. They were historically seen as related to the Anguidae within the microorder Diploglossa, the sister taxon to the Platynota (Camp, 1923; McDowell and Bogert, 1954). Cladistic analysis places xenosaurids among the basal Anguimorpha (Gauthier et al., 2012) or Platynota (Conrad, 2008). The platynotan hypothesis concerns *Shinisaurus* and related fossil forms. We consider it to be in contradiction with the key morphological features of the taxa being compared.

It should be pointed out that *Shinisaurus*, similarly to all the other Diploglossa (except Anniella: Alifanov, 2000a, 2012) is characterized by the diploglossopalatine condition (the absence of a connection between the lateral processes of ectopterygoid and palatine bones which doesn't form the margin of the suborbital fenestra). This type can be contrasted with another type of the platynotopalatine condition, where maxillaries are isolated from the suborbital fenestrae by a contact of the lateral process of palatine and the ectopterygoid. Our data shows that the two conditions can not be reduced to one, as they form the different conditions of two different branches of semogenetic tree and one cannot be derived from the other directly, without intermediate stages (Alifanov, 2012, 2016).

Considering the issues and data just discussed, we should draw attention to tooth structure in *Shinisaurus* and *Xenosaurus*. In the former, the central cusp has indistinct symmetric shoulders (Conrad, 2004, text-figs. 17A, 17C), whereas in the latter the cusp has a rostral arms that makes the tooth look asymmetrical. If Xenosauridae s.l. are related to the Dorsetisauridae, then we have to deal with something that has not been addressed in previous work, including our own (Figs. 3a, 3b). Namely, the two modern forms must then stand in different relationship to the fossil family. In particular, *Xenosaurus* appears morphologically isolated within the group of a comparison. Based on this fact, it is possible to talk about two modern xeno-
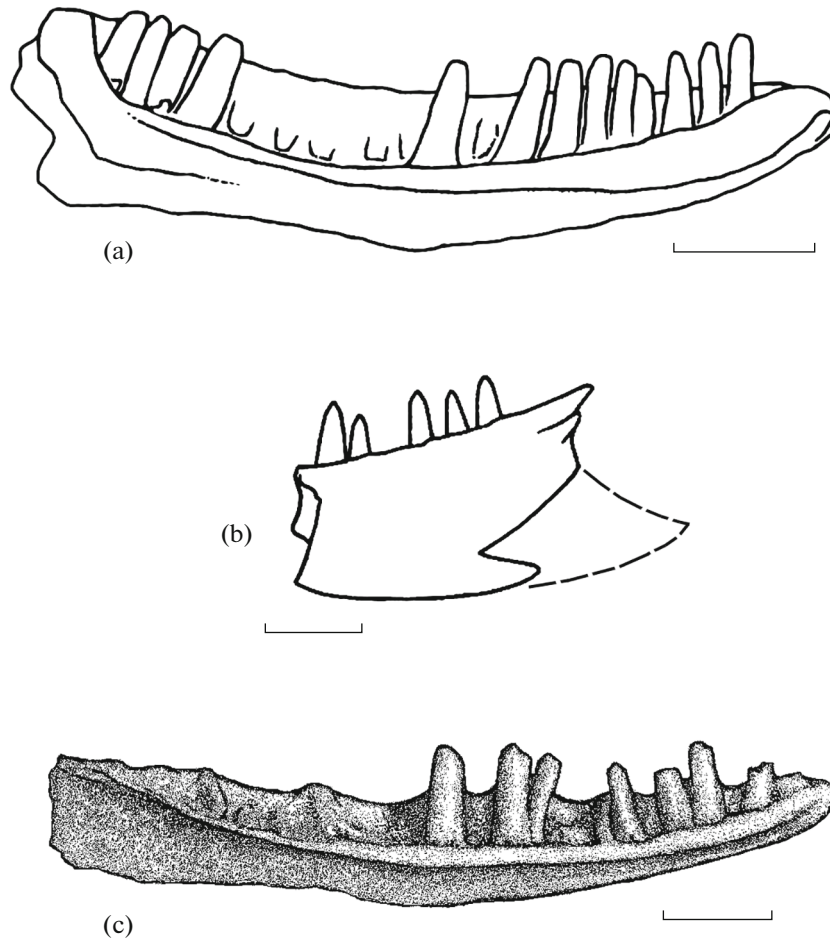
Fig. 4. Lizards of the family Xenosauridae (Anguimorpha): (a) *Oxia karakalpakensis* Nessov, 1985; holotype CMGE 28/12000 (from Gao and Nessov, 1998, fig. 3, in partim), left dentary in lingual view; Uzbekistan, Upper Aptian; (b) "Xenosauridae" gen. indet. (?Ardeosauridae fam. indet.); PIN 3334/515 (Alifanov, 2000, text-fig. 28d), posterior region of the left dentary in labial view; (c) *Xenostius futilus* gen. et sp. nov. (Xenosauridae, Anguimorpha), holotype PIN 3334/522, left dentary in lingual view; Mongolia, Övörkhangai aimag, Khoobur locality; early Cretaceous, Upper Aptian−Lower Albian, Hühteeg Horizon. Scale 3 mm for (a), 1 mm for (b) and (c).

saurid forms in different families (Fig. 3c), a suggestion previously made more than once (Bever et al., 2005; Conrad, 2008).

A group sometimes synonymized with Xenosauridae s.l. are the late Cretaceous Carusiidae Borsuk-Białynicka, 1987 or its type genus (Gao and Norell, 1998, 2000; Conrad, 2008). Such attribution is contradicted, however, by the structure of the dentaries. Carusiids have scincomorph dentaries with the surangular process either incipient or absent, the angular process wide at the base and often lengthened, the coronoid process overlapping the lateral surface of the labial and/or the dorsal process of the coronoid. Scincomorph morphology of the dentaries was discussed in the first description of the group (Borsuk-Białynicka, 1985, 1987). Recent research places it either basally within the Scincoidea (Gauthier et al., 2012) or as one of the families of the superfamily Ardeosauroidea (Alifanov, 2012, 2016). The members of the

type family of this last taxon are usually seen, in cladistic analyses, as related to the Gekkota (e.g., Conrad, 2008; Gauthier et al., 2012).

In North America, Xenosauridae s.str. are represented by the fossil genera *Exostinus* Cope, 1873 (late Cretaceous−early Oligocene, includes two species, possibly not monophyletic, see Bhullar, 2011) and *Restes* Gauthier, 1982 (late Paleocene). The oldest fossils here are Cenomanian in age (Nydam, 2013). In Asia, the family is represented by *Oxia karakalpakensis* Nessov, 1985 (Fig. 4a) from the late Albian of Uzbekistan (Gao and Nessov, 1998). The species is described from a dentary carrying blunted teeth and having a posterior region typical for the anguimorphs: the coronoid process is well-developed; the surangular process and the angular process do not reach occipitally beyond the center of the coronoid.

The discovery of *Oxia karakalpakensis* Nessov, 1985 is evidence of an early origin (earlier than late
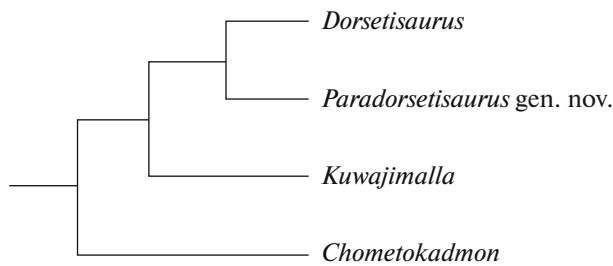
Fig. 5. Proposed phylogenetic relationships of the family Dorsetisauridae

Cretaceous) of xenosaurids. The hypothesis of Central Asian origin must be supported with older fossils. We previously considered PIN 3334/515 from Khoobur (Fig. 4b) as a possible candidate (Alifanov, 2000a). However, a reexamination of the specimen, which is a fragment of the dentary with teeth, showed that the posterior region, which, as noted previously, is diagnostic, is missing but resembles the dentary structure in the Anguimorpha. It likely belongs to a scincomorph. However, xenosaurids are found in the Khoobur assemblage, as shown by specimens in this article.

The origin of the Shinisauridae the distribution of which are now confined to a small area in Southern China and Northern Vietnam, is enigmatic. Its wider distribution in the past is attested by fossil finds in the Eocene of North America (Conrad, 2006) and the Miocene of Europe (Klembara, 2008). Apparently, the group originated in one of the three areas. We believe that its most likely origin is Cretaceous Europe, from which it subsequently migrated into Southwestern Asia in post-Mesozoic times either through North America and Central Asia or through Asia Minor and the Indian subcontinent. The latter may have been originally zoogeographically related with Europe rather than with the southern continents: Kalandadze and Rautian (1992; 1997).

SYSTEMATIC PALEONTOLOGY

Order LACERTILIA

Infraorder ANGUIMORPHA

Microorder DIPLOGLOSSA

Superfamily Xenosauroidea Cope, 1868

D i a g n o s i s. Diploglossian lizards characterized by the presence of free scutelike osteoderms in the head region and their absence in the trunk region.

C o m p o s i t i o n. Xenosauridae Cope, 1868; early Cretaceous of Uzbekistan and Mongolia, late Cretaceous to Modern, North America; Dorsetisauridae Hoffstetter, 1967; late Jurassic of North America, Tithonian to early Neocomian of Europe, early Cretaceous of Central Asia; Shinisauridae Ahl, 1930;

Eocene of North America, early Miocene of Europe, Modern S. China and N. Vietnam.

R e m a r k s. As noted above, anguimorphs of the microorder Diploglossa, here taken to circumscribe the superfamilies Xenosauroidea and Anguoidea, are characterized by a diploglossopalatine type of the palate fenestration. Superfamilies are distinguished according to the degree to which osteoderms are developed. In Xenosauridae these are concentrated in the head region, whereas in Anguoidea they extend over the whole body forming armour. The circumscription as well as the phylogenetic affinities of the superfamily Anguoidea is in need of a revision, just as the Xenosauridae s. str. The revision should include the fossil Glyptosauridae, as well as the living Anguidae (this latter group may have to be split into two to three families). Based on palatal morphology, the family Anniellidae forms part of the Platynota, not of the Diploglossa, as is usually assumed. Within the platynotan, the Anniellidae share some cranial characters with the Lanthanotidae to which it is likely related (Alifanov, 2012).

Family Dorsetisauridae Hoffstetter, 1967

T y p e   g e n u s. *Dorsetisaurus* Hoffstetter, 1967; late Jurassic of North America, late Jurassic to early Cretaceous of Europe.

D i a g n o s i s. Nares openings elongate. Frontals paired. Lateral processes of the postfrontals are bifurcated for articulation with the medial process of the postorbitals. Osteodermal sculpture of skull roof bones is of the medium-sized scutes type. Tooth attachment eupleurodont or subpleurodont. Tooth crown lancet-shaped.

C o m p o s i t i o n. In addition to the type genus, genera: *Chometokadmon* Costa, 1864; early Cretaceous of Italy; *Kuwajimalla* Evans et Manabe, 2008; early Cretaceous of Japan; *Paradorsetisaurus* gen. nov.; early Cretaceous of Mongolia.

R e m a r k s. Family diagnosis takes into account the new composition. The phylogenetic affinities of dorsetisaurid genera are shown in Fig. 5. The diagram shows the undoubted close affinity between *Dorsetisaurus* Hoffstetter, 1967 and *Paradorsetisaurus* gen. nov., based on considerable similarities in tooth structure; as well as the basal position of *Chometokadmon* Costa, 1864 based on weak expansion of the crown apex and a larger tooth count.

Genus *Paradorsetisaurus* Alifanov, gen. nov.

E t y m o l o g y. From the Greek *para* (near) and *Dorsetisaurus*.

T y p e   s p e c i e s. *Paradorsetisaurus postumus* sp. nov.

D i a g n o s i s. Premaxillary and jugal processes of the maxillary relatively long, the jugal process with a sharp tip. The medial branch of the premaxillary pro-

cess carries a tubercle. The largest teeth are located in the middle of the toothrow. Their tips are flattened, somewhat curved inwards, turned at a small angle to the axis of the jaw and protrude by half their height beyond the maxilla. Tooth tip edge long and smooth. Upper tooth number—15.

S p e c i e s   c o m p o s i t i o n. Type species.

C o m p a r i s o n. The new species is distinguished from other genera of the same family by the development of a dorsal tubercle on the medial branch of the premaxillary process and by a smaller tooth count. Compared with the type genus it is unique in a relatively long premaxillary and jugal processes of the maxillaries and in the arrangement of tooth crowns at an angle to the jaw axis. Further, the new genus is distinguished from *Kuwajimalla* Evans et Manabe, 2008 in having smooth cutting edges and from *Chometokadmon* Costa, 1864, in having taller teeth and expanded tooth tips.

Paradorsetisaurus postumus Alifanov, sp. nov.

Plate 14, figs. 1—4

Dorsetisaurus [sp.]: Alifanov, 1993, p. 9; 2000b, p. 382.

E t y m o l o g y. From the Latin *postumus* (born last).

H o l o t y p e. PIN 3334/5l7, right maxilla; Mongolia, Övörkhangai aimag, Khoobur Locality; early Cretaceous, Upper Aptian to Lower Albian, Hühteeg Horizon.

D e s c r i p t i o n (Fig. 2g). The dorsal process of the maxillary passes gradually into the occipital process. The occipital process makes up half of the bone's length. Premaxillary process wide at the base, its length more than a quarter of the total length of the maxilla. According to our reconstruction of the broken-off lateral part of the rostral process, the nares were enlarged. The base of the dorsal process makes up a third of the total length. The outer surface of the maxilla carries labially numerous foramina, no less than seven in the lower row. The supradental shelf wide, especially in the third quarter of the bone, at the level of teeth 8—11. The alveolar foramen is located on the dorsal surface of the supradental shelf below tooth 10. The tooth edge of the maxilla festoon-like. Teeth are set in shallow sockets, tooth implantation subpleurodont. At the base of the teeth a small resorption foramen is usually formed. There is also some cement deposition. Teeth project by half their height beyond the dental parapet.

H o l o t y p e   s i z e   i n   m m. Length of the maxilla (reconstructed) 14.5 (15.5), height 4.3, height of the highest maxillary tooth 2.5.

R e m a r k s. An interesting specimen, PIN 3334/519 (Pl. 14, fig. 5), is found in the collection of fossils from the Khoobur locality. It is an unpaired frontal belonging to a relatively large form. The bone is wide, with a sculptured dorsal surface and a series of foramina for the passage of nutrient vessels, arranged in two rows on either side of an imaginary middle line. Subolfactory processes are low and wide in the occipital part, thin and high in the rostral part of the bone. The facets for the attachment of the prefrontals are deep. Their posterior margin is located on the level of the middle of the orbit. Generally, the form represented by the specimen PIN 3334/519 is similar in appearance to *Dorsetisaurus* but is distinct in being unpaired and lacking transverse sulci on the dorsal surface. Quite possible this specimen belongs to the described species, though until further and more complete material becomes available, it cannot be identified more precisely than just Lacertilia fam. indet.

M a t e r i a l. Holotype.

Family Xenosauridae Cope, 1868

T y p e   g e n u s. *Xenosaurus* Cope, 1886, modern Mexico.

D i a g n o s i s. The bones of the skull roof are usually covered in granular or small-scute ornamentation. Frontals always unpaired and narrow. Squamosals flattened occipitally. Teeth blunt, with a rostral shoulder.

C o m p o s i t i o n. In addition to the type genus, genera *Exostinus* Cope, 1873, late Cretaceous to early Oligocene of North America; *Restes* Gauthier, 1982, late Paleocene of North America; *Oxia* Nessov, 1985, early Cretaceous of Uzbekistan; *Xenostius* gen. nov., early Cretaceous of Central Mongolia.

### Genus *Xenostius* Alifanov, gen. nov.

E t y m o l o g y. Anagram of *Exostinus*.

T y p e   s p e c i e s. *Xenostius futilus* sp. nov.

D i a g n o s i s. Dentaries long, slim, straightened and weakly expanded occipitally. Posterior margin does not develop a deep notch. The flank of the subdental ridge narrow along its whole length. Teeth relatively large, straight and with an slightly expanded base. The part of the teeth projecting beyond the dorsal edge of the dentary makes up a third to a half of its total length. The largest teeth form in the middle of the tooth row. There is a small rostral shoulder on the tooth tips. Total tooth count 20.

S p e c i e s   c o m p o s i t i o n. Type species.

C o m p a r i s o n. The new genus is unique within the family, judging by the small size and the gracility of the dentary. It is additionally distinguished from *Oxia* Nessov, 1985 in the weakly expanded flank of the subdental ridge, the presence of a distinct rostral shoulder near the tooth tip, as well as by a large part of the teeth extending beyond the dental parapet.

Plate 14

3

1

Tpmx

3 mm

Tpmx

2

4

5

1 mm

6

3 mm
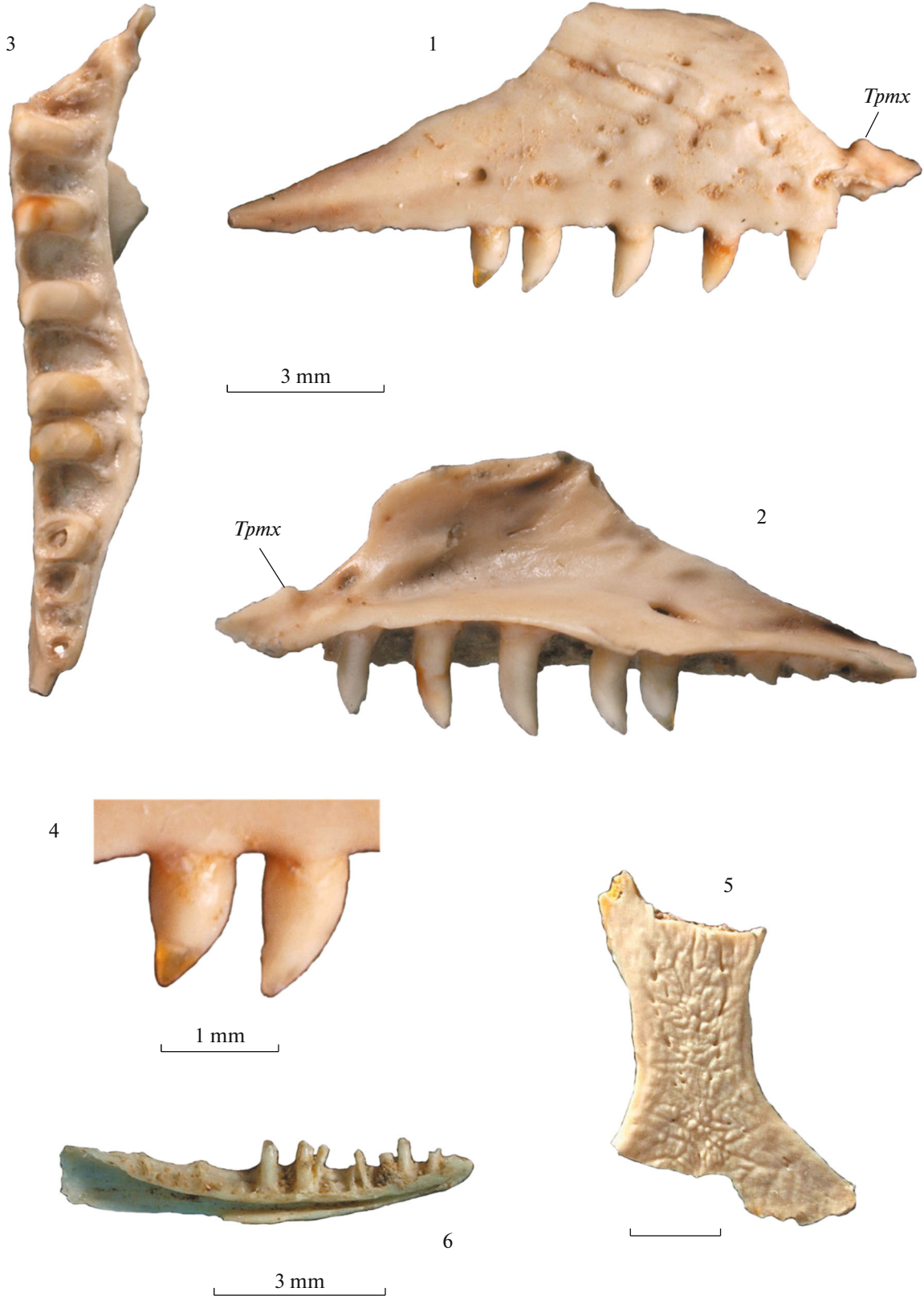
Xenostius futilus Alifanov, sp. nov.

Plate 14, fig. 6

E t y m o l o g y. From the Latin *futilus* (fragile).

H o l o t y p e. PIN 3334/522, left dentary, Mongolia, Övörkhangai aimag, Khoobur locality; early Cretaceous, Upper Aptian−Lower Albian, Hühteeg Horizon.

D e s c r i p t i o n (Fig. 4c). Dentary shallow and almost straight, its labial side notably rounded. The rostral part of the Meckelian canal is oriented ventromedially, which is usually typical for anguimorphs. The expanded base of the larger teeth does not have a transitional zone towards the tip. All of the teeth are generally oriented vertically, sometimes slightly deviating forward or back. In the Khoobur specimen, we have not been able to find the facet separating the central cusp of the tooth from its rostral shoulder.

H o l o t y p e   s i z e   i n   m m. Length of the dentary: 7.4, height of its posterior margin: 1.2 (reconstructed height 1.5), height of the highest dentary tooth: 1.1.

M a t e r i a l. In addition to the holotype, PIN 3334/521; left dentary with teeth, type locality.

THE DIVERSITY OF THE LIZARDS OF CENTRAL ASIA IN THE JURASSIC AND THE EARLY CRETACEOUS

The lizard families of the Khoobur assemblage can be split into two groups (Fig. 1). Part of the first group was widely distributed not only in the early Cretaceous of Central Asia, but also beyond it in the Jurassic of Europe, North America (Paramacellodidae and Dorsetisauridae) and Africa (Paramacellodidae). The other group is found in the Jurassic (Ardeosauridae) and early Cretaceous of Europe (Globauridae). All representatives of this group likely were distributed within the Jurassic Laurasia or Afrolaurasia, e.g., Laurasia connected with Africa.

The second group within the assemblage is endemic to early Cretaceous Central Asia. The all families composing this group (Eoxantidae, Gekkonidae s.l., Hodzhakuliidae, Temujiniidae, and Xenosauridae) first appeared in early Cretaceous of Central Asia and their appearance is tied with the territorial isolation of this paleocontinent which lasted during the final Jurassic and most of the early Cretaceous. The isolation of Central Asia, as part of the breakup of Afrolaurasia, was suggested by N.N. Kalandadze and A.S. Rautian (1992, 1997).

Outside of Mongolia, the Khoobur assemblage can certainly be compared in age with two lizards of the family Hodzhakuliidae: *Pachygenys thlastesa* Gao et Cheng, 1999 from the Doushan Formation (found to be Aptian-Albian in age by S. Lucas (2006)) in China (Shandong); and another species of the same genus, *P. adashii* Ikeda et al., 2015 from the lower part of the Sasayama Formation (Aptian−Albian boundary) in Japan (Hyogo).

The makeup of the only post-Khoobur (late Albian) assemblage from the lower part of the Hodzhakul Formation in Uzbekistan is remarkable, with four groups identified so far (Gao and Nessov, 1998). Our identifications suggest that, in addition to the already mentioned Xenosauridae, the Hodzhakul assemblage also includes members of the families Hodzhakuliidae, Ardeosauridae gen. indet. and Temujiniidae gen. indet. This family composition, even taking into account incomplete material, indicates lower lizard diversity in post-Khoobur times. Based on the material from the late Cretaceous of Mongolia, the only families to go extinct among those found in Khoobur are Hodzhakuliidae and Dorsetisauridae. The family Xenosauridae s. str. also disappears from Central Asia but appears in the late Cretaceous of another continent, North America.

The diversity of lizards at the Aptian−Albian boundary stands in contrast with the low diversity of lizards in earlier times. For instance, only one family is found in the Jurassic deposits of Central Asia, the Paramacellodidae (*Changetisaurus estesi* Nessov, 1992, middle Jurassic of Kazakhstan; *Sharovisaurus karatauensis* Hecht et Hecht, 1984, late Jurassic of Kazakhstan; *Mimobecklesisaurus gansuensis* Li, 1991, late Jurassic of China). The only Neocomian lizard fossil found in Central Asia comes from the Hodzhiabat Formation of Kyrghyzstan (Lacertilia gen. indet.: Averianov and Fedorov, 2004; Ardeosauridae: Alifanov, 2012).

Among the pre-Khoobur lizards fossils of Mongolia we should note *Norellius nyctisaurops* Conrad et Daza, 2015 (Ardeosauridae, our identification) from the Undurukhinsk Formation (Oosh Formation), exposed in Central Mongolia, and Bavarisauridae gen. indet. (Alifanov, 2000a, 2012) from the Tsagantsab Formation in Western Mongolia. Both stratigraphic units occur within the Tsagantsab Group, for which absolute dates are known. These fall within the range of 141−119 Ma (Shuvalov, 2000), which is closer to the Hauterivian−Barremian, rather than the entire Neo-
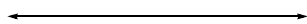
Explanation of Plate 14

Figs. 1−4. *Paradorsetisaurus postumus* gen. et sp. nov. (Dorsetisauridae), holotype PIN 3334/517, right maxilla: (1) labial view, (2) lingual view, (3) ventral view; (4) teeth in labial view, enlarged. Abbreviation: (*Tpmx*) dorsorostral tubercle.

Fig. 5. Lacertilia (?Dorsetisauridae) fam. indet., PIN 3334/519, fragment of a frontal in dorsal view.

Fig. 6. *Xenostius futilus* gen. et sp. nov. (Xenosauridae s.str.), holotype PIN 3334/522, left dentary in lingual view.

Mongolia, Övörkhangai aimag, Khoobur locality; Lower Cretaceous, Upper Aptian−Lower Albian, Hühteeg Horizon.

comian (Shuvalov, 2000) or the Barremian–Aptian (Lucas, 2006).

Outside of Mongolia, lizards of Barremian–Aptian age are known from the Tetori Group in Japan: *Kaganaias hakusanensis* Evans et al., 2006 (Dolichosauridae), *Kuwajimalla kagaensis* Evans et Manabe, 2008 (Dorsetisauridae; our identification) from the Kuwajima Formation (Ishikawa Prefecture) and *Sakurasaurus shokawensis* Evans et Manabe, 1999 (Ardeosauridae; our identification) from the Okurodani Formation (Gifu Prefecture). Fossil finds of similar age have been reported from the Ilek Formation in the Kemerovo District, Russia (Paramacellodidae indet., Xenosauridae indet.: Averianov, Fayngerts, 2001) and the Murtoy Formation in Transbaikalia, Russia (Paramacellodidae indet.: Averianov and Skutchas, 1999). There are numerous lizard fossils in the deposits of the Jehol Group (Barremian–Aptian) of Northeastern China (*Jehololacerta formosa* Ji et Ren, 1999; *Dalinghosaurus longidigitus* Ji, 1998; *Liaoningolacerta brevirostra* Ji, 2005; *Liushusaurus acanthocaudata* Evans et Wang, 2010; *Yabeinosaurus tenuis* Endo et Shikama, 1942). All of these, most likely, belong to scincomorphs of the family Ardeosauridae which, in our view, was the dominant group in Central Asia throughout the whole early Cretaceous.

Compared to this low diversity of early Cretaceous lizards in Central Asia, all the more notable is the Aptian-Albian diversity maximum established using the material from the Khoobur locality. Increased fossil diversity is not only reflective of taphonomic conditions favorable for the accumulation of fossil remains but also of environmental conditions (climate warming, increased insect diversity and biomass). This was the first of the two Cretaceous diversity peaks in Central Asia since their appearance in the fossil record. The second, much higher peak is registered in the Campanian (Alifanov, 2000a).

It should be emphasized that the Jurassic to early Cretaceous time interval forms a distinct historical stage in lizard faunas. Its notable feature is the predominance of the scincogekkonomorphs, especially the Scincomorpha (Paramacellodidae in the Jurassic, Ardeosauridae in the early Cretaceous in general, Hodzhakuliidae in the Upper Aptian and Albian). This composition of dominant taxa is in stark contrast with other such stages: the late Cretaceous with the predominance of members of the infraorder Chamaeleomorpha (Macrocephalosauria, and Priscagamia) and the Paleogene, when the microorder Pachyglossa (Changjiangosauridae, Uromastycidae, and Agamidae) reached its maximum diversity.

In summary, several phases can be reconstructed within the Jurassic to early Cretaceous stage in the development of lizard faunas of Central Asia. These are the second half of the Jurassic (the dominance of Paramacellodidae), Neocomian to early Aptian (the dominance of Ardeosauridae and the maintenance of archaic diversity), late Aptian to early Albian (maximum diversity achived with the appearance of endemic groups), and late Albian (reducing compared to the previous phase).

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