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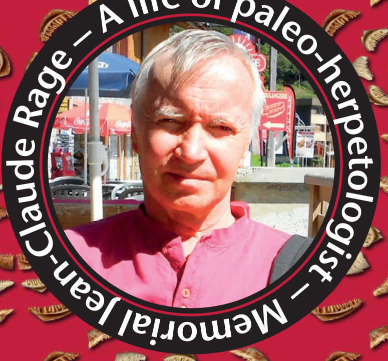
Andrej ČERŇANSKÝ & Marc Louis AUGÉ



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The Oligocene and Miocene fossil lizards (Reptilia, Squamata) of Central Mongolia

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ABSTRACT

Lizard material from the early Oligocene and early and late Miocene of the Valley of Lakes, Central Mongolia is described. Besides the Oligocene fossorial squamate published elsewere, the material can be allocated to several major clades: Agamidae, Lacertidae and Anguidae (Glyptosaurinae). The presence of *Pseudotinosaurus* Alifanov, 1991 in early and late Rupelian localities shows that this taxon has a continuous history in this area from the Eocene to the Oligocene. The same is true for the clade Glyptosaurinae, represented by isolated osteoderms in the early Oligocene locality Hsanda Gol. This might suggest that the Eocene-Oligocene transition did not have such a strong or rapid impact in East Asia, in contrast to the Grande Coupure in Europe, at least among some lizard clades. The early Oligocene (early Rupelian) lacertids from Taatsiin Gol, Hsanda Gol and Tatal Gol represent one of the oldest evidences of Asiatic dispersal of this clade. It might reflect the dispersal pathways after closure of the Turgai Strait between Europe and Asia. Some of the material closely resembles the common European Oligocene taxon *Lacerta* s.l. *filholi* Augé, 1988. In the early Miocene locality Olon Ovoony Khurem, two clades can be recognized – Lacertidae and a scincoid with a specialized dentition (family indeterminate). The clade Lacertidae forms a dominant component of the late Miocene lizard fossils in Mongolia. The material from the locality Builstyn Khudag shows differences compared to the early Miocene lacertids and represents the oldest evidence of the tribe Eremiadini in this area.

KEY WORDS
Asia,
Paleogene,
Neogene,
Squamata,
lizards.

RÉSUMÉ

Les lézards fossiles de l'Oligocène et du Miocène de Mongolie Centrale.

Des faunes de lézards du début de l'Oligocène, du début et de la fin du Miocène de Mongolie sont décrites. Elles comptent des membres de plusieurs groupes, Agamidae, Lacertidae and Anguidae (Glyptosaurinae). La présence de l'agamidé *Pseudotinosaurus* Alifanov, 1991 dans des gisements du Rupélien ancien et récent montre que ce genre était présent en Mongolie depuis l'Éocène jusqu'à l'Oligocène, ce qui vaut aussi pour les Glyptosaurinae, dont on a trouvé les ostéodermes dans le gisement de l'Oligocène inférieur de Hsanda Gol. Ceci suggère que la transition Éocène/Oligocène a eu un effet moins marqué sur les faunes de lézards de Mongolie que sur les faunes européennes. Les Lacertidae trouvés dans les gisements de Taatsiin Gol, Hsanda Gol et Tatal Gol représentent les premiers membres de la famille connus en Asie, peut-être issus d'une dispersion permise par la fermeture du détroit de Turgai qui a séparé l'Europe de l'Asie durant la première partie du Paléogène. Plusieurs fossiles apparaissent très proches de l'espèce *Lacerta* s.l. *filholi* Augé, 1988, le lacertidé le plus commun en Europe durant l'Oligocène. Si cette interprétation est correcte, elle indique une large répartition de ce lézard, de l'Asie à l'Europe durant l'Oligocène. Dans la localité de Olon Ovoony Khurem (Miocène ancien) deux taxons sont reconnus, un membre des Lacertidae et un scincoïde montrant une dentition très spécialisée. Les Lacertidae dominent largement l'assemblage de lézards du Miocène récent de Mongolie. Le matériel du gisement de Builstyn Khudag diffère des Lacertidae du Miocène inférieur, avec la première apparition des Erimiadinae en Mongolie.

MOTS CLÉS
Asie,
Paléogène,
Néogène,
Squamata,
lézards.

INTRODUCTION

The lizard material described herein comes from the Oligocene and Miocene localities of the Valley of Lakes in Central Mongolia (Fig. 1). It forms a part of the herpetofauna that was previously briefly discussed by Böhme (2007). Mongolian fossil lizards are well documented from the Mesozoic (e.g., Alifanov 1989, 2016; Borsuk-Białynicka 1984, 1985, 1990, 1991; Norell *et al.* 1992; Gao & Lianhai 1995; Norell *et al.* 2008; Conrad & Norell 2006; Daza *et al.* 2014; Tałanda 2016, 2017), but have only rarely been reported from Palaeocene and Eocene localities (e.g., Gilmore 1943; Alifanov 1993, 2009, 2012; Wu *et al.* 1996; Gao & Dashzeveg 1999; Van Itterbeeck *et al.* 2007; Dong *et al.* 2016). Except for a possible arretosaurid described by Alifanov (2012) and a potential dibamid described by Čerňanský (2019), the evolution of lizards remains largely unknown during the Oligocene and Miocene in Mongolia (it should be noted that *Crythiosaurus mongoliensis* Gilmore, 1943, described by Gilmore [1943] from the lower Oligocene of the Hsanda Gol locality as an amphisbaenian, is interpreted by several authors as a snake [see Hoffstetter 1962; Estes 1983; Kearney 2003]).

The Oligocene represents a particularly important time period because of global climatic changes that characterize the Paleogene. The most major warming can be observed in the Palaeocene/Eocene boundary, whereas a distinct mean annual temperature and precipitation drop started during the late Eocene and early Oligocene (see e.g., Cavelier *et al.* 1981; Burchardt 1978; Rea *et al.* 1990; Prothero & Berggren 1992; Janis 1993; Rage 2013). The most significant cooling was at 33.5 Ma, slightly after the Eocene/Oligocene boundary. This event is also characterized by changes in vegetation from Eocene dense forests to Oligocene more open country (Prothero & Heaton 1996). Nowadays, Mongolia is the largest inland arid region in the mid-latitudes on Earth (this is very likely influenced by the collision between India and Asia that could have occurred at 35 Ma, creating the rain shadow of the Himalaya, see Ali & Aitchison 2008; Najman *et al.* 2010). Aridity here most likely began by the late Oligocene to the early Miocene (Dong *et al.* 2013). Eolian deposits within Asian arid regions (see Sun *et al.* 2010) show that an arid pattern similar to that of today may have formed before the late Oligocene.

Asiatic paleofaunas are crucial for our understanding of dispersals of squamate clades between Europe and Asia (and their distribution there) and further to North America. Beringia formed a land bridge between North America and Asia for a long period during the Cenozoic, although affected by climatic conditions that limited migration of land animals at certain times (see McKenna 1983; Janis 1993; Beard 2008) or favored such dispersal during other periods, like the Paleocene/Eocene boundary. With respect to Europe, the Turgai Strait became dry land during the early Oligocene (Rögl 1999; Hou *et al.* 2011), and this formed a terrestrial connection with Asia. This opened a dispersal corridor for land-dwelling animals between these two continents (Haq *et al.* 1987) and allowed to migrate many taxa, among them Lacertidae and Anguinae, presumably from Europe to Asia (see e.g., Alifanov 1993; Vasilyan *et al.* 2017; Čerňanský *et al.* 2017a). According to several authors (Akhmetiev & Beniamovski 2009; Akhmetiev *et al.* 2012), the Turgai Strait was terrestrially passable prior to the Oligocene. Godinot & de Broin (2003) even suggested that the Turgai Strait did not act as a barrier as previously thought and that the Turgai region allowed the dispersal of land vertebrates, affected by sea level conditions and environmental changes. In any case, the material of Lacertidae from the early Oligocene described here represents one of the oldest known occurences of this clade in Asia.

The lizard materials studied here come from several Mongolian localities of different age (see Table 1) located in the Valley of

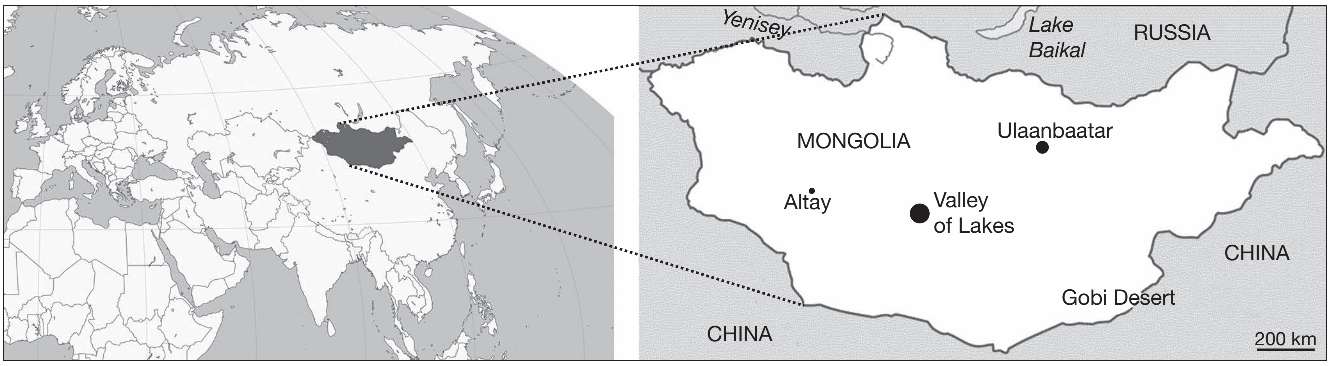

FIG. 1. — Location of the Valey of Lakes in Mongolia.

TABLE 1. — List of taxa examined from the Oligocene and Miocene localities of Valley of Lakes in Central Mongolia.

		Iguania	Lacertidae		Scincoidea	Anguimorpha
late Miocene	Builstyn Khudag section BUK-A/12-14	–	–	Eremiadini	–	–
early Miocene	Olon Ovoony Khurem ODO-A/6	–	–	–	? Scincoidea indet.	–
	Olon Ovoony Khurem ODO-A/2	–	–	Lacertidae indet.	–	–
late Rupelian	Taatsin Gol left TGL-A/11a	–	?	Lacertidae indet.	–	–
	Hsanda Gol SHG-A/1a	*Pseudotinosaurus* cf. *asiaticus* (Gilmore, 1943)			–	Glyptosaurinae indet.
	Ikh Argalatyn Nuruu IKH-A/1	Iguania indet.	?	Lacertidae indet.	–	–
early Rupelian	Taatsiin Gol left TGL-A/2	–	cf. *Lacerta* s.l. *filholi*	Lacertidae indet.	–	–
	Taatsiin Gol right TGR-ZO/2	–	–	–	–	–
	Taatsiin Gol right TGR-A/13	*Pseudotinosaurus* cf. *asiaticus*	–	–	–	? Anguimorpha indet.
	Taatsiin Gol right TGR-A/14	–	?	Lacertidae indet.	–	–
	Hsanda Gol SHG-C/2	–	?	Lacertidae indet.	–	–
	Tatal Gol TAT-D/1	–	?	Lacertidae indet.	–	–

Lakes (Fig. 1; for geology, topography and stratigraphy, see Höck *et al.* 1999 and Daxner-Höck *et al.* 2017). The lower Oligocene, early Rupelian, is represented by the localities Taatsiin Gol right (right side of the river Taatsiin; western plateau, sections TGR-A/13, TGR-ZO/2), Taatsiin Gol left (section TGL-A/2), Tatal Gol (section TAT-D/1) and Hsanda Gol (section SGH-C). The late Rupelian is represented by the locality Taatsiin Gol left (section TGL-A/11), Hsanda Gol (section SHG-A) and Ikh Argalatyn Nuruu (section IKH-A/1). The lower Miocene is represented by the locality Olon Ovoony Khurem (section ODO-A/6) and upper Miocene by Builstyn Khudag (section BUK-A/12-14).

MATERIAL AND METHODS

All material was collected during the field seasons 1995-1997 in the Valley of Lakes in Central Mongolia by Austrian-Mongolian expedition (see Höck *et al.* 1999). The lizard specimens are housed in the Natural History Museum Vienna (Austria), prefixed under individual NHMW numbers. The specimens were photographed under using a Leica M125 binocular microscope with axially mounted DFC500 camera (LAS software [Leica Application Suite] version 4.1.0 [build 1264]). Several specimens were photographed under a scanning electron microscope (SEM; FEI Inspect F50) at the Slovak Academy of Sciences in Banská Bystrica (Slovakia). The standard anatomical orientation system is used throughout this paper. The image processing program ImageJ (Schneider *et al.* 2012) was used for measurements.

The type material of *Lacerta* s.l. *filholi* from Oligocene localities of the Phosphorites du Quercy in France was originally published by Augé (1988). However, only outlines of this material were figured in the original paper. Because this taxon represents an important Paleogene lacertid, we decided to provide high quality images here. Photographs were taken with a canon EOS 5 DSr, objectif Canon MPe 65. The holotypic left dentary from Pech-du-Fraysse (Phosphorites du Quercy) is housed in the collection of the Muséum national d'Histoire naturelle, Paris (France) and is prefixed by MNHN.F.PFR11001. The paratypic left dentary from Coderet is housed in Claude Bernard University in Lyon and prefixed by UCBL 97

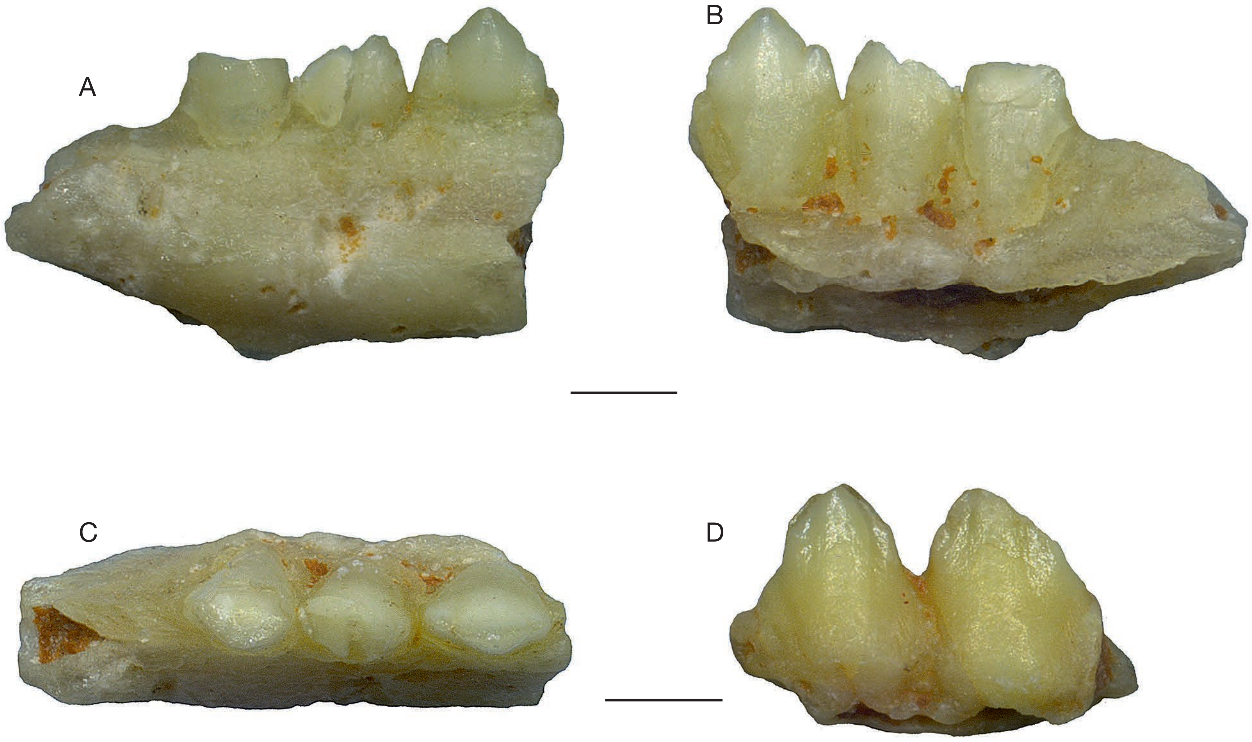

Fig. 2. — *Pseudotinosaurus* cf. *asiaticus* (Gilmore, 1943) from the lower Oligocene of the locality Taatsiin Gol right (**A**-**C**), section TGR-A/13b (early Rupelian of Central Mongolia) and the locality Hsanda Gol (**D**), section SHG-A/1a (late Rupelian): jaw fragments NHMW 2016/0203/0001 in: **A**, lateral; **B**, medial; **C**, dorsal aspects. Jaw fragment NHMW 2016/0201/0001 in: **D**, medial aspect. Scale bars: 500 μm.

689, whereas the paratypic left dentary from Roqueprune 2 is housed in University of Montpellier and prefixed by USTL ROQ2 411. The extant lacertid *Takydromus sexlineatus* Daudin, 1802 from the collection of Department of Ecology, Comenius University in Bratislava (DE 134) is used here for comparative purposes. The specimen was scanned at the micro-computed tomography (CT) facility at the Slovak Academy of Sciences in Banská Bystrica, using a a Phoenix mikro-CTv|tome|x L240. The CT data set was analyzed using VG Studio Max 3.2.

SYSTEMATIC PALAEONTOLOGY

Part 1: Oligocene

SQUAMATA Oppel, 1811
IGUANIA Cope, 1864
Agamidae Gray, 1827
Pseudotinosaurus Alifanov, 1991

Pseudotinosaurus cf. ***asiaticus*** (Gilmore, 1943)
(Fig. 2)

Locality, horizon and material. — **1.** Taatsiin Gol section right TGR-A/13b; biozone A, lower Oligocene (early Rupelian): right one jaw fragment (NHMW 2016/0203/0001). — **2.** Hsanda Gol section SHG-A/1a; biozone B, lower Oligocene (late Rupelian): jaw fragment (NHMW 2016/0201/0001).

Description

Only two fragments are preserved. The specimen from Hsanda Gol (NHMW 2016/0201/0001) represents only two teeth, whereas a fragment of jaw from Taatsiin Gol (NHMW 2016/0203/0001) is slightly more complete (see Fig. 2). Here, three teeth are preserved, although only the anterior-most one is complete. The teeth are mediolaterally compressed. In all cases, teeth are acrodont, tricuspid, with a dominant triangular cusp and smaller mesial and distal ones. Teeth are very close to each other, with almost no interdental gaps.

Remarks

The material described here as *Pseudotinosaurus* is fragmentary (listed in Böhme [2007] as *Tinosaurus* sp.). Moreover, the problem of "*Tinosaurus*" is that tricuspid teeth of a similar form are probably present in some 200 living species of Agamidae, more precisely members of Draconinae and *Leiolepis* Cuvier, 1829 (Smith *et al.* 2011). Previously, *Tinosaurus* Marsh, 1872 in Mongolia was recognized by Gilmore (1943), who described the right dentary fragment from the middle Eocene of Shara Murun area as a new species, *T. asiaticus* (Gilmore, 1943). Later, a new generic name – *Pseudotinosaurus* – was erected for this material by Alifanov (1991), who also referred the material from Khaychin Ula II locality to this taxon. This taxon can be distinguished from *T. stenodon* Marsh, 1872 and *T. pristinus* Leidy, 1872 by having more closely spaced teeth and it differs from *T. lushihensis* Dong, 1965 by its laterally compressed teeth (see also Estes 1983). Our material corresponds with this

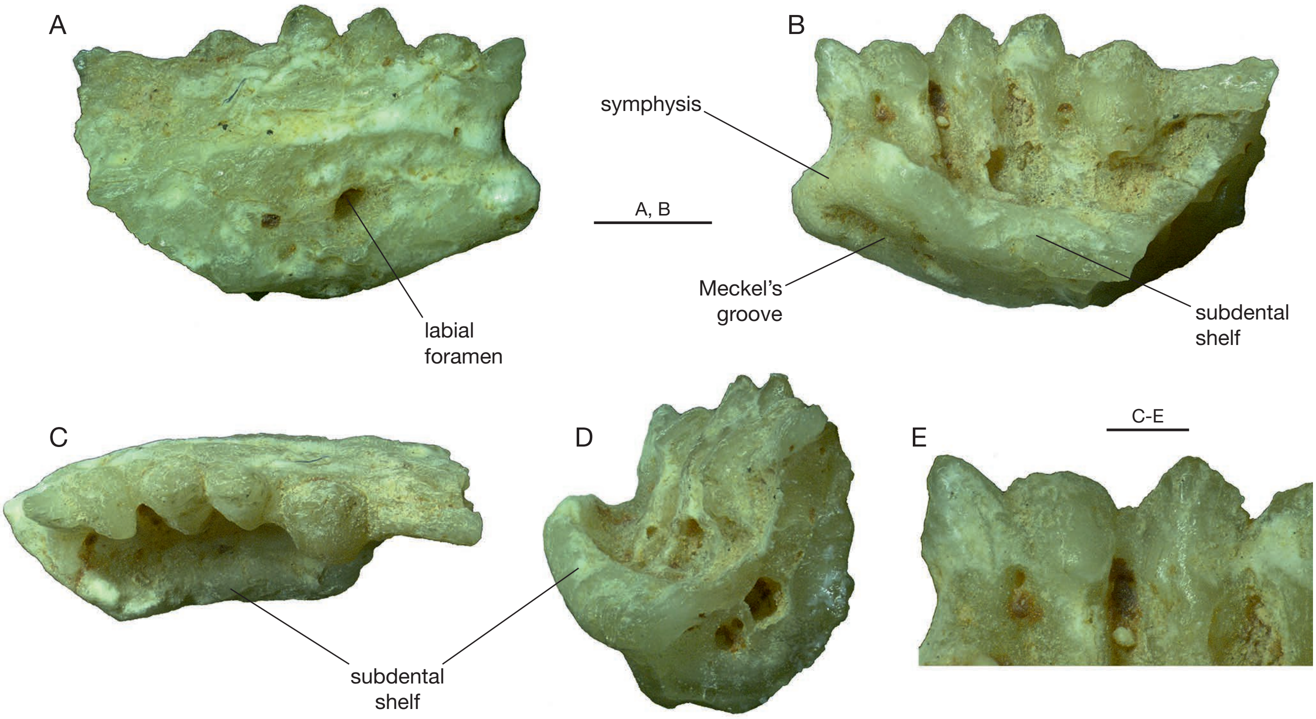

Fig. 3.— Iguania indet. from the locality Ikh Argalatyn Nuruu (**E**-**H**), section IKH-A/1, Central Mongolia: right dentary NHMW 2016/0199/001 in **A**, lateral; **B**, medial; **C**, dorsal; and **D**, posterior aspects. **E**, detail of tooth crowns in medial aspect. Scale bars: A, B, 500 µm; C-E, 200 µm.

definition. In addition, Alifanov (1991) described a new species, *P. ascriptivus* Alifanov, 1991. Several other acrodontan lizards have been described from the middle Eocene of Mongolia (Gao & Dashzeveg 1999; Alifanov 2009).

IGUANIA indet.
(Fig. 3)

Locality, horizon and material. — Ikh Argalatyn Nuruu, section IKH-A/1; biozone B, early Oligocene (late Rupelian); right dentary NHMW 2016/0199/001.

Description

Only a fragment of the anterior dentary portion is referred to an indeterminate iguanian. It is robustly built and the preserved portion is medially curved. It bears five teeth. Meckel's groove is shallow, deeper at the anterior end. Posteriorly, it becomes shallower, only superficially developed. The subdental shelf is medially expanded, and its dorsal margin forms a slightly concave platform. In medial aspect, the bone is tall. The surface is pierced by a labial foramen located at the level between the third and fourth tooth position.

Dentition

Teeth in this anterior region appear to be more-or-less pleurodont, but acrodont implantation cannot be excluded posteriorly. The teeth are damaged, but some tooth crowns have triangular appearance, although the apices of teeth are blunt. The mesial and distal cutting edges in the best preserved tooth (the third tooth, counted from anterior) appear to be slightly serrated (Fig. 3E). In medial aspect, the tooth crowns are flared compared to the tooth shafts. The anterior-most tooth is slightly more anteriorly inclined compared to others in the preserved tooth row.

LACERTOIDEA
Estes, De Queiroz & Gauthier, 1988
LACERTIDAE Oppel, 1811

cf. ***Lacerta*** s.l. ***filholi*** Augé, 1988
(Fig. 4)

Locality, horizon and material. — Taatsiin Gol left section TGL-A/2; biozone A, lower Oligocene (early Rupelian): right dentary (NHMW 2016/0213/0001), left dentary (NHMW 2016/0213/0002).

Description

Dentary

Only two incomplete dentaries are tentatively referred to this taxon (Fig. 4). Meckel's groove is fully open along the entire preserved length. The ventral margin of the dentary is not parallel with the subdental shelf, but forms an angle with it. This ventral margin is almost straight in the preserved portion (Fig. 4D), rising gradually dorsally in the anterior direction. The subdental shelf is thin and more-or-less straight in the preserved portion of both dentaries. The lateral surface of the bone is smooth. In NHMW 2016/0213/0002, it is pierced by two elliptical labial foramina located in the

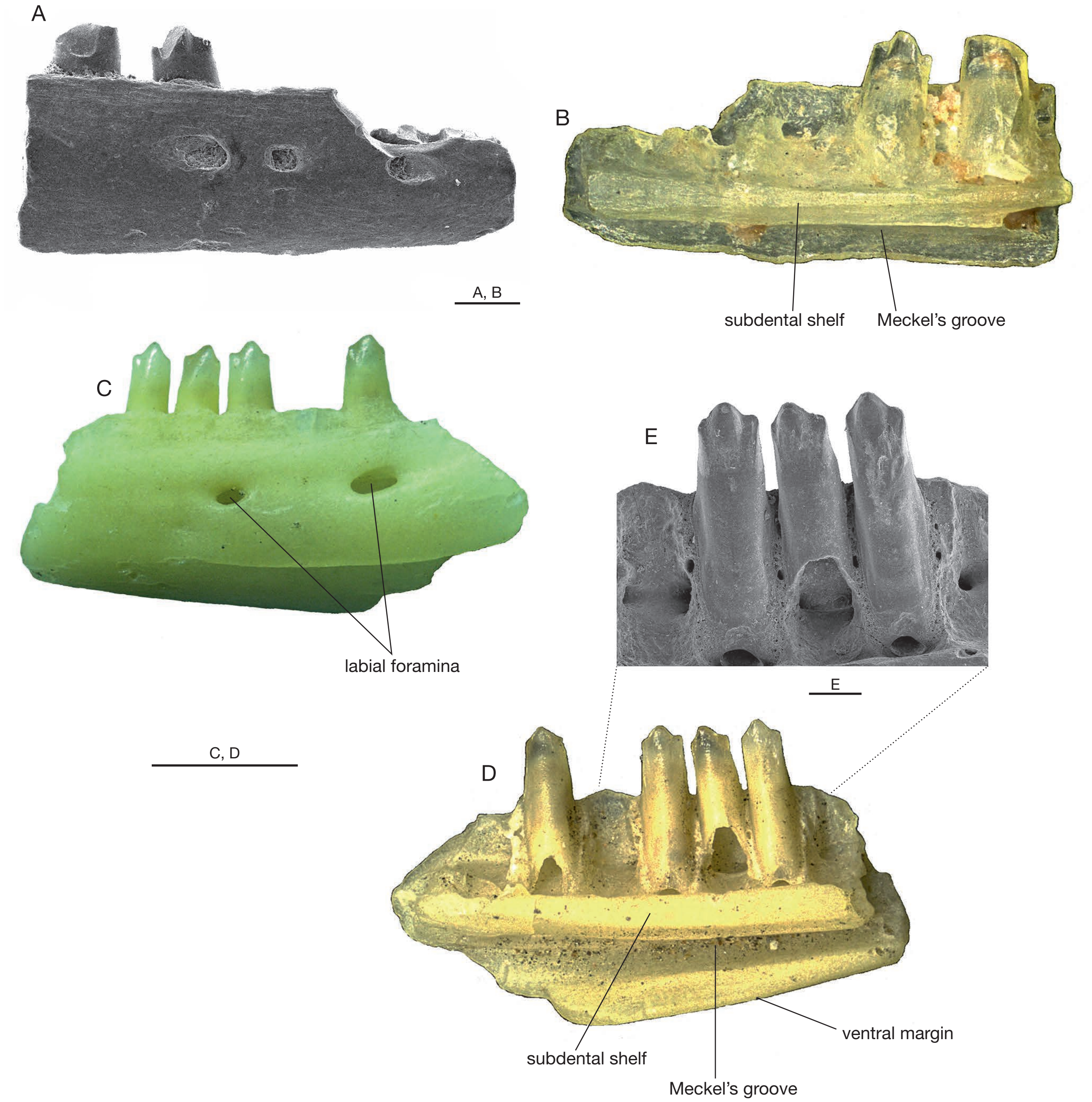

FIG. 4. — cf. *Lacerta* s.l. *filholi* Augé, 1988 from the lower Oligocene of the locality Taatsiin Gol, Central Mongolia: right dentary NHMW 2016/0213/0001 in lateral (**A**) and medial (**B**) spects; left dentary NHMW 2016/0213/0002 in lateral (**C**) and medial (**D**) aspects. Scale bars: 200 µm.

dorsal half of the bone. The posterior one is larger in size than the anterior one. In NHMW 2016/0213/0001, there are three preserved labial foramina, the posteriormost one being the largest.

Dentition

The tooth implantation is pleurodont. Teeth are quite thick but their morphology changes along the tooth row: the shaft of the anterior teeth (Fig. 4C, D) is rather thin, whereas the shaft of the posterior teeth is distinctly thicker (Fig. 4A, B). Their tooth crowns are tricuspid, with a dominant central cusp and smaller mesial and distal cusps. The distal cusp is slightly smaller than the mesial one. Their tooth bases have resorption pits of various sizes, all located lingually. The teeth surpass the jaw parapet by one-third of their height and are densely spaced. The left dentary (Fig. 4C, D) reveals an interesting feature: on the apex of the first preserved tooth (or most anterior tooth), the distal cusp is weakly developed, incipient, and its mophology is therefore quite similar to that of a bicuspid tooth. So it could be assumed that some of the anterior teeth in the complete tooth row were bicuspid.

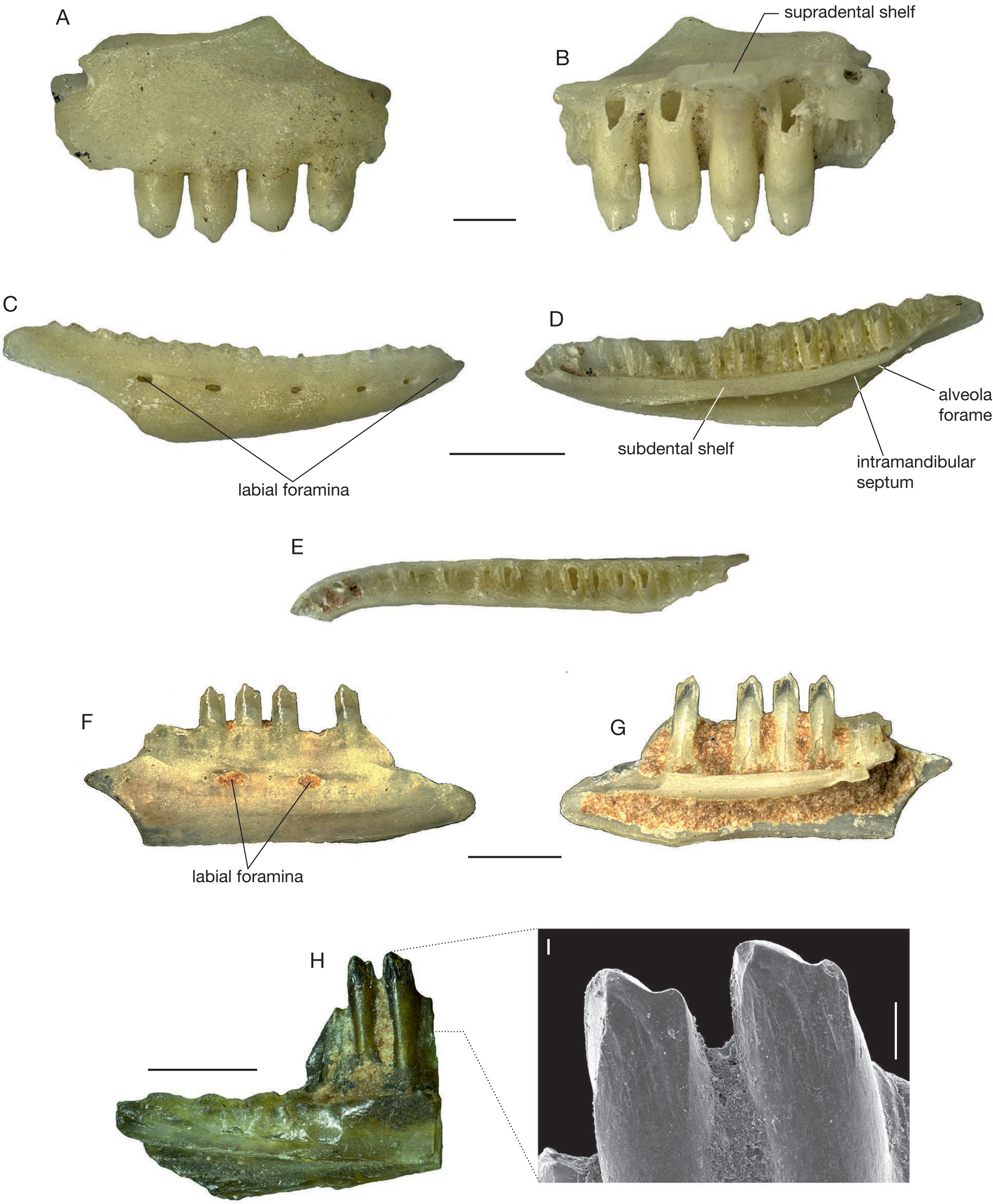

Fig. 5. — Lacertidae indet. from the lower Oligocene (early Rupelian) of the locality Taatsiin Gol left, section TGL-A/2, Central Mongolia: left maxilla NHMW 2016/0214/0001 in: **A**, lateral; **B**, medial aspects. Right dentary NHMW 2016/0214/0003 in **C**, lateral; **D**, medial; and **E**, dorsal aspects. Right dentary NHMW 2016/0214/0004 in **F**, lateral; and **G**, medial aspects. Left dentary NHMW 2016/0214/0002 in **H**, medial aspect with a detail of teeth (**I**). Scale bars: A, B, 200 µm; C-E, 1 mm; F-H, 500 µm; I, 100 µm.

Remarks

Besides some members of the clade Lacertidae (e.g., *Lacerta agilis* Linnaeus, 1758, see Kosma 2004), tricuspid teeth (the presence of mesial and distal accessory cusps separated by lingual and labial grooves from the main cusp) in the posterior region of tooth row are often present in members of Iguanidae and Teiidae as well. However, other potential synapomorphies of Iguanidae clade are absent from the material described herein, e.g., the upfolded lower margin of the Meckelian groove (Gauthier *et al.* 2012; infra- and supra-Meckelian lips *sensu* Smith 2009a, b). Moreover, in Iguanidae, the distal accessory cusps tends to appear first in the anterior position, the mesial cusp later, whereas in "scincomorphs" the mesial cusp appears first, then the distal cusp. The tooth crown in Mongolian material is asymmetric because of the greater prominence of the mesial cusp, which is also inconsistent with Iguania but consistent with "scincomorphs" (K. T. Smith, pers. comm. 2018). In the present material, the mesial cusp is larger than the distal one, so we consider it likely that the mesial cusp appeared first in the tooth row. For all these reasons, we allocate this material to Lacertidae. Extensive, heavy deposit of cementum on tooth bases, typical for teiids (see Presch 1974; Estes *et al.* 1988), is absent here.

The preserved material from Taatsiin Gol left section TGL-A/2 is basically identical to the European lacertid taxon *Lacerta* s.l. *filholi* in the following features: 1) presence of tricuspid teeth (together with the possible presence of bicuspid teeth in the anterior region; 2) one-third of tooth height projects beyond jaw parapet; 3) teeth are densely spaced with small interdental gaps (there is a change in posterior teeth, where the distance can be larger); 4) increase of the tooth robustness posteriorly – estimation based on both specimens here; 5) distinct inclination of the ventral margin relative to the subdental shelf (see Augé & Smith 2009: 150, fig. 1); and 6) position of labial foramina in the preserved portion.

A potential problem of this attribution is that the diagnosis of *Lacerta* s.l. *filholi* (Augé 2005: 129) is based on both dentary and maxillary elements. But as recognized above, the morphology of these dentaries and their teeth is sufficient to distinguish them from all other fossil or recent members of the family. In addition, these diagnostic characters are also cited in the original diagnose of *Lacerta* s.l. *filholi*. Due to the variations in tooth morphology of the specimens from the Phosphorites du Quercy (France, type locality Pech-du-Fraysse) attributed to *Lacerta* s.l. *filholi*, the present referral should be regarded as tentative, and a revision of this species is certainly needed.

LACERTIDAE indet.
(Figs 5, 6, 7, 8)

MATERIAL, HORIZON AND LOCALITY. — **1.** Taatsiin Gol left section TGL-A/2; biozone A, lower Oligocene (early Rupelian): left maxilla (NHMW 2016/0214/0001), one left dentary (NHMW 2016/0214/0002), two right dentaries (NHMW 2016/0214/0003 and 0004). — **2.** Taatsiin Gol right section TGR-A/14; biozone A, lower Oligocene (early Rupelian): two left dentaries (NHMW 2016/0205/0001 and 0002), left maxilla (NHMW 2016/0205/0003). — **3.** Hsanda Gol section SHG-C/2; biozone A, lower Oligocene (early Rupelian): two right dentaries (NHMW 2016/0215/0001 and 0002). — **4.** Tatal Gol section TAT-D/1; biozone A, lower Oligocene (early Rupelian): three left maxillae (NHMW 2016/0211/0001 and 0002 and 0003), two right dentaries (NHMW 2016/0211/0004 and 0005). — **5.** Taatsiin Gol left section TGL-A/11a; biozone B, lower Oligocen (late Rupelian): left maxilla (NHMW 2016/0209/0001), right dentary (NHMW 2016/0209/0002). — **6.** Ikh Argalatyn Nuruu section IKH-A/1; biozone B, lower Oligocene (late Rupelian): left dentary (NHMW 2016/0210/0001), right dentary (NHMW 2016/0210/0002).

DESCRIPTION

Maxilla

All maxillae are fragmentary (see Figs 5A, B; 6A; 7A-F; 8A, B). The supradental shelf is thin but well medially expanded. In NHMW 2016/0211/0001 (Fig. 7B), the opening of the superior alveolar foramen is present at the level of the fourth tooth (counted from posterior, but the posterior region of the maxilla is broken off, so the real number of this tooth position was certainly higher). Posterior to this opening is a shallow groove (the jugal facet). Otherwise the smooth external surface of the bone is pierced by several large labial foramina. They are located ventral to the nasal process (the nasal process is, however, damaged in all specimens).

Dentary

The description is based on several fragments (Figs 5C-H; 6C-G; 7G-K; 8C-H). Dentary NHMW 2016/0214/0003 is straight in dorsal aspect, with a slight medial curvature at its anterior end. Meckel's groove is fully open, but narrow. This is especially true in the anterior region, where it opens ventrally. The symphysis is rectangular in shape, slightly elevated dorsally. The subdental shelf is concave. It is robust anteriorly and gradually narrows posteriorly, partly as a result of the presence of the facet for the splenial, situated on its ventral margin. This facet reaches anteriorly to the level of the eighth tooth position (counted from anterior). The alveolar foramen is located at the level of the fourth tooth position (counted from posterior). The intramandibular septum has no free ventral margin. The exact tooth count is unknown, but if NHMW 2016/0214/0003 represents the same taxon as fragments described here, the tooth count is around 23.

The external surface is smooth, pierced by a serie of labial foramina located more-or-less at mid-heigh of the lateral surface. In NHMW 2016/0214/0003, there are six labial foramina.

Dentition

The implantation is pleurodont. Teeth are tall and conical (or cylindrical). The interdental gaps are wide; the gap size forms one-third or more of the mesiodistal length of the tooth shaft in the middle region. Teeth are bicuspid with a dominant distal (central) cusp and smaller mesial one, except for the anterior teeth, that are unicuspid. The distal cusp is triangular and pointed in lingual aspect. Maxillary tooth crowns in NHMW 2016/0211/0002 (Fig. 7C, D), an anterior fragment, are slightly posteriorly recurved. The crowns of some teeth bear weak striae lingually. Oval resorption pits are present in some tooth bases.

REMARKS

The description of the dentition is based on several dentaries from different lower Oligocene localities which display a similar, almost identical morphology. All are incomplete except for NHMW 2016/0214/0003 which is more-or less complete. However, all teeth in this specimen are broken off. All preserved specimens show bicuspidity. In most of the specimens of *L. filholi* from the Phosphorites du Quercy tricuspid teeth are present but often inconspicuous and show significant variation, even in specimens from the same locality. Tricuspid teeth like those seen in specimens in Figure 4 are only known in *L. filholi* from

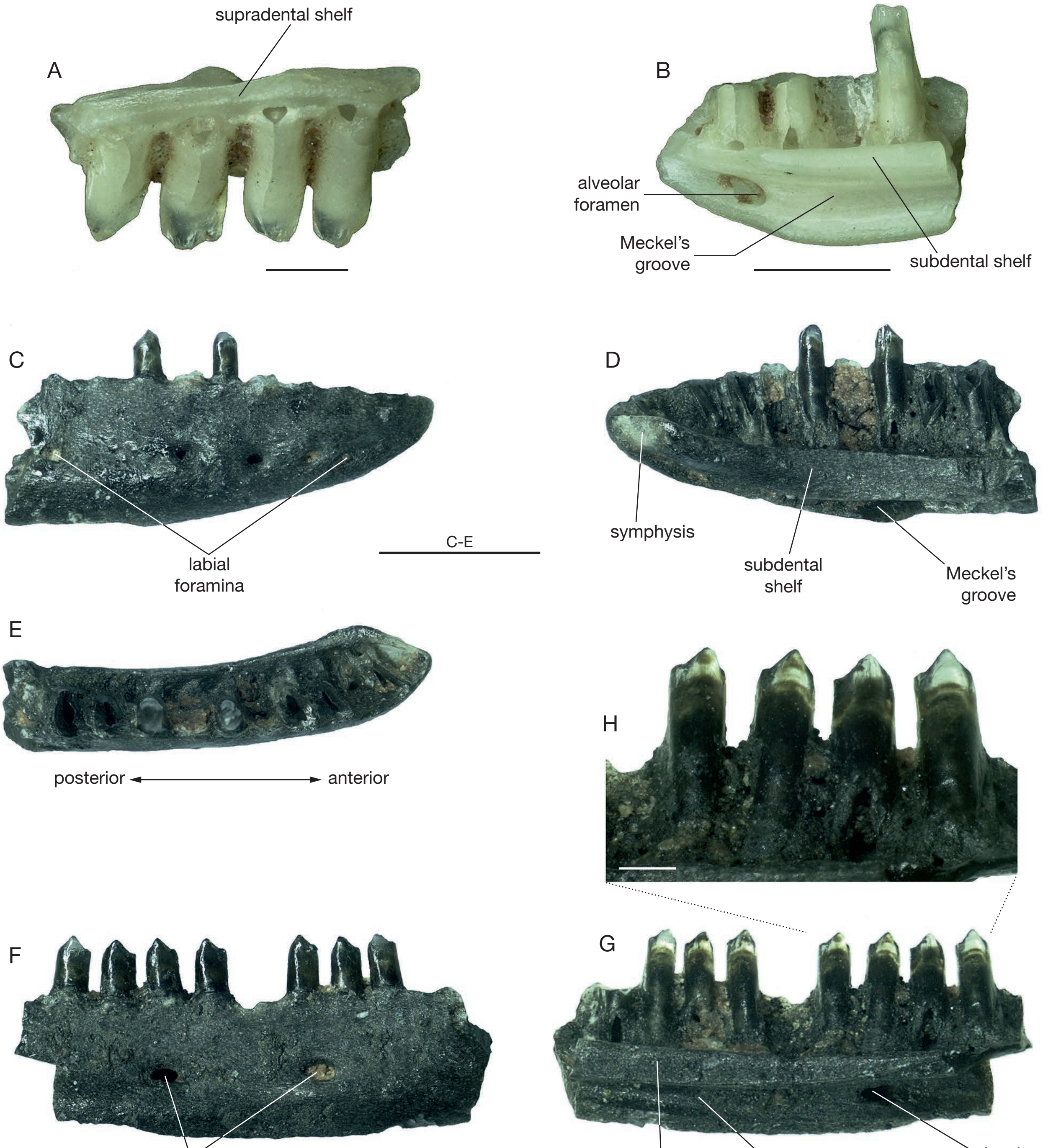

Fig. 6. — Lacertidae indet. from the lower Oligocene (early Rupelian) of the locality Taatsiin Gol right (**A**, **B**), section TGR-A/13 and Hsanda Gol (**C**-**G**), section SHG-C/2, Central Mongolia: Left maxilla NHMW 2016/0205/0003 in **A**, medial aspect. Left dentary NHMW 2016/0205/0001 in **B**, medial aspect. Right dentary NHMW 2016/0215/0001 in **C**, lateral; **D**, medial; and **E**, dorsal aspects. Right dentary NHMW 2016/0215/0002 in **F**, medial; and **G**, medial aspects with detail of teeth (**H**). Scale bars: A, G, 200 μm; B, 500 μm; C-E, F, G, 1 mm; H, 200 μm.

Boutersen (in Augé & Smith 2009: fig. 2). However, the fact that this Mongolian form described here as Lacertidae indet. is clearly bicuspid, whereas *L. filholi* tends to be tricuspid, might show that there is a second unidentified lacertid. Moreover, the teeth in the Mongolian material show some variation in robustness or posterior curvature of the crown (see Fig. 7C, D). Although these differences might be caused by individual (or ontogenetic) variability and position within the tooth row (anterior teeth are usually more posteriorly recurved than those in the posterior section in extant lacertids), the presence of several species cannot fully be excluded due to the limitation of such fragmentary material.

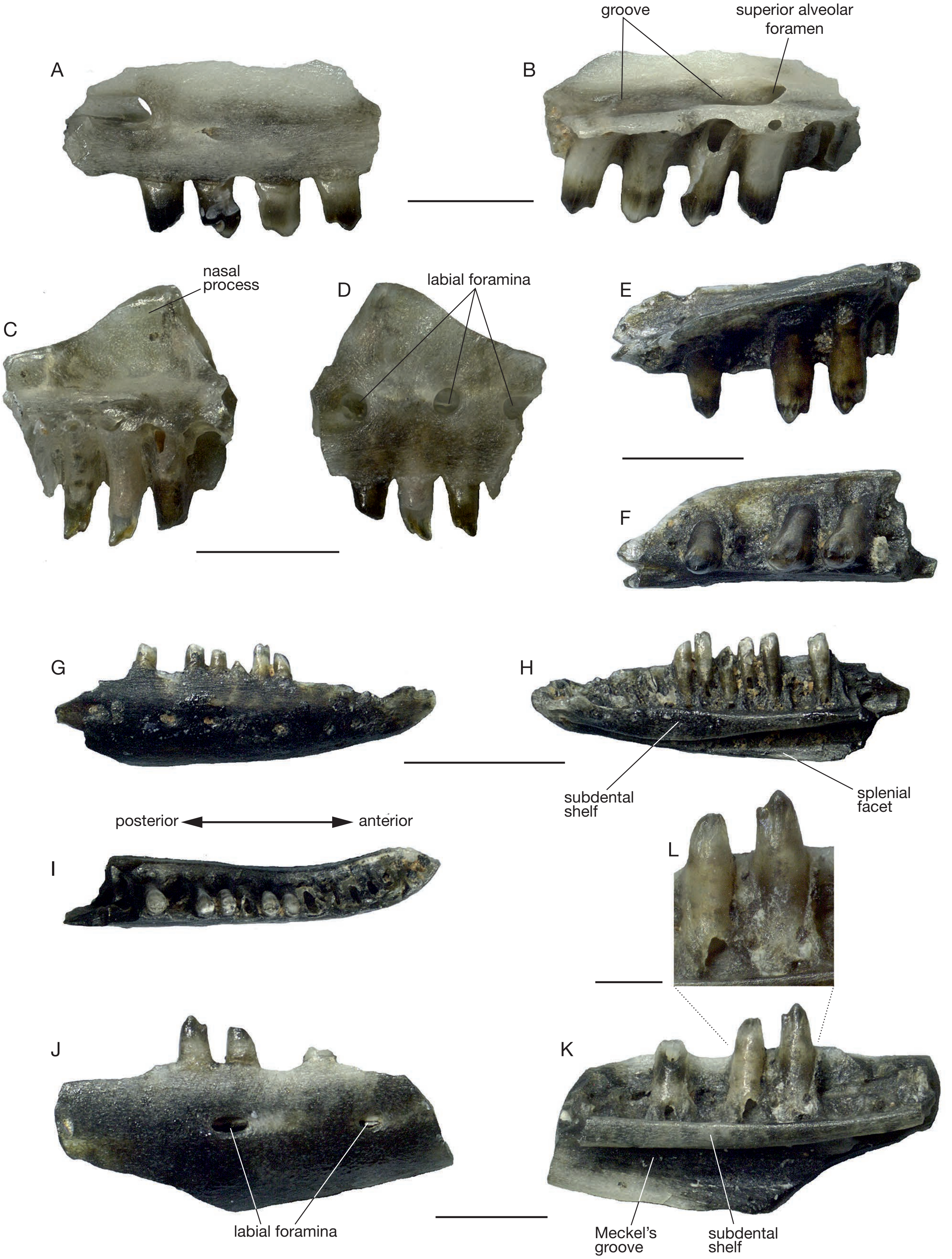

FIG. 7. — Lacertidae indet. from the lower Oligocene (early Rupelian) of the locality Tatal Gol, section TAT-D/1, Central Mongolia: Left maxilla NHMW 2016/0211/0001 in **A**, lateral; and **B**, medial aspects. Left maxilla NHMW 2016/0211/0002 in **C**, medial; and **D**, lateral aspects. Left maxilla NHMW 2016/0211/0003 in **E**, medial; and **F**, ventral aspects. Right dentary NHMW 2016/0211/0004 in **G**, lateral; **H**, medial; and **I**, dorsal aspects. Right dentary NHMW 2016/0211/0005 in **J**, lateral; and **K**, medial aspects with detail of teeth (**L**). Scale bars: A-F, J, K, 500 μm; G-I, 1 mm; L, 200 μm.

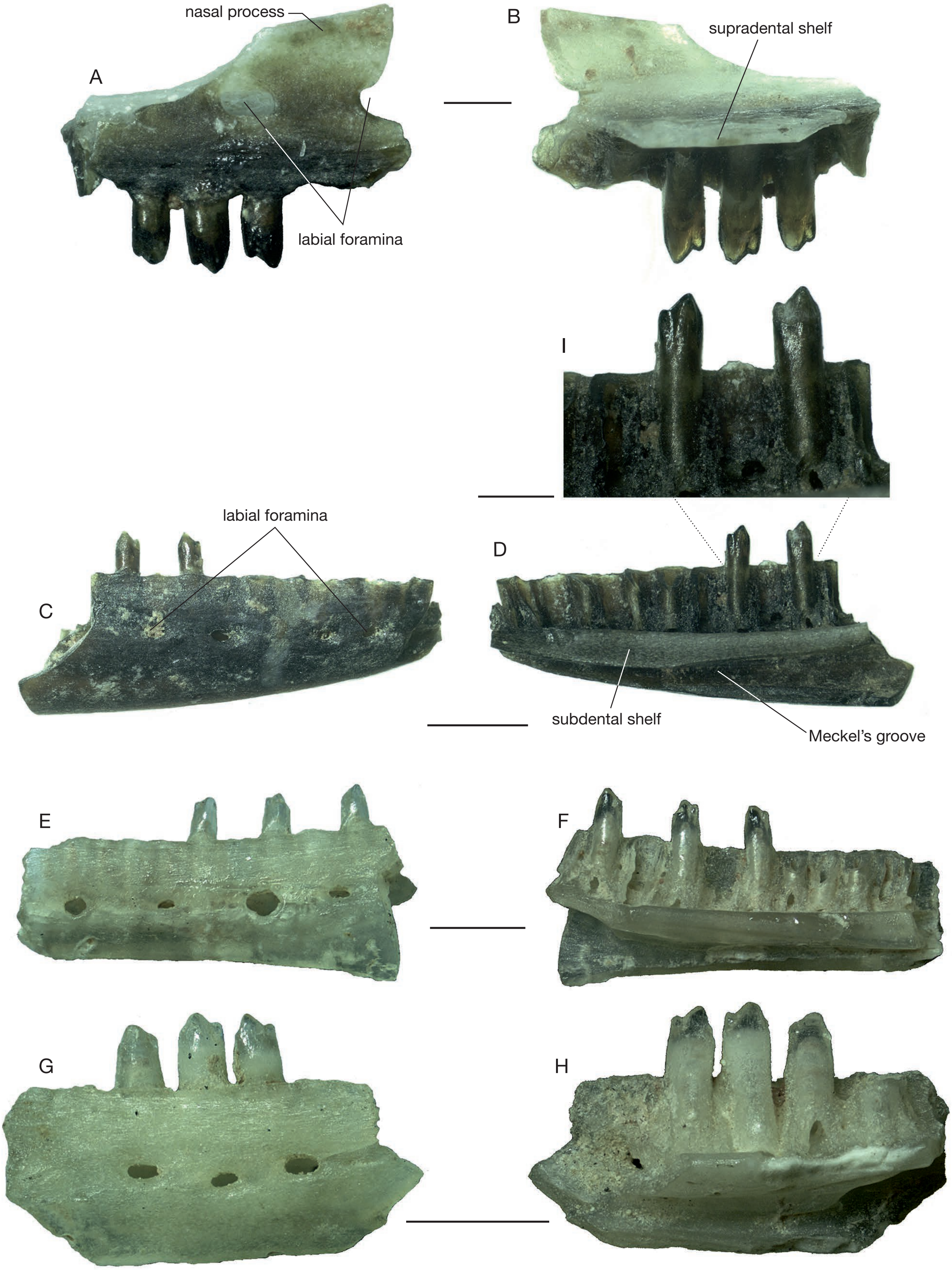

Fig. 8. — Lacertidae indet. from the lower Oligocene (late Rupelian) of the locality Taatsiin Gol left (**A**-**D**), section TGL-A/11 and Ikh Argalatyn Nuruu (**E**-**H**), section IKH-A/1, Central Mongolia: Left maxilla NHMW 2016/0209/0001 in **A**, lateral; and **B**, medial aspects. Right dentary NHMW 2016/0209/0002 in **C**, lateral; and **D**, medial aspects with detail of teeth (**I**). Left dentary NHMW 2016/0210/0001 in **E**, lateral; and **F**, medial aspects. Right dentary NHMW 2016/0210/0002 in **G**, lateral; and **H**, medial aspects. Scale bars: A, B, I, 200 µm; C-H, 500 µm.

ANGUIMORPHA Fürbringer, 1900
ANGUIDAE Gray, 1825
GLYPTOSAURINAE Marsh, 1872

cf. Glyptosaurini Sullivan, 1979
(Fig. 9)

LOCALITY, HORIZON AND MATERIAL. — Hsanda Gol; section SHG-A/1, biozone B, lower Oligocene (late Rupelian): seven osteoderms (NHMW 2016/0200/0001-0007).

DESCRIPTION
The osteoderms are thick and robust. They can be divided into two groups based on shape. The first type is rectangular. The anteroposterior length of NHMW 2016/0200/0001 (Fig. 9A-C) is 6.5 mm, and its width 4.4 mm. Its maximum thickness is 1.6 mm. The external surfaces of osteoderms possess a tuberculated ornamentation, formed by discrete tubercles of various sizes (usually smaller centrally). A blunt oblique keel is present, rising up in the posterior section of the ornamented region. Its location in the preserved specimens is not on the midline but is slightly displaced toward the margin. In two osteoderms, a keel is absent. In the first one, NHMW 2016/0200/0003, however, tubercles in central region are more-or-less connected to form an indistinct but continuous ridge (Fig. 9G) located in the midline. This osteoderm is not rectangular, but trapezoidal in shape. The second one (NHMW 2016/0200/0004; Fig. 9J-L) is rectangular but very narrow (length 6.4 mm, width 3.2 mm). Here the tubercles are connected as well, forming an indistinct ridge. This ridge is not on the midline and is oblique.

The smooth articular surface is anteroposteriorly narrow. It is only partly preserved in some osteoderms. It is separated from the ornamented portion by a transverse groove. The lateral edge of some osteoderms is not smooth, but shows that they were interdigitated with adjacent osteoderms (Fig. 9B, E, K). The osteoderms are not flat but tend to have a weakly concave exterior surface (Fig. 9C). The interior surface is characterized by a longitudinal depression bounded by the expanded lateral articular surfaces, which tend to be more prominent posteriorly than anteriorly. The internal surface is pierced by several small neurovascular foramina. The osteoderms slightly narrow anteriorly.

The second type of osteoderm (NHMW 2016/0200/0005; Fig. 9M-O) is rhombic and smaller (diagonal lengths 3 mm and 4.4 mm). Its external ornamentation is the same as described in the first type.

REMARKS
The two different types of osteoderm most likely reflect topographic position in the body. Among Anguimorpha, the tuberculate ornamentation observed on those osteoderms is an autapomorphy of the anguid clade Glyptosaurinae, which Sullivan (1979) divided into the tribes Melanosaurini and Glyptosaurini (see Estes 1983; Cicimurri *et al.* 2016).

In Glyptosaurini, subhexagonal (or polygonal) osteoderms are present on the skull, whereas they have rectangular osteoderms on the body (the situation on limbs is more complicated). Böhme (2007) placed the osteoderms from Hsanda Gol section SHG-A/1 in Melanosaurini. Several genera have been attributed to that clade: *Melanosaurus* Gilmore, 1928, *Arpadosaurus* Meszoely, 1970, *Peltosaurus* Cope, 1873, *Xestops* Cope, 1873 and *Paraplacosauriops* Augé & Sullivan, 2006 (see Sullivan 1979; Augé & Sullivan 2006). The morphology of the Hsanda Gol osteoderms might indicate their affinity to Melanosaurini in two points: 1) rectangular overall shape (except for NHMW 2016/0200/0005; see Fig. 9M-O); and 2) the presence of a keel. However, Melanosaurini are generally considered to have been plesiomorphic in most characters with respect to Glyptosaurini, including their osteoderms. They appear to be less heavily tuberculate, less robust and more rectangular in shape if compared to Glyptosaurini osteoderms. However, the keel in Hsanda Gol osteoderms is not as strongly developed as it is, for example, in *Xestops* (see Meszoely *et al.* 1978: 162, fig. 4). They are also very robust and strongly tuberculate. In fact, they are very similar to body osteoderms of the glyptosaurine lizard *Helodermoides tuberculatus* Douglass, 1903 (see Sullivan 1979: 35, fig. 15c, d). These are also rectangular and keeled in the way as osteoderms described here. Moreover, the presence of a subhexagonal osteoderm (Fig. 9M, N, O) only occurs in glyptosaurins whereas melanosaurins have only rectangular osteoderms and osteodermal shields on the skull roof. *Stenoplacosaurus mongoliensis* (Sullivan, 1979) was described from the upper Eocene of Mongolia (Sullivan & Dong 2018; *Helodermoides mongoliensis* in Sullivan 1979). This taxon is based on the frontal morphology, whereas the body osteoderms are unknown. In any case, it is plausible that the osteoderms described here might belong to this lineage, showing its survival into the Oligocene.

? Anguimorpha indet.
(Fig. 10)

LOCALITY, HORIZON AND MATERIAL. — Taatsiin Gol right section TGR-A/13a; biozone A, lower Oligocene (early Rupelian): left dentary (NHMW 2016/0202/0001).

DENTARY
The posterior and middle portion of the left dentary is preserved (Fig. 10), but the anterior region is broken off. The dentary is anteroposteriorly elongated and narrow. In dorsal view, the preserved portion is straight. The jaw parapet alveolar crest is low and supports eleven tooth positions; three teeth are still attached. In medial aspect, Meckel's groove is narrow and gradually narrows anteriorly. The ventral margin of the bone is damaged, preserved only in the anterior region. The alveolar foramen is located at the level of the fourth tooth (counted from posterior). The intramandibular septum lacks a free ventral margin. The subdental shelf is thin. It starts to slightly rise dorsally in posterior direction from the level of the sixth tooth position (counted from posterior). Here, it is much thinner than anteriorly. A sulcus dentalis is absent. The coronoid process is short and pointed. The ventral part of

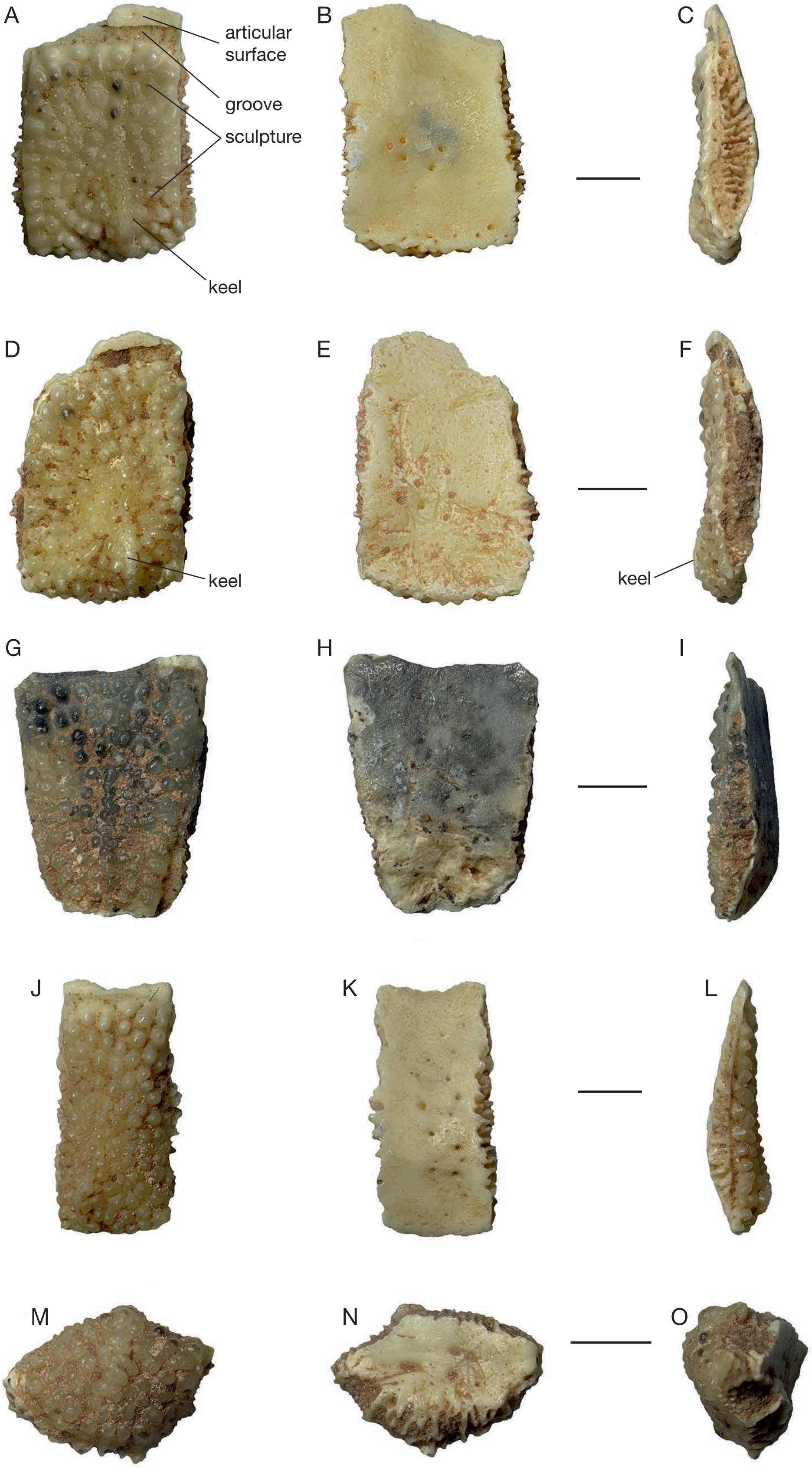

FIG. 9. — Glyptosaurinae indet. from the lower Oligocene of the locality Hsanda Gol, section SHG-A/1, Central Mongolia: Osteoderms NHMW 2016/0200/0001-0005 in **A**, **D**, **G**, **J**, **M**, external; **B**, **E**, **H**, **K**, **N** internal; and **C**, **F**, **I**, **L**, **O** lateral aspects. Scale bars: 1 mm.

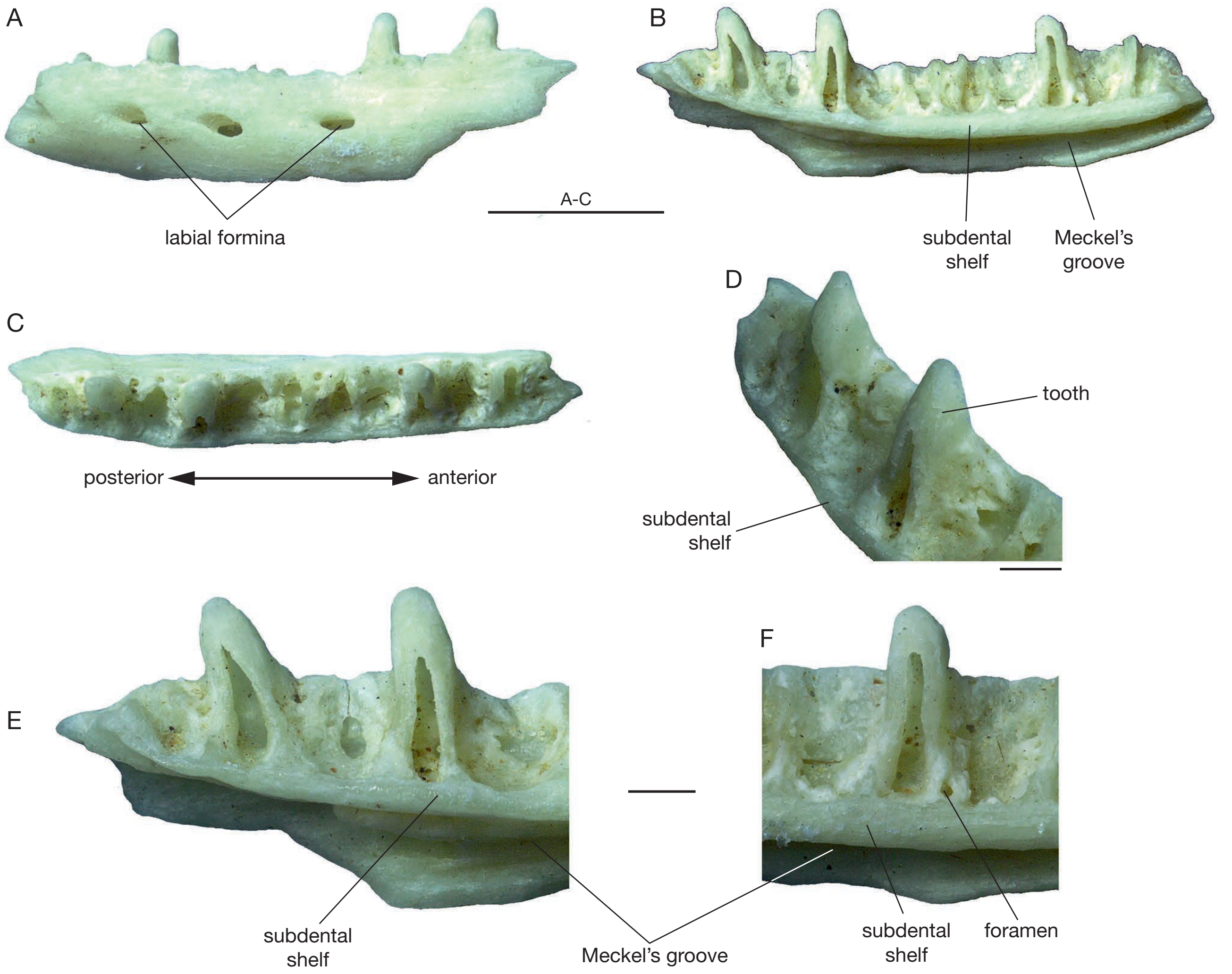

Fig. 10. — ?Anguimorpha indet. from lower Oligocene (early Rupelian) of the locality Taatsiin Gol right, section TGR-A/13a, Central Mongolia: the left dentary NHMW 2016/0202/0001in **A** lateral, **B** medial and **C** dorsal aspects. **D**, posterior section in anterodorsomedial aspect, **E**, the detail of posterior section in medial aspect, the detail of anteriorly located tooth in **F**, medial aspect. Scale bars: A-D, 1 mm; E, F, 200 µm.

the posterior portion is not preserved. The preserved external surface, which is otherwise smooth, is pierced by three labial foramina. They increase in size posteriorly and become more anteroposteriorly elongated (elliptical). The openings are directed anterodorsally, as indicated by depressions.

Dentition

The dentition is subpleurodont (*sensu* Hoffstetter 1954, 1955), the jaw parapet is low and the bases of the teeth are attached to a sloping, concave surface, without any angle between two different planes. Moreover, subpleurodont implantation is often associated with reduction of the subdental shelf. Teeth are large in relation to the size of the dentary. Estimated from the morphology of just those three teeth, it seems that their overall size increases posteriorly. Two of them are only slightly recurved, whereas the posterior preserved tooth (second tooth position) is more posteriorly inclined. The tooth crowns are blunt and appear to be highly corroded. All teeth have huge pits, reaching almost to their tooth crowns. It should be noted that this feature might be probably related to an artifact of preservation. In the first anteriorly preserved tooth, a small foramen is located slightly anteriorly to the tooth.

Remarks

The position of the resorption pit preserved close to the nine tooth position (counted from posterior) indicates the tooth replacement pattern which resembles that of modern anguimorphs in being of the interdental type (McDowell & Bogert 1954). This, together with the combination of the slightly recurved teeth and the subpleurodont implantation (although this is not unique to Anguimorpha) of the teeth, supports a tentative allocation of this material to Anguimorpha. The splenial anterior inferior alveolar foramen is located between the splenial and the dentary in many anguimorphs (Estes *et al.* 1988). In an isolated dentary, this can be often easily recognized by the presence of the splenial spine (or at least impression of the foramen) in subdental shelf (see e.g., Klembara *et al.* 2014). This is true especially for members of Anguidae (thus this clade can be excluded here), but this

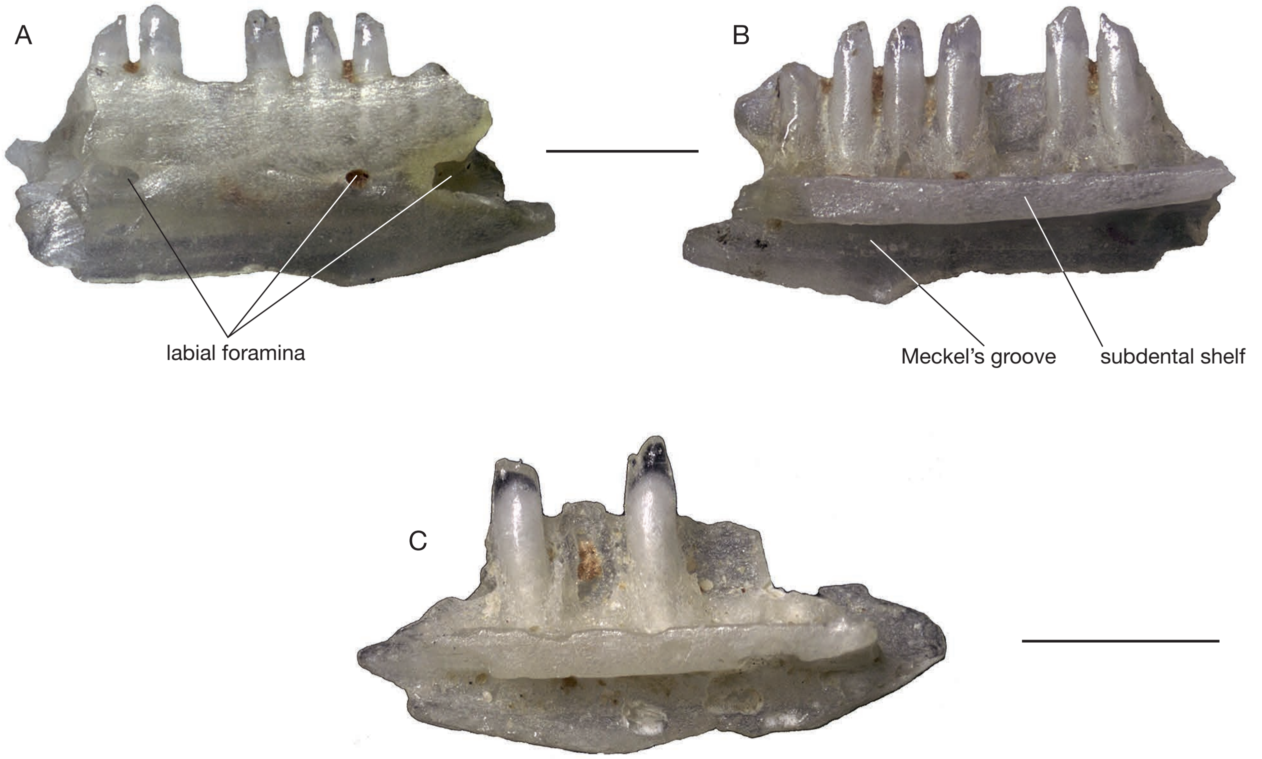

Fig. 11. — Lacertidae indet. from the lower Miocene of the locality Olon Ovoony Khurem, section ODO-A/2, Central Mongolia: right dentary NHMW 2016/0206/0001 in **A**, lateral; **B**, medial aspects; right dentary NHMW 2016/0206/0002 in **C**, medial aspect. Scale bars: 500 μm.

feature on the subdental shelf is absent in *Shinisaurus* Ahl, 1930, *Heloderma* (Wiegmann, 1829) and some others (see Rieppel 1980; Conrad 2004). This character is also absent here in NHMW 2016/0202/0001.

PART 2: MIOCENE

SQUAMATA Oppel, 1811

LACERTIDAE indet. (Fig. 11)

LOCALITY, HORIZON AND MATERIAL. — Olon Ovoony Khurem; section ODO-A/2, biozone D1, lower Miocene: two right dentaries (NHMW 2016/0206/0001 and 0002).

DESCRIPTION

Only fragments of two right dentaries are available. NHMW 2016/0206/0001 bears seven tooth positions (five teeth are still attached; Fig. 11A, B) whereas only four tooth positions (with two complete teeth) are preserved in NHMW 2016/0206/0002 (Fig. 11C). The jaw parapet is tall, teeth projecting only one-third of their height above it. Meckel's groove is fully open and is bounded by the subdental shelf. The subdental shelf gradually narrows posteriorly. The otherwise smooth external surface of the bone is pierced by a series of labial foramina located in the middle portion. Foramina are elliptical, slightly anteroposteriorly elongated.

Dentition

The tooth implantation is pleurodont, the interdental gaps are broad (the gap forms around one-third of the mesiodistal width of the tooth shaft). Teeth are bicuspid with a dominant distal cusp and small mesial cusp. Some of the tooth bases bear resorption pits.

?SCINCOIDEA Oppel, 1811

Family indet.
(Fig. 12)

LOCALITY, HORIZON AND MATERIAL. — Olon Ovoony Khurem; section ODO-A/6, biozone D1, lower Miocene; left maxilla (NHMW 2016/0204/0001).

DESCRIPTION

Maxilla

Only a fragment of the posterior portion of the left maxilla is available (Fig. 12). It is robustly built and bears seven teeth. The supradental shelf is thin but broad, well medially expanded. The superior alveolar foramen is located around the level of the position of the third preserved posterior tooth. It appears large, but this is most likely caused by the fact that the bone roof that covered it partly collapsed during fossilization. The posterior section is broken off and the posterior branch of the canal is exposed in posterior aspect. The nasal process is heavily damaged, only

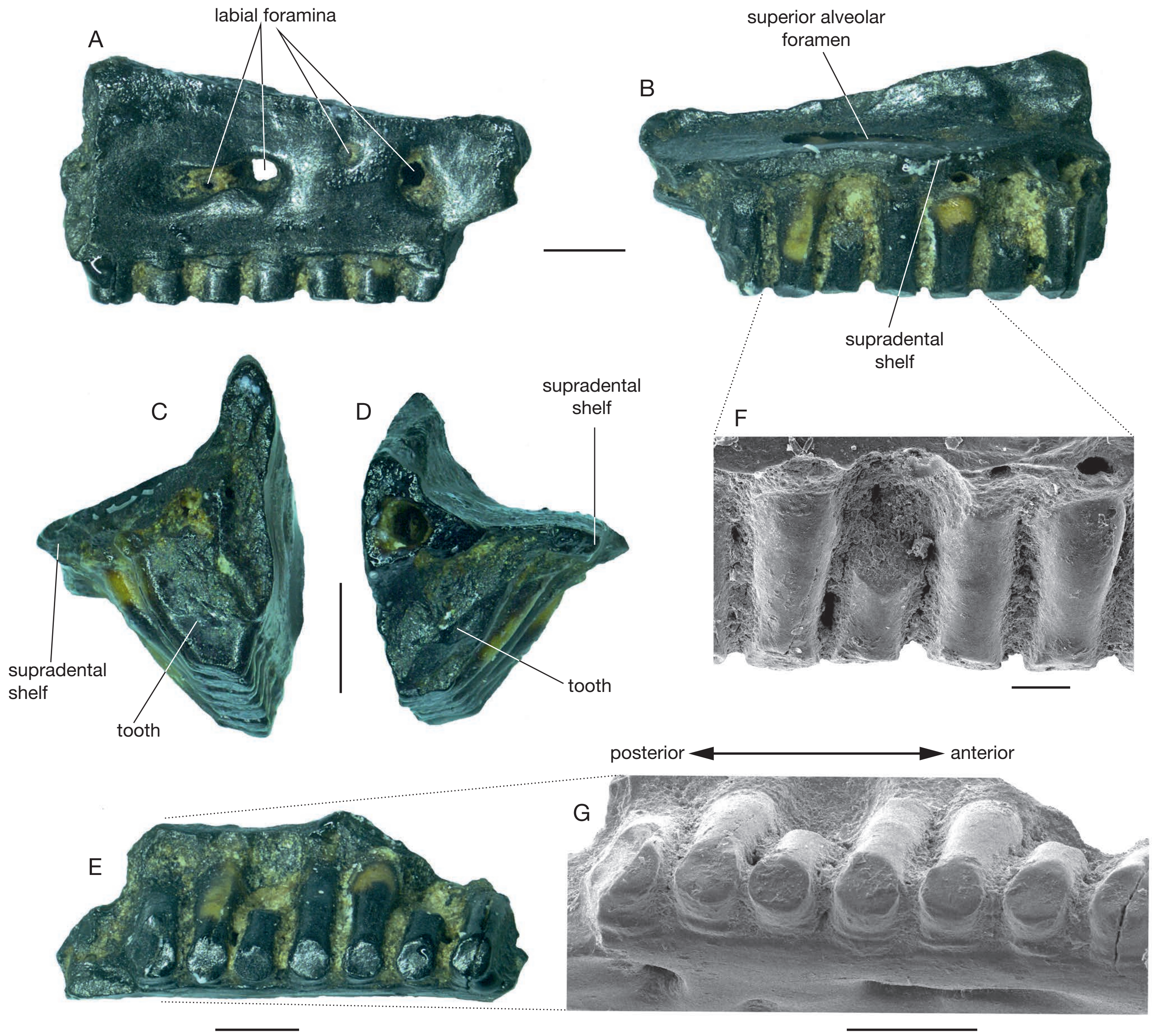

Fig. 12. — ? Scincoidea indet. from the lower Miocene of the locality Olon Ovoony Khurem, section ODO-A/6, Central Mongolia: left maxilla NHMW 2016/0204/0001 in **A**, lateral; **B**, medial; **C**, anterior; **D**, posterior; and **E**, ventral aspects. Scale bars: A-E, G, 500 μm; F, 200 μm.

its base is preserved (Fig. 12A, B). The posterior process slopes gently towards the supradental shelf but becomes horizontal well above it. The external surface of the bone is pierced by four large labial foramina. They are located inside of the depressions which surround them. In the anterior two foramina, the depressions are confluent.

Dentition

The teeth show pleurodont implantation. They are tall (in medial aspect) and closely spaced with small interdental gaps. In lingual aspect, the teeth are columnar, only slightly wider around their bases. However in mesial or distal aspect, the teeth are gradually swollen lingually in the direction to their bases. For this reason, they are mesiodistally compressed, with a gradually lingually expanded portion basally, so that their base occupies the entire width of the supradental table. The tooth crowns are blunt, ended with an oval flat surface (hammer-like). This gives them a horizontally clipped off appearance. The position of these surfaces is, however, not absolutely horizontal, but they are slightly inclined lingually. Some of those surfaces appear to be gently concave in mesial or distal aspects, and the labial margin of this surface reaches slightly more ventrally if compared to the lingual margin.

REMARKS

The equivalent height of each crown suggests that this was related to occlusal surface and not formed due to diagenetic processes. Although mammalian carnivores with high stomach acidity can destroy the entire crown

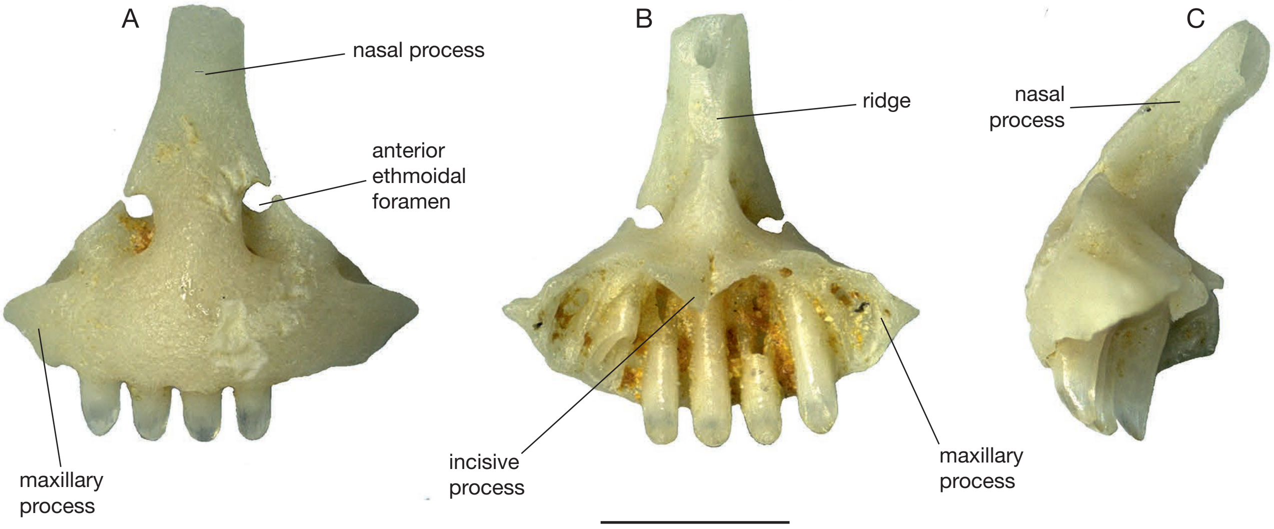

Fig. 13. — Eremiadini indet. from the upper Miocene of the locality Builtsin Khudag, Central Mongolia: premaxilla NHMW 2016/0208/0001 in **A**, external; **B**, internal; and **C**, lateral aspects. Scale bar: 500 µm.

without touching the shaft (Smith Pers. Comm. 2019) and slightly similar morphology sometimes can be a result of a corrosion, we believe that this is not the case of NHMW 2016/0204/0001. The support for that is: 1) the pulp cavities are not exposed (although it depends on how far the pulp cavity penetrates into the crown); and 2) there is no difference in texture between the tooth occlusal surface margin vs. its internal section in ventral aspect (no micro-canals can be observed in the central section, so there is no indication of an exposed dentine). The occlusal surfaces appear to be present as a normal enamel condition. In fact, exactly the same morphology can be observed in all preserved seven teeth here. Moreover, bone surface does not seem to be affected by such digestive process at all. In contrast to that, specimens which have been subjected to digestive action by carnivores, as can be expected, bear marks of this process that are visible on the entire specimen. Moreover, the results on each tooth are usually very different and pulp cavities are exposed in many cases. A similar condition as that present in NHMW 2016/0204/0001 can be observed in the supposedly durophagous *Catactegenys solaster* Nydam, Rowe & Cifelli, 2013, a potential xantusiid from the Campanian of Texas (see Nydam *et al.* 2013). However, several other differences are present, e.g., the tooth bases of the Miocene Mongolian taxon extend all the way to the supradental shelf whereas in *C. solaster* they taper on approaching the supradental shelf.

The dentition of NHMW 2016/0204/0001 is so unique that it can be easily recognizable. It suggests a presence of a new taxon, however, we do not make it here because of the limitation of the present material. Moreover, its relationhips within Squamata are difficult to elucidate. Several characters of this maxilla suggest scincid affinities, such as lingually swollen tooth shafts (although this is also present in many Glyptosaurinae and *Palaeoxantusia* Hecht, 1956, see e.g., Meszoely 1970; Schatzinger 1980) and low crowns in external aspect (only slightly exceeding the level of the ventral margin of the maxillary jaw parapet). The nasal (= facial) process becomes horizontal posteriorly and remains fairly tall. This character state is common in Scincoidea (and Acrodonta), where there is also frequently a small triangular process of maxilla, in contact with the jugal (see Smith 2009b). The large labial foramina also accord well with scincid morphology (Estes 1983; Greer 1989; Evans 2008). However, there are conflicting characters with this attribution, like the posterior position of the superior alveolar foramen and the presence of labial foramina on the posterior margin of the maxilla. According to Lee *et al.* (2009, they studied taxa from Australasia and New Caledonia), in skinks the superior alveolar foramen has an anterior position and labial foramina are absent on the posterior margin. However, it is worth noting that the posterior portion of this maxilla is broken off.

Tooth morphology of this fossil also departs from the scincoid or scincid dental type as defined by Richter (1994) and Kosma (2004): teeth with chisel-shaped tooth crowns bearing several striations on the crown. However, scincoids and specially scincids present a great variability in tooth shape (Bolet & Augé 2014). In particular, the extant Australian scincid *Cyclodomorphus gerrardii* (Gray, 1845) has hammer-like teeth used to crush the shells of snails; in addition *Cyclodomorphu*s Fitzinger, 1843 also eats slugs, insects, spiders and fruits (Arena *et al.* 2011). Moreover, blunt teeth are present in e.g., the amblyodont blue-tongued skink *Tiliqua* Gray, 1825 from Australia, the diet of which also includes plant matter such as seeds (Christian *et al.* 2003; Shea 2006). Hence, the NHMW 2016/0204/0001 is referred, with some doubts, to scincoid lizards.

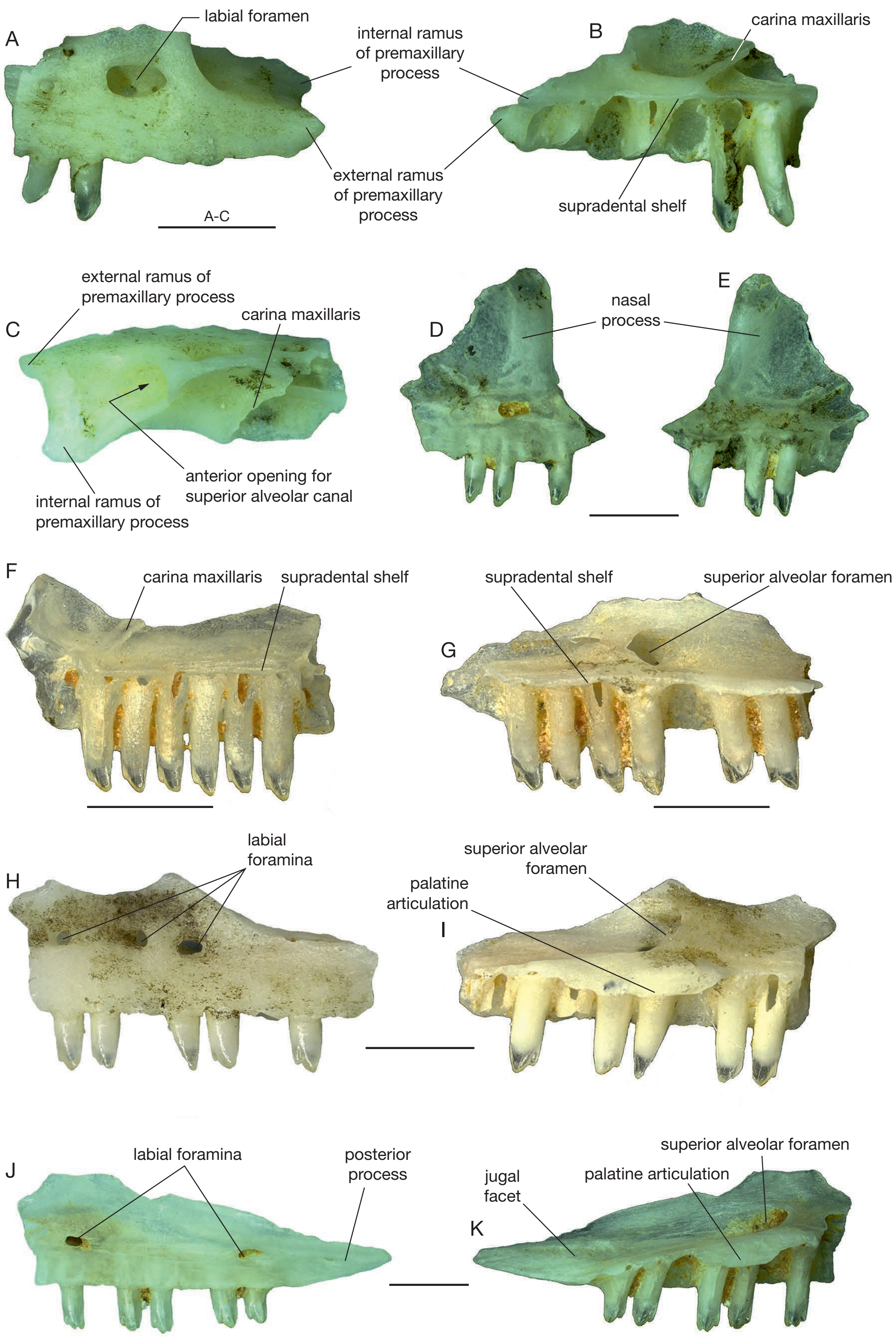

FIG. 14. — Eremiadini indet. from the upper Miocene of the locality Builtsin Khudag, section BUK-A/12-14, Central Mongolia: Right maxilla 2016/0208/0002 in **A**, lateral; **B**, medial; and **C**, dorsal aspects. Right maxilla NHMW 2016/0208/0003 in **D**, lateral; and **E**, medial aspects. Right maxilla 2016/0208/0004 in **F**, medial aspect. Right maxilla 2016/0208/0005 in **G**, medial aspect. Left maxilla NHMW 2016/0208/0006 in **H**, lateral; and **I**, medial aspects. Left maxilla NHMW 2016/0208/0007 in **J**, lateral; and **K**, medial aspects. Scale bars: 500 μm.

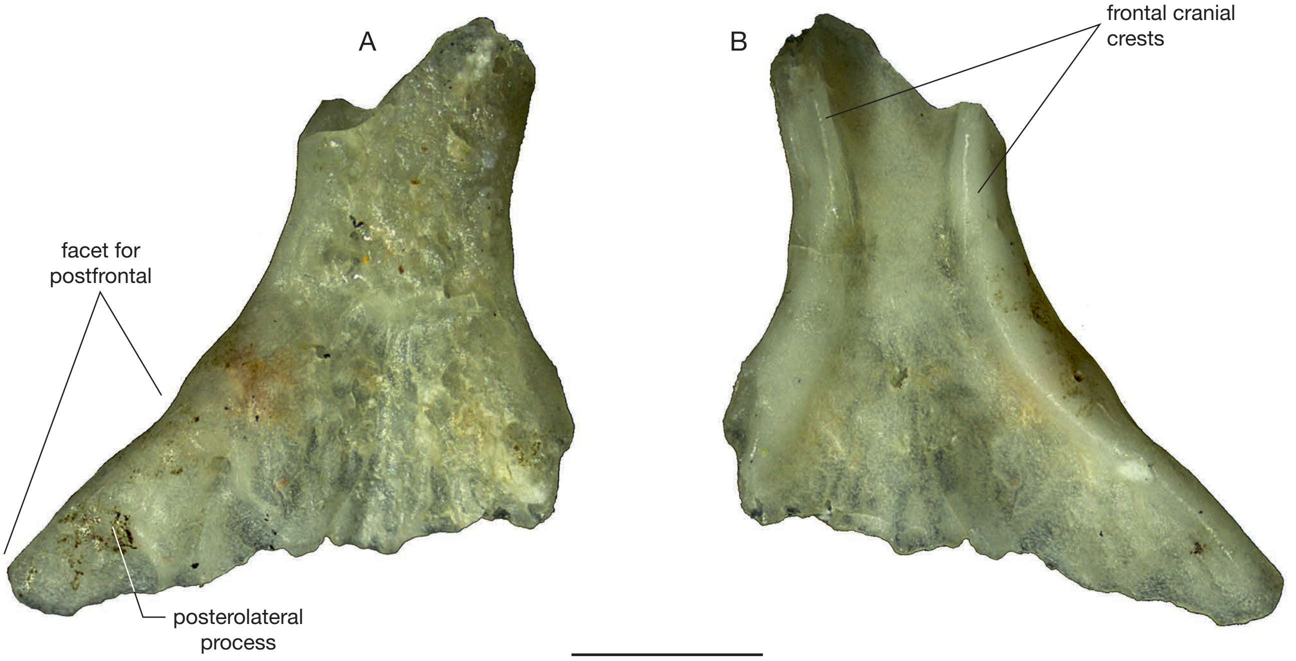

Fig. 15. — Eremiadini indet. from the upper Miocene of the locality Builtsin Khudag, section BUK-A/12-14, Central Mongolia: Frontal NHMW 2016/0208/0019 in **A**, dorsal; and **B**, ventral aspects. Scale bar: 1 mm.

EREMIADINI Shcherbak, 1975

EREMIADINI indet.
(Figs 13, 14, 15, 16, 17)

LOCALITY, HORIZON AND MATERIAL. — Builstyn Khudag; section BUK-A/12-14, biozone E, upper Miocene: premaxilla (NHMW 2016/0208/0001), four right maxillae (NHMW 2016/0208/0002-0005), two left maxillae (NHMW 2016/0208/0006-0007), four left dentaries (NHMW 2016/0208/0008-0011), four right dentaries (NHMW 2016/0208/0012-0015), three vertebrae (NHMW 2016/0208/0016-0018); frontal (NHMW 2016/0208/0019).

COMMENT
The location of the material described in the following section (below Lacertidae indet.) reflects its stratigraphic position. The lizard material described here was discovered at the Builtsin Khudag, upper Miocene and therefore is younger.

DESCRIPTION
Premaxilla

The premaxilla is unpaired, small, but robustly built (Fig. 13). It is a triradiate, T-shaped element, bearing seven tooth positions (four teeth are still attached). The ventral margin of the parapet is curved. The nasal process gradually tapers posterodorsally, but it is incomplete distally. At its base, the anterior ethmoidal foramina pierce the premaxillary body. The nasal process bears a median ridge on its interior surface. The maxillary processes are well defined, but short (relatively to those in e.g., *Lacerta viridis*; see Čerňanský & Syromyatnikova 2019). The short, weakly bilobed median incisive process is located ventral to the supradental shelf. This premaxilla bears seven tooth positions with four teeth preserved; the crowns are unicuspid, like the anterior maxillary teeth of maxillae referred to the same taxon.

Maxilla

The maxillae are poorly preserved. The description is based on several specimens in which, however, many aspects of the overall morphology can be observed. A jaw parapet supports the teeth. The total number of maxillary teeth is unknown. The premaxillary process is divided into a short external ramus and a broader, more medially oriented and slightly more dorsally developed internal ramus. A very shallow notch is present between these rami. Posteriorly to it, the oval anterior opening of superior alveolar canal is located at the base of the nasal process. The nasal process is only partly preserved, and in most specimens only its basal portion is present. One exception is NHMW 2016/0208/0003 (Fig. 14D, E), where the anterior portion is preserved. It is tall, rapidly rising dorsally behind the external naris. Its dorsal section is bent medially. The external surface of the preserved portion of the process is smooth. Its medial surface bears a posterodorsally directed ridge in anterior section, the *carina maxillaris* (*sensu* Müller 1996), which passes between the vestibulum and the cavum nasi (see Hallermann 1994). However, only its lower portion is preserved in several specimens. This ridge is directed at an angle of *c.* 45°. The supradental shelf is thin but well medially expanded. The superior alveolar foramen is located at the level between the sixth and seventh tooth position (counted from posterior). At this level, and slightly posteriorly, the supradental shelf slightly medially protrudes and bents ventrally, forming a palatine articulation. The posterior section of maxilla tapers into a pointed posterior process, so this portion is not stepped. This section bears a facet for the jugal mediodorsally. The smooth lateral surface is pierced by a series of labial foramina. The most posterior one is located at the level between the ultimate and penultimate teeth.

Frontal

Frontals are fused to form a single hourglass shaped element (Fig. 15). The central region is narrow, having concave lateral margins. Anteriorly, the frontal gradually widens. However, the further anterior portion is broken off and missing. The posterior portion of the frontal widens posteriorly. It is well laterally expanded and markedly broader than the central portion. Here, long and distinct posterolateral processes are developed. However, only the left one is complete. It is posterolaterally directed. On its anterolateral margin, an elongate facet for the postfrontal is located. It shows that the lateral margin of the frontal in the central region was not exluded from the orbital border. The suture, which forms the contact with the parietal, is only slightly interdigitated. The dorsal surface is somewhat weathered, but the shallow interfacial sulcus located posterior to the mid-orbital constriction is still visible. Posteriorly from its mid-point, the additional sulcus runs to the posterior end of the bone.

On the ventral side, the frontal cranial crests are developed. Their lateral walls are pierced by three small foramina. The cranial crests expand anteriorly. They gradually run deeper ventrally and become sharp. Although their anterior regions are not preserved, at least the root portion of the subolfactory process is preserved on the right side. In the posterior region, an indistinct triangular facet for the parietal tab is present medial to the cranial crest.

Dentary

All dentaries are incomplete (Fig. 16). In dorsal aspect, the dentary is straight with only gentle medial curvature in its anterior end. In medial aspect, Meckel's groove is fully open, but very narrow, especially anteriorly. The alveolar foramen is located at the level between fourth and fifth tooth positions (counted from posterior). The subdental shelf has a concave course. Around the symphyseal region, it is elevated. The symphysis is small and rectangular in shape. The lateral surface is pierced by a series of anteroposteriorly elongated labial foramina.

Dentition

The tooth implantation is pleurodont. The teeth are closely spaced with small interdental gaps (the gap forms only around one-fourth of the mesiodistal length of the tooth shaft). The first five dentary teeth are unicuspid whereas posteriorly located teeth are all bicuspid. The bicuspidity is distinct, with the dominant triangular, pointed and in some cases posteriorly recurved central cusp and well-developed mesial cusp. Teeth are slender. The anteriormost teeth are more anteriorly inclined compared to more posterior teeth. On some tooth bases, circular or dorsally elongated resorption pits are preserved. Based on the preserved material, the teeth in the posterior region are more robust (i.e., tooth robustness increases posteriorly). The premaxillary teeth are all unicuspid with slightly recurved crowns.

Vertebrae

The description is based on three dorsal vertebrae (Fig. 17). Differences in vertebrae might be caused by topographic and individual/ontogenetic variability. The pentagonal neural canal is large. In anterior aspect, there is a pair of foramina located close to the anterior margin of the internal wall of the neural canal. This is especially clear in NHMW 2016/0208/0017. The position of these foramina varies slighty. In NHMW 2016/0208/0018, they are located slightly deeper in the neural canal. The cotyle and condyle are depressed (this is less developed in NHMW 2016/0208/0018). The neural spine is low and markedly posteriorly inclined (such a morphology in present among members of Eremiadini, e.g., *Acanthodactylus* Fitzinger, 1834; pers. obs. of A. Č. 2018). Anteriorly, it continues as a median ridge. In dorsal aspect, the anterior margin of the neural arch forms a triangular incision. The articulation facets on pre- and postzygapophyses are large and elliptical. Zygosphene-zygantrum accessory intervertebral articulations are only incipient, weakly developed as small facets located at the base of the neural arch and continuous with pre- or postzygapophyseal articulations (character 468, state 2 in Gauthier *et al.* 2012). In dorsal aspect, the interzygapophyseal constriction is weak, shallowly developed. For this reason, the vertebrae have a broad appearance. Synapophyses are well developed, located in the anterior portion of the vertebrae. In lateral view, NHMW 2016/0208/0016 is more anteroposteriorly elongate compared to the other two. The ventral margin is concave in this aspect. In ventral aspect, there is a low median ridge running along the centrum, from the cotyle to almost the anterior border of condyle. Lateral to this ridge, subcentral foramina are located in the anterior third of the centrum. The ridge is almost absent in NHMW 2016/0208/0016.

REMARKS

Today, only three genera of the clade Lacertidae are present in Mongolia (see Munkhbayar & Munkhbaatar 2012) – *Eremias* Fitzinger, 1834 (multiple species), *Lacerta* (*L. agilis* Linnaeus, 1758) and *Zootoca* Wagler, 1830 (*Z. vivipara* (Lichtenstein, 1823)). The teeth and dentaries described here from Builstyn Khudag differ from those from the early Miocene locality Olon Ovoony Khurem (see Discussion). The dentary material from Builstyn Khudag strongly resembles members of Eremiadini, such as the extant taxon *Acanthodactylus* (see Kosma 2004), in the following respects: 1) in *Acanthodactylus boskianus* (Daudin, 1802), the first five teeth of the dentary are unicuspid and following teeth are bicuspid. In *Eremias arguta* (Pallas, 1773), four anteriormost teeth are unicuspid, whereas all others are bicuspid. In *L. agilis*, unicuspidity is restricted to the two anteriormost teeth, while tricuspidity can be observed in posterior teeth (see Kosma 2004). In *Z. vivipara*, the first six or seven anteriormost teeth are unicuspid whereas all posteriorly located teeth are bicuspid (several posterior teeth might have a tendency towards tricuspidity); 2) the teeth are slender (the slender teeth is a condition of some members of Eremiadini – in *E. arguta*, teeth are bulbous);

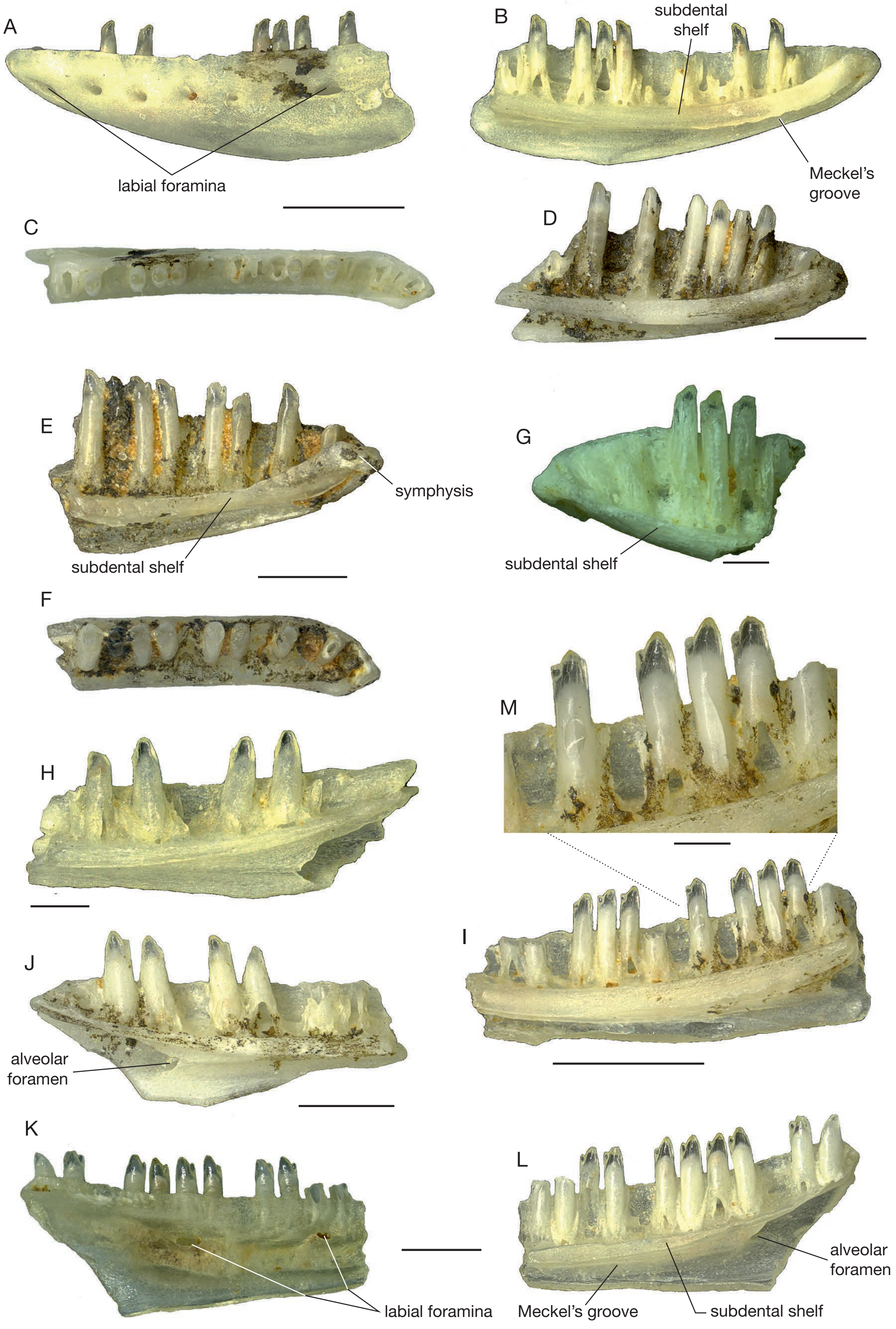

FIG. 16. — Eremiadini indet. from the upper Miocene of the locality Builtsin Khudag, section BUK-A/12-14, Central Mongolia: Left dentary NHMW 2016/0208/0008 in **A**, lateral; **B**, medial; and **C**, dorsal aspects. Left dentary NHMW 2016/0208/0009 in **D**, medial aspect. Left dentary NHMW 2016/0208/0010 in **E**, medial; and **F**, dorsal aspects. Right dentary NHMW 2016/0208/0012 in **G**, medial aspect. Right dentary NHMW 2016/0208/0013 in **H**, medial aspect. Right dentary NHMW 2016/0208/0014 in **I**, medial aspect with detail of teeth. Left dentary NHMW 2016/0208/0011 in medial **J**, aspect. Right dentary NHMW 2016/0208/0015 in **K**, lateral; and **L**, medial aspects. Scale bars: A-C, I, 1 mm; D-F, J-L, 500 µm; G, H, M, 200 µm.

3) the anteriormost teeth are more anteriorly inclined; 4) The teeth are very closely spaced, with small interdental gaps (they are much larger in *Z. vivipara* and the teeth have more robust appereance); 5) resorption pits are circular or slightly elongated in dorsal direction; 6) alveolar foramen located at the level of the fourth tooth (counted from posterior); and 7) the symphyseal region is elevated compared to the subdental shelf posteriorly (see also Evans 2008: 171, fig. 1.66). This is not so pronounced in *Z. vivipara*.

The overall morphology of premaxilla is slightly different. The premaxilla has seven teeth in *Acanthodactylus* (Evans 2008). However seven teeth are present in *Mesalina watsonata* (Stoliczka, 1872) and six or seven in *Eremias persica* Blanford, 1875 (see Khorsravani *et al.* 2011). The same tooth number can be observed in *Gallotia* Boulenger, 1916 as well, whereas in *Psammodromus* Fitzinger, 1826 and Lacertini it is nine or more (Čerňanský *et al.* 2016a).

The posterior process of maxilla is pointed, gradually narrows to its end and is not stepped. This condition is identical to that in many members of the tribe Eremiadini (see Evans 2008; Khosravani *et al.* 2011), but it contrasts with a stepped termination of this process in *Lacerta agilis*. It should be noted that non-stepped termination is present in *Zootoca vivipara* as well (see Rauscher 1992).

The frontal from the Builstyn Khudag locality shares the following combination of features with the frontals of the extant members of the tribe Eremiadini (see e.g., Evans 2008; Khosravani *et al.* 2011): 1) frontals are fused to form a single element; 2) the central region of the bone is narrow, having a distinct mid-constriction between the orbits; and 3) the suture between frontal and parietal is only slightly interdigitating.

The combination of all above mentioned features supports the allocation of the material the Builstyn Khudag locality to the tribe Eremiadini, but more precise allocation is impossible (some of the present characters states might be plesiomorphic within Eremiadini).

DISCUSSION

Early Oligocene

The great abundance of rodents and the absence of many large herbivores, according to Mellett (1968), might suggest that the Hsanda Gol area was an open country and not forested during the Oligocene (except near waterways). This is consistent with the results of Meng & McKenna (1998), which show a distinct pattern of faunal turnovers in Mongolia: perissodactyl-dominant faunas of the Eocene were abruptly replaced by rodent/lagomorph-dominant faunas of the Oligocene. They interpreted the turnovers as reflecting global climatic shifts and name the prominent biotic reorganization across the Eocene-Oligocene boundary the Mongolian Remodelling, which correlates to the European *Grande Coupure*. In contrast to mammals, Paleogene lizard faunas are poorly studied in this area. However, it appears that several taxa cross the Eocene-Oligocene boundary here: e.g., *Pseudotinosaurus* – its presence in early and late Rupelian localities shows that this taxon has more likely a continuous history in this area at least until the Oligocene, like the clade Glyptosaurinae. Glyptosaurinae is an extinct clade of anguid lizards that inhabited Asia and North America from the Cretaceous to the late Paleogene-Oligocene (Sullivan 1979; Conrad & Norell 2008; Keller 2009). In Europe they are only known during the Eocene and they disappear from the continent at the Eocene-Oligocene boundary (see e.g., Rage 2013).

It is also worth noting that anguimorph lizards have been recorded in the late Paleocene of Mongolia (Van Itterbeeck *et al.* 2007). The incomplete jaws in their figure 9 (11-13) are interesting as they show subpleurodont, recurved and pointed teeth but without plicidentine on their base. In addition, one of the teeth (Van Itterbeeck *et al.* 2007: fig. 9, no. 13) bears a huge pit on its medial aspect. This resembles condition present in the dentary from the early Oligocene of Taatsiin Gol described here (Fig. 10; although if it is related to an artifact of preservation, it is not taxonomically informative). In the Paleocene material, there is no trace of a splenial spine on the subdental shelf, but these jaws admittedly are too incomplete to assess the state of this character. In any case, if new, better-preserved materials of these forms showed their close relationship, this might represent further support for the persistence of taxa in Mongolia during the Eocene-Oligocene boundary. In addition, such features as the absence of the splenial spine among anguimorphs can be observed in many taxa, e.g., in the extant Asian taxon *Shinisaurus* as well.

Members of the clade Lacertidae are very abundant among the recovered fossil material, showing their successful adaptation to paleoenvironments of Central Mongolia. The presence of Lacertidae is mentioned in the lower Oligocene Ergiliin Zoo Formation (as *Lacerta* sp. by Alifanov 1993; however, this material was not described nor figured). Based on present knowledge, this clade is absent in older formations of Mongolia (see also Alifanov 2000). Thus, this clade appears to be a newcomer in the Oligocene of Asia. Such a story fits well with the timing of the closure of the Turgai Strait (Haq *et al.* 1987; Rögl 1999; Hou *et al.* 2011) and is highly possible. However, the poor knowledge of the Eocene lizard record in Mongolia and generally in the whole continent (fossil lizards have only rarely been reported from the Paleogene of Asia; Cleary *et al.* 2018) may throw doubts on the direction of the dispersal of these specific lineages. The clade Lacertidae is considered to have a European origin (Arnold *et al.* 2007; Čerňanský & Augé 2013; Čerňanský *et al.* 2016a; Čerňanský & Smith 2018) which is consistent with the observation of crown or near-crown lacertids in the Eocene of Europe (Borsuk-Białynicka *et al.* 1999; Čerňanský & Augé 2013) along with sister (or stem) taxa (Čerňanský & Smith 2018). However, except for *Plesiolacerta* (Čerňanský & Augé 2013), these Eocene forms disappeared at the Eocene-Oligocene boundary (see Rage 2013). Immediately after the Grande Coupure, lacertid lizards diversified during the Oligocene in Europe (see

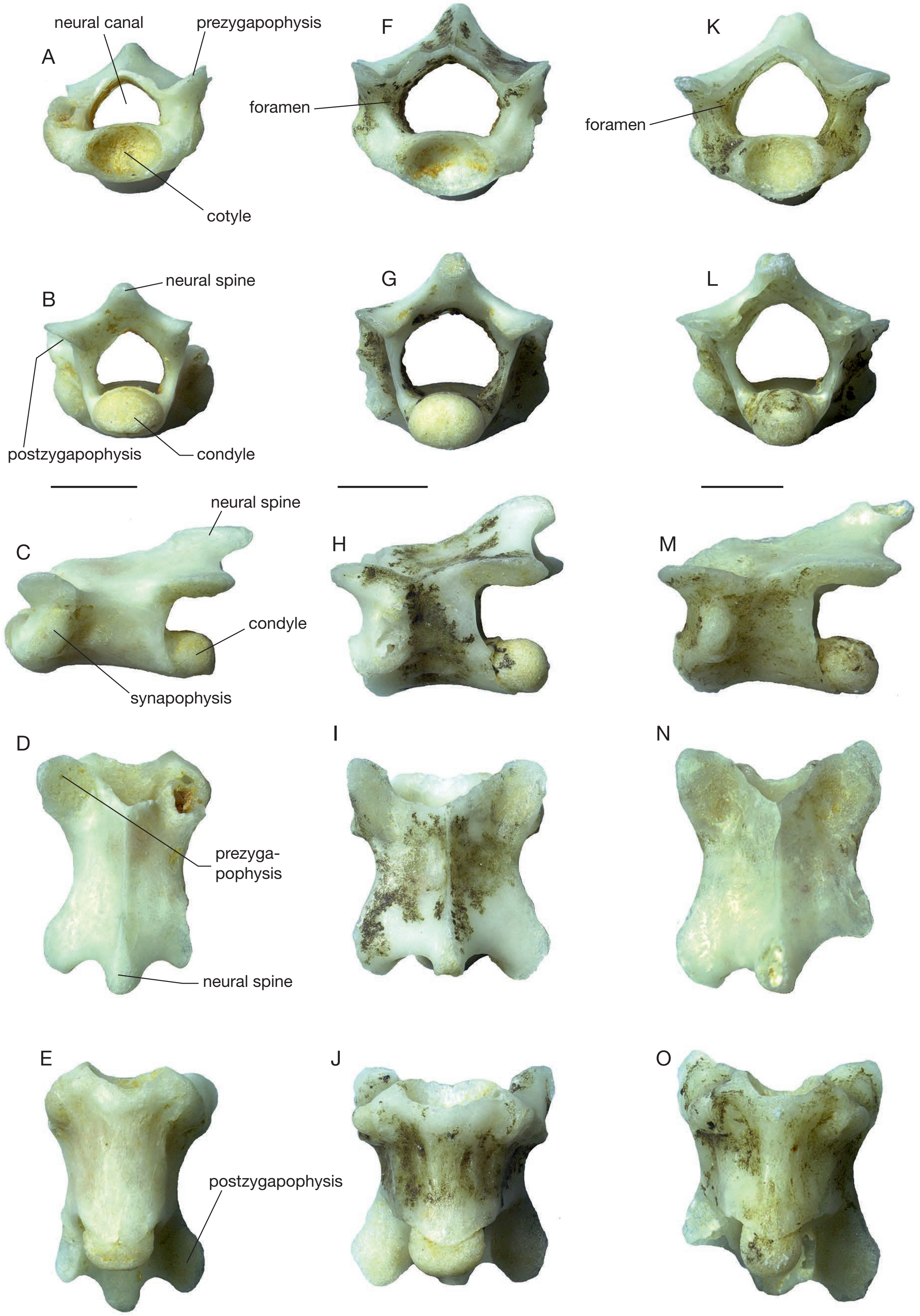

Fig. 17. — Eremiadini indet. from the upper Miocene of the locality Builtsin Khudag, section BUK-A/12-14, Central Mongolia: Dorsal vertebrae NHMW 2016/0208/0016-0018 in **A**, **F**, **K**, anterior; **B**, **G**, **L**, posterior; **C**, **H**, **M**, lateral; **D**, **I**, **N**, dorsal; and **E**, **J**, **O**, ventral aspects. Scale bars: 500 µm.

e.g., Augé 2005). However, these taxa represent different forms than the Eocene species, and it remains unknown if these new species could result from an episode of speciation in situ or if they could come from another region. Whether at least a part of the Oligocene lacertid diversity in Europe resulted from a radiation that took place in Asia is unknown. In any case, this cannot be fully excluded, based on current knowledge, mainly if the Turgai Strait did not act as an ultimate barrier before the Oligocene (see Akhmetiev & Beniamovski 2009; Akhmetiev *et al.* 2012; Godinot & de Broin 2003). Although in the Oligocene of Europe many forms with amblyodont dentition are present (see e.g., Augé 2005; Čerňanský *et al.* 2016b, 2017b), based on available material, these forms are absent in the early Oligocene of Mongolia.

In the early Oligocene of Europe, lacertids with tricuspid teeth are represented by the taxon *Lacerta* s.l. *filholi* (Fig. 18A-F) described by Augé (1988) and *Plesiolacerta* (see e.g., Čerňanský & Augé 2013). The first taxon represents the most common Oligocene lacertid and is known throughout the period in western Europe (Rage & Augé 1993; Augé 2000; Augé & Smith 2009). It should be noted that it is very plausible that this taxon does not represent the today living genus *Lacerta* and therefore is placed as *Lacerta* s.l. in the literature (see e.g., Augé & Smith 2009). The preserved fragmentary material from Taatsiin Gol left section TGL-A/2 is basically identical to this European taxon. However, interpretations of the incomplete fossil elements always need to be met with caution and therefore we decided to allocate this material as cf. *Lacerta* s.l. *filholi*. If this attribution is correct, it shows a broad paleobiogeographical distribution of this taxon, occuring from the areas from Western Europe to East Asia during the early Oligocene, with the first documented occurence in Asia during the early Rupelian (*c.* 32.5 Ma). For Lacertidae, this seems to be not so unusual even in modern ecosystems, where *Lacerta agilis* and *Zootoca vivipara* – taxa which occupy areas in Europe – occur in Mongolia today as well (Ananjeva *et al.* 2006; Munkhbayar & Munkhbaatar 2012; Uetz *et al.* 2018). Nowadays, tricuspidity also occurs in some Asian taxa such as *Takydromus sexlineatus*, where the tooth size increases posteriorly as well. However, the dentary and the dentition of this species differ from that of *L.* s.l. *filholi* in many aspects (see Fig. 18G here; Kosma 2004), e.g.: 1) the dentary is markedly narrow, long and rather straight in medial aspect (Meckel's groove is narrow almost along the entire length of the dentary); 2) the higher tooth number (28-30 tooth positions); 3) large interdental gaps; and 4) the teeth in the anterior half of the tooth row are pointed and unicuspid, whereas those in the posterior are all at once tricuspid. The size of the mesial and distal cusp is equal here, thus the tooth crown appears to be symmetrical in medial aspect.

All other fossil lacertids from Mongolia described here have bicuspid teeth. The absence of tricuspidity might indicate the presence of at least two taxa in the lower Oligocene of Mongolia. However, all this material is fragmentary, and we lack knowledge about the tooth morphology in the posterior portion of the jaws. It cannot be excluded that at least a part of the material might represent the same taxon as the material mentioned above, but there is no evidence to support it.

The persistence of several clades of Mongolian lizards across the Grande Coupure, while mammalian fauna are abruptly replaced by other assemblages (see above), gives an interesting though discordant signal. Lizards, as ectothermic vertebrates, are known to be strongly affected by climatic conditions and changes (e.g., Markwick 2002). Yet, the fate of lizards in Mongolia shows that diversity and extinction might depend not only on the physical environment but also on biological interactions (e.g., competition, synergy, dispersal). Deciphering these interactions is certainly a demanding challenge and comparisons between major faunal turnovers like the Grande Coupure in Europe and the Mongolia Remodelling may provide useful insights.

Miocene

In the studied Miocene material, only two lineages can be recognized – the possible scincid and Lacertidae. Based on the morphology of massive teeth and robustness of the preserved portion of the maxilla NHMW 2016/0204/0001, we can suggest a durophagous (or omnivorous) diet in this animal. Eremiadini can be certainly recognized at least in the upper Miocene of Mongolia, namely in the locality Builtsin Khudag. Nowadays, members of this clade are distributed in Africa and arid southwest and central Asia, where they usually inhabit desert and steppe regions (Rastegar-Pouyani & Rastegar-Pouyani 2001; Arnold *et al.* 2007). They are present in Mongolia as well – e.g., *Eremias argus* (see Zhao *et al.* 1999). The habitats of *E. argus* in coastal sand dunes are characterized by approximately 75% plant coverage and medium-sized sand grains (Kim *et al.* 2010). Their presence in the late Miocene might suggest an arid paleoenvironment. The material from the locality Builtsin Khudag differs from lacertids in the lower Miocene of the locality Olon Ovoony Khurem in the following respects: 1) the teeth are very closely spaced. The interdental gap about one-fourth of the mediodistal length of the tooth shaft in the middle of the jaw, whereas it is one-third in lower Miocene forms; 2) the teeth appear to be taller, projecting almost half their height above the jaw parapet, whereas it is only one-third in lower Miocene forms; 3) the central cusp is more pointed. Consequently, we suggest the presence at least of two different taxa in the Miocene of Mongolia. This might be consistent with the hypothesis of Arnold *et al.* (2007), who suggested a date of the separation of the Eremiadini from the Lacertini around 16 My ago, in the mid-Miocene, associated with the dispersal into Africa, where one set of xeric forms (*Eremias*, *Acanthodactylus*, *Ophisops* Ménétries, 1832 and *Mesalina* Gray, 1838) also dispersed into Asia. Rage (1976) lists *Eremias* sp. from the middle Miocene of Beni Mellal (Casablanca, Morocco) and our late Miocene Mongolian material represents the oldest evidence of the tribe Eremiadini in the area of East Asia.

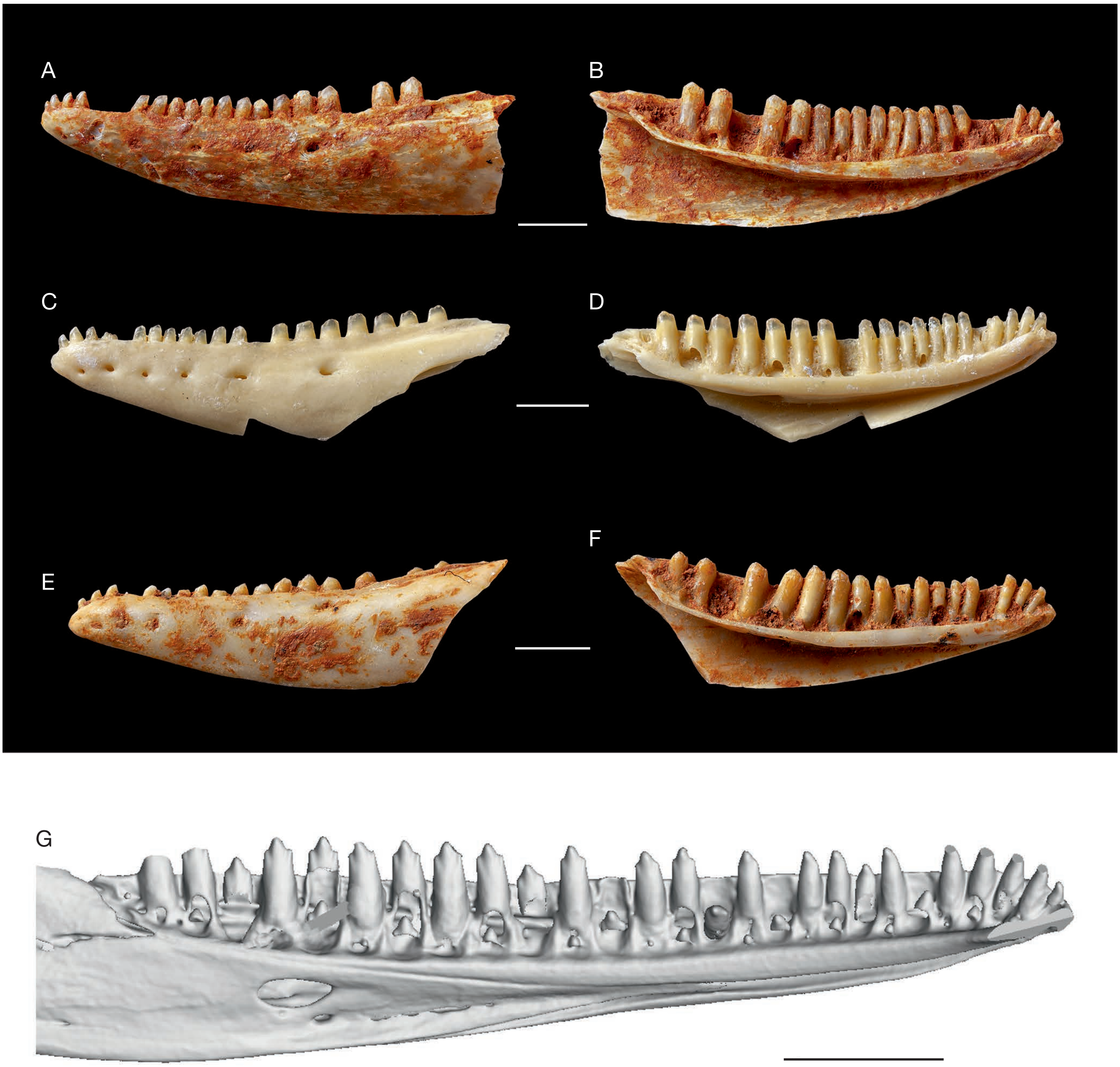

Fig. 18. — *Lacerta* s.l. *filholi* from the Oligocene of France (**A**-**F**) and the extant *Takydromus sexlineatus* (G). The holotypic left dentary MNHN.F.PFR11001 (**A**, **B**) from the locality Pech du Fraysse, left dentary UCBL 97 689 (**C**, **D**) from the locality Coderet, left dentary USTL ROQ2 441 (**E**, **F**) from the locality Roqueprune 2: in lateral (**A**, **C**, **E**) and medial (**B**, **D**, **F**) aspects. The dentary region of mandible of *T. sexlineatus* DE 134 in (**G**) medial aspect. Scale bars: A-F, 2 mm; G, 1 mm.

Although agamids are present in the Oligocene of Mongolia (see above) and several taxa inhabit the area today (see Munkhbayar & Munkhbaatar 2012) – Mongolian agama (*Paralaudakia stoliczkana altaica* (Blanford, 1875)), Toad-head Agama (*Phrynocephalus versicolor* Strauch, 1876), Sunwatcher Toad-head Agama (*Ph. helioscopus* (Pallas, 1771)) – they are absent among the Miocene material available to us. Members of the clade Gekkota are also absent in our material and thus the history of this clade in Asia remains known exclusively from Cretaceous localities (see Borsuk-Białynicka 1990; Daza *et al.* 2014, 2016). Nowadays, this clade is represented in Mongolia by several taxa (see Munkhbayar & Munkhbaatar 2012): the Caspian Even-fingered Gecko (*Alsophylax pipiens* (Pallas, 1827)), Przewalski's Wonder Gecko (*Teratoscincus przewalskii* Strauch, 1887) and Gobi Naked-toed Gecko (*Tenuidactylus elongatus* (Blanford, 1875)). This shows that many crucial aspects of the lizard evolution are still unknown in the East Asia and can be resolved only by future systematic research and studies of new material from this part of the world.

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