

The first potential fossil record of a dibamid reptile (Squamata: Dibamidae): a new taxon from the early Oligocene of Central Mongolia

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Dibamid reptiles have a known current distribution on two continents (Asia and North America). Although this clade represents an early-diverging group in the Squamata and thus should have a long evolutionary history, no fossil record of these peculiar burrowing squamate reptiles has been documented so far. The fossil material described here comes from the early Oligocene of the Valley of Lakes in Central Mongolia. This material consists of jaws and is placed in the clade Dibamidae on the basis of its morphology, which is further confirmed by phylogenetic analyses. In spite of the fragmentary nature of this material, it thus forms the first, but putative, fossil evidence of this clade. If correctly interpreted, this material demonstrates the occurrence of Dibamidae in East Asia in the Palaeogene, indicating its distribution in higher latitudes than today. The preserved elements possess a unique combination of character states, and a new taxon name is therefore erected: *Hoeckosaurus mongoliensis* sp. nov. The dentary of *Hoeckosaurus* exhibits some characters of the two extant dibamid taxa. However, the open Meckel's groove, together with other characters, show that this group was morphologically much more diverse in the past.

ADDITIONAL KEYWORDS: Squamata – osteology – phylogeny – Palaeogene – Asia.

INTRODUCTION

The clade Dibamidae represents a peculiar group of poorly known squamate reptiles that are distributed in tropical or subtropical climates. The extant members of this clade are fossorial and basically limbless (except for males that have small, flaplike hindlimb vestiges near the cloaca), with reduced eyes covered by an immovable head scale (see Greer, 1985; Grismer, 2011). This clade contains only two extant genera, *Dibamus* and *Anelytropsis*, distributed on two continents (Townsend *et al.*, 2011). Members of the genus *Dibamus* occur in scattered localities across tropical Southeast Asia (Vietnam, Cambodia, Thailand, Peninsular Malaysia, Borneo and Indonesia) and are also found west to the Nicobar Islands and east to the Philippines and New Guinea. In contrast, *Anelytropsis* is distributed in a relatively small area of northeastern Mexico (for

example, see Greer, 1985; Darevsky, 1992; Das & Lim, 2003, 2005, 2009; Das & Yaakob, 2003; Neang *et al.*, 2011; Quah *et al.*, 2017). All dibamid species are small to medium sized (*Dibamus*, snout–vent length 52–203 mm; *Anelytropsis papillosus* Cope, 1885, snout–vent length 77–180 mm), and all representatives have a small skull (5–7 mm in length; see Greer, 1985; Evans, 2008).

The systematic position of this clade and its biogeography have been enigmatic for a long time. According to molecular analyses (Townsend *et al.*, 2004; Vidal & Hedges, 2005; Wiens *et al.*, 2010; Pyron *et al.*, 2013), dibamids are an early-diverging group in Squamata, sister to all other clades either alone or with Gekkota (although there is limited anatomical support for such a basal placement in morphological data sets, for example, see Gauthier *et al.*, 2012). The stem clade is estimated to have diverged in the Mesozoic (potentially even the Late Triassic, see Vidal & Hedges, 2005; or close to Triassic/Jurassic boundary, see Simões *et al.*, 2018), but the complete absence of a fossil record is a significant knowledge gap in our understanding of their evolutionary history. For this

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reason, several authors (Estes, 1983; Townsend *et al.*, 2011) suggested that these animals most probably did not fossilize well (burrowing animals generally do not have a good fossil record, although amphisbaenians leave many more vertebrae than skull bones).

The material described here from the early Oligocene forms part of a herpetofauna that was previously discussed by Böhme (2007). Although fragmentary, the material described here represents the first potential evidence of a dibamid history in East Asia. Although fossil lizards are well documented from the Mesozoic of Mongolia (e.g. Borsuk-Biafinicka, 1984, 1985, 1990, 1991; Alifanov, 1989, 2016; Norell *et al.*, 1992, 2008; Conrad & Norell, 2006; Talanda, 2016), they are less commonly known from Palaeocene and Eocene deposits (e.g. Gilmore, 1943; Alifanov, 1993, 2009, 2012; Gao & Dashzeveg, 1999; Dong *et al.*, 2016). However, except for a possible arretosaurid described by Alifanov (2012), the evolution of lizards in Mongolia remains largely unknown during the Oligocene and Miocene. *Crythosaurus mongoliensis* Gilmore, 1943, from the Early Oligocene of the Hsanda Gol locality in the Valley of Lakes, described as an amphisbaenian, is interpreted as a snake by other authors (see Hoffstetter, 1962; Estes, 1983).

MATERIAL AND METHODS

SPECIMENS EXAMINED, PHOTOGRAPHY AND MEASUREMENTS

All material was collected during the field seasons of 1995–1997 in the Valley of Lakes in Central Mongolia (Fig. 1) by an Austrian–Mongolian expedition (see Höck *et al.* 1999). The relevant localities are Taatsiin Gol right (right side of the river Taatsiin; western plateau) and Taatsiin Gol left (for geology, topography

and stratigraphy, see Höck *et al.*, 1999; Daxner-Höck *et al.*, 2017). The lizard specimens are housed at the Natural History Museum, Vienna (Austria), prefixed under individual NHMW numbers.

Specimens were photographed under a Leica M125 binocular microscope with axially mounted DFC500 camera [LAS software (Leica Application Suite) v.4.1.0 (build 1264)]. Several specimens were imaged 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.

SPECIMENS USED FOR COMPARISONS, X-RAY MICROTOMOGRAPHY AND THREE-DIMENSIONAL VISUALIZATION

The following specimens of extant lizard species were used for comparison: *Acontias meleagris* (Linnaeus, 1758) (NHMW 10653:1); *Anelytropsis papillosus* Cope, 1885 (FMNH 100410); *Aprasia pulchella* Gray, 1839 (NHMW 18082); *Blanus strauchi* (Bedriaga, 1884) (NHMW 12311:1); *Dibamus leucurus* (Bleeker, 1860) (NHMW37479:1); *Dibamus novaeguineae* Duméril & Bibron, 1839 (NHMW10671:1); *Dibamus nicobaricum* (Steindachner, 1867) (NHMW23461:1 – holotype); *Feylinia currori* Gray, 1845 (NHMW 10664); *Ophiomorus punctatissimus* (Bibron & Bory de St. Vincent, 1833) (NHMW 23527); *Rhineura floridana* (Baird, 1858) (NHMW 12360:1); and *Trogonophis wiegmanni* Kaup, 1830 (NHMW 12380:1). All

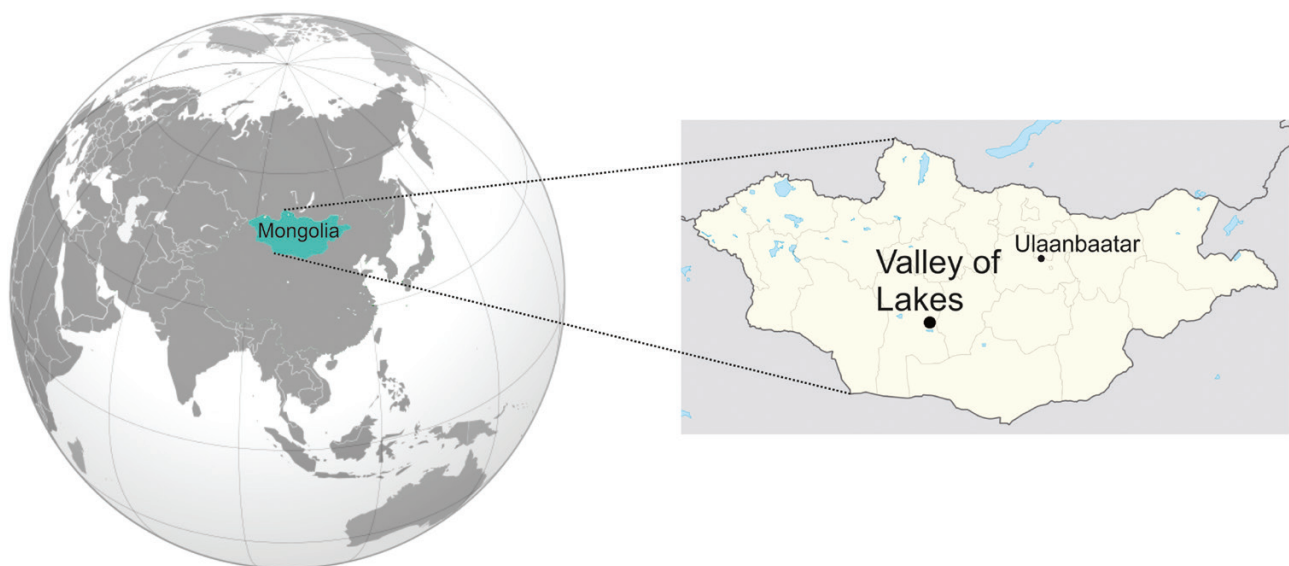


Figure 1. Location of Taatsiin Gol (the Valley of Lakes) in Mongolia.

specimens, except those of *Anelytropsis papillosus*, were scanned using the micro-computed tomography (CT) facility at the Slovak Academy of Sciences in Banská Bystrica, using a Phoenix v|tome|x L 240 micro-CT. The CT data sets were analysed using Avizo v.8.1. *Anelytropsis papillosus* was scanned using the University of Texas High-Resolution X-ray CT Facility (see Digimorph.org, 2002–2012).

Institutional Abbreviations: FMNH, the Field Museum of Natural History (USA); NHMW, the Natural History Museum Vienna (Austria).

PHYLOGENETIC ANALYSIS

A morphological data matrix (see [Supporting Information, Appendix S1](#)) was developed and modified using characters taken primarily from [Kearney \(2003\)](#); see [Supporting Information, Appendix S2](#)). Twenty-one characters of relevance for lizards and amphisbaenians were added (see [Supporting Information, Appendix S2](#)).

The matrix comprises 183 characters scored for 24 extant squamate ingroup taxa [*Acontias meleagris*, *Agama agama* (Linnaeus, 1758), *Amphisbaena alba* Linnaeus, 1758, *Anniella pulchra* Gray, 1852, *Bipes biporus* (Cope, 1894), *Blanus cinereus* Vandelli, 1797, *Cadea blanooides* (Stejneger, 1916), *Chalcides chalcides* (Linnaeus, 1758), *Cordylus mossambicus* (Fitzsimons, 1958), *Dibamus leucurus*, *Feylinia grandisquamis* Müller, 1910, *Gekko gecko* (Linnaeus, 1758), *Gymnophthalmus underwoodi* Grant, 1958, *Heloderma suspectum* Cope, 1869, *Lacerta viridis* (Laurenti, 1768), *Phrynosoma douglasii* (Bell, 1829), *Plestiodon obsoletus* Baird & Girard, 1852, *Pygopus lepidopus* (Lacépède, 1804), *Rhineura floridana*, *Shinisaurus crocodilurus* Ahl, 1930, *Teius teyou* (Daudin, 1802), *T. wiegmanni*, *Tupinambis teguixin* (Linnaeus, 1758) and *Varanus salvator* (Laurenti, 1768)], in addition to the extinct taxon represented by the Mongolian material described here. *Sphenodon punctatus* (Gray, 1842) was used as the outgroup.

The principal goal of this analysis is to understand the relationship of the Mongolian Oligocene taxon among Squamata. The data matrix was analysed using maximum parsimony as an optimality criterion in the program TNT and the NT (New Technology) search (with ratchet) and 1000 iterations ([Goloboff et al., 2008](#)). All characters were treated as unordered and were equally weighted. Support was estimated through Bremer support indices ([Bremer, 1994](#)). Mesquite v.2.75 was used to visualize all trees (build 566; [Maddison & Maddison, 2011](#)). The molecular phylogeny of [Pyron et al. \(2013\)](#) was used to constrain the ingroup relationships. The command used was: [force = (23) ((11 12) (((12 8 9 10) (((4 5 6 7 (3 (22 (17 18 19 20 21))))((13 14 15 16)(24 25)))))); constrain=;].

Hoeckosaurus was the only taxon excluded from the constraint tree, leaving it free to float. To test the results further, the phylogenetic relationships of the Mongolian taxon were also based on the character–taxon matrix of [Gauthier et al. \(2012\)](#); see [Supporting Information, Appendix S3](#)), which included 610 characters (see [Supporting Information, Appendix S4](#)).

SYSTEMATIC PALAEOLOGY

SQUAMATA OPPEL, 1811

DIBAMIDAE BOULENGER, 1884

HOECKOSAURUS GEN. NOV.

urn:lsid:zoobank.org:act:FE7BC446-89D9-49DA-B702-49865F6A83D4

Type and only species: Hoeckosaurus mongoliensis Čerňanský, sp. nov.

Etymology: The genus is named in recognition of Austrian palaeontologist Gudrun Höck, who undertook research in Mongolia and collected the type material, and from Greek σαύρα [*saura*], lizard. The epithet is derived from Mongolia, where the type specimen was collected.

Diagnosis: As for *Hoeckosaurus mongoliensis*, the only known species.

HOECKOSAURUS MONGOLIENSIS SP. NOV.

(FIGS 2–4)

2007 Squamata indet. – Böhme: p. 46, text figures 1, 2a, b

urn:lsid:zoobank.org:act:8A581C67-C0F7-4106-84AC-91406471872A

Holotype: NHMW 2007z0054/0001, an almost complete right dentary (section TGL-A/2, [Fig. 2A–C](#)); figured by [Böhme, 2007](#): text figures 1, 2a, b).

Paratypes: Right dentary NHMW 2016/0198/0001 (section TGR-ZO/2); right dentary NHMW 2007z0054/0003 (section TGL-A/2); and left dentary NHMW 2007z0054/0004 (section TGL-A/2).

Referred material: Left maxilla NHMW 2007z0054/0002 (section TGL-A/2).

Localities and horizons: (1) Mongolia, Taatsiin Gol left river side, section TGL-A/2, biozone A, lower Oligocene (early Rupelian); and (2) Mongolia, Taatsiin Gol right river side, section TGR-ZO/2, biozone B, lower Oligocene (late Rupelian).

Diagnosis: A dibamid that differs from other extant forms in the following combination of features: (1) open

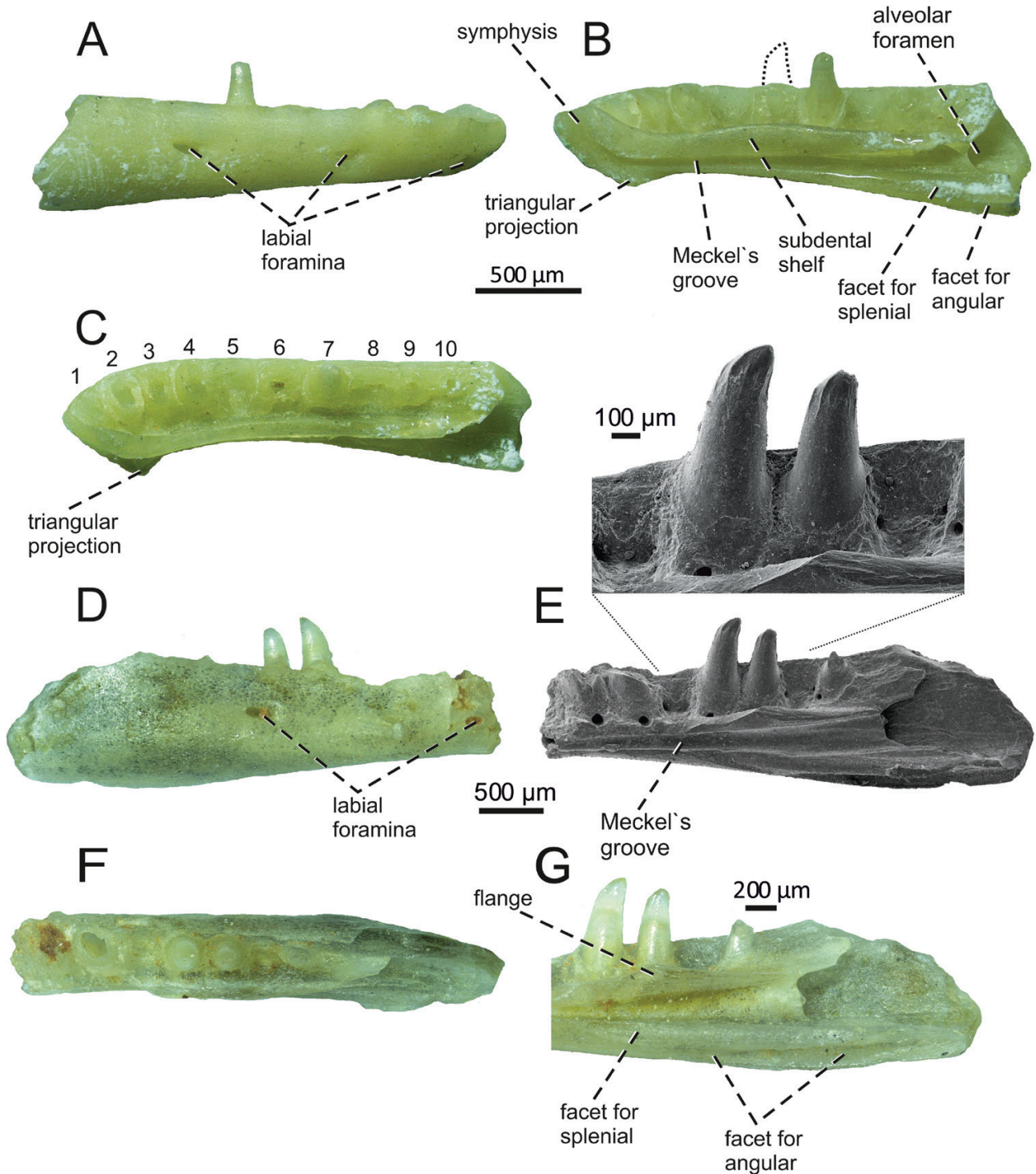


Figure 2. *Hoekosaurus mongoliensis* from the lower Oligocene (Rupelian) of Taatsiin Gol left, section TGL-A/2 (A–C) and Taatsiin Gol right, section TGR-ZO/2 (D–G). A–C, the holotypic right dentary NHMW 2007z0054/0001 in lateral (A), medial (B) and dorsal (C) aspects. D–F, paratypic right dentary NHMW 2016/0198/0001 in lateral (D), medial with detail of teeth (E) and dorsal (F) aspects. G, detail of the posterior region in ventromedial aspect. The dotted line in B indicates the missing tooth figured by [Böhme \(2007\)](#).

Meckel's groove; (2) three labial foramina; and (3) lingual side of tooth crowns bearing fine striations. Besides these features, this taxon is characterized by the combination of the following characters: (4) dentary is long and slender (if its dorsoventral size is compared with its anteroposterior length); (5) subpleurodont implantation; (6) number of teeth in dentary is ten; (7) pointed teeth that more-or-less increase in size anteriorly; (8) presence of the triangular medioventral projection on the ventral section of the symphyseal region; (9) symphyseal region is slightly angled; (10) a deep subdental shelf, forming a raised flange lingual to the dentition; and (11) an intramandibular septum along the entire tooth row.

Description

Dentary: The description is based on one left and three right dentaries. The almost complete dentary (Fig. 2A–C) from Taatsiin Gol left (NHMW 2007z0054/0001) is designated as the holotype. Its length is 3.8 mm. A specimen from Taatsiin Gol right (NHMW 2016/0198/0001) lacks the anterior region (Fig. 2D–G) but preserves more of the postdental process. The dentary is slender. The holotype specimen has preserved an entire tooth row bearing ten tooth positions. Unfortunately, only one tooth is still attached, which is the seventh, counting from anterior (in Böhme, 2007: p. 46, figs 1, 2a, b, two teeth were preserved). The incomplete specimen NHMW 2016/0198/0001 bears seven tooth positions, but three teeth are still attached (Fig. 2D–G).

In dorsal aspect, the dentary is straight, with only its anterior region slightly curved medially. In medial aspect, the dentary is slender, becoming slightly taller posteriorly. The symphyseal region is angled and dorsally elevated. The angle between the long axis of the symphysis and the posteriorly located subdental shelf is 144°. In its ventral region, the symphyseal region bears a small triangular projection that is directed ventromedially. Meckel's groove is fully open, but narrow. The alveolar foramen is large. It is separated from Meckel's groove by a vertical intramandibular septum, the end of which is fused with the bone. The septum itself extends until the posterior end of tooth row (slightly beyond the last tooth position). Ventral to it, there is a wedge-shaped facet that most probably represents the facet for the splenial. This facet reaches anteriorly to the level of the fourth tooth position (counted from posterior). Below this facet, there is a second facet that reaches to the level of the second tooth position (counted from posterior) and was probably for articulation with the angular (or compound bone). This facet forms a narrow but well-developed groove. The subdental shelf (*sensu* Rage & Augé, 2010) is straight; its medial portion forms a low, dorsally convex (rounded) edge (or flange, especially

in its mid-region). The presence of this flange is also evident posteriorly in the paratype dentaries (Figs 2G, 3B, F), although the anterior sections are broken. The posterior region of the holotype dentary (NHMW 2007z0054/0001) is broken off, but this region is partly preserved in NHMW 2016/0198/0001 (Fig. 2D–G). The posteroventral process (*sensu* Gans & Montero, 2008) is broad and well expanded posteriorly, with no indication of a bifurcation. The posterodorsal process (*sensu* Gans & Montero, 2008; = coronoid process) is broken here, but is preserved in specimen NHMW 2007z0054/0004. This process is small and slightly elevated dorsally (Fig. 3D, E), but it appears not to be preserved completely. Dorsally, the preserved portion reaches the level of the apex of the third tooth (counted from posterior).

The external surface of the holotype dentary is pierced by three large labial (neurovascular) foramina. The posteriormost one is oval (anteroposteriorly elongated). Only two foramina are preserved in NHMW 2016/0198/0001, but the anterior region is broken away and probably had the same number of foramina.

Maxilla: Only a small fragment of the left maxilla is preserved (Fig. 4). It bears two teeth, the anterior one being larger. The tooth morphology is identical to that of the dentary. The preserved lateral portion of the bone is smooth.

Dentition: The implantation is subpleurodont (*sensu* Hoffstetter, 1954, 1955), with the tooth bases ankylosed to their sockets and surrounded by a ring of bony tissue. The teeth are unicuspid and pointed, with the apex being slightly curved distally. The tooth crowns have fine mesial and distal cutting edges. A concavity at the base of the crown is present. The lingual side of the tooth crowns bears fine, almost indistinct striations (visible with scanning electron microscopy, see Fig. 2E). Although only the tooth bases are preserved for most teeth, it appears that tooth size decreases posteriorly. Based on preserved teeth and on the size of the tooth bases in dorsal aspect, the largest tooth was the second from the symphysis. Small circular resorption pits are present in some tooth bases.

Remarks

The dentary NHMW 2007z0054/0001 (TGL-A/12) was originally described by Böhme (2007: text figures 1, 2a, b) as Squamata indet. The sixth tooth, which is present in Böhme's figure, is now broken off and missing.

PHYLOGENETIC ANALYSIS

All phylogenetic trees presented here are based on limited fossil material, and more complete fossil specimens of this taxon are needed to draw more robust

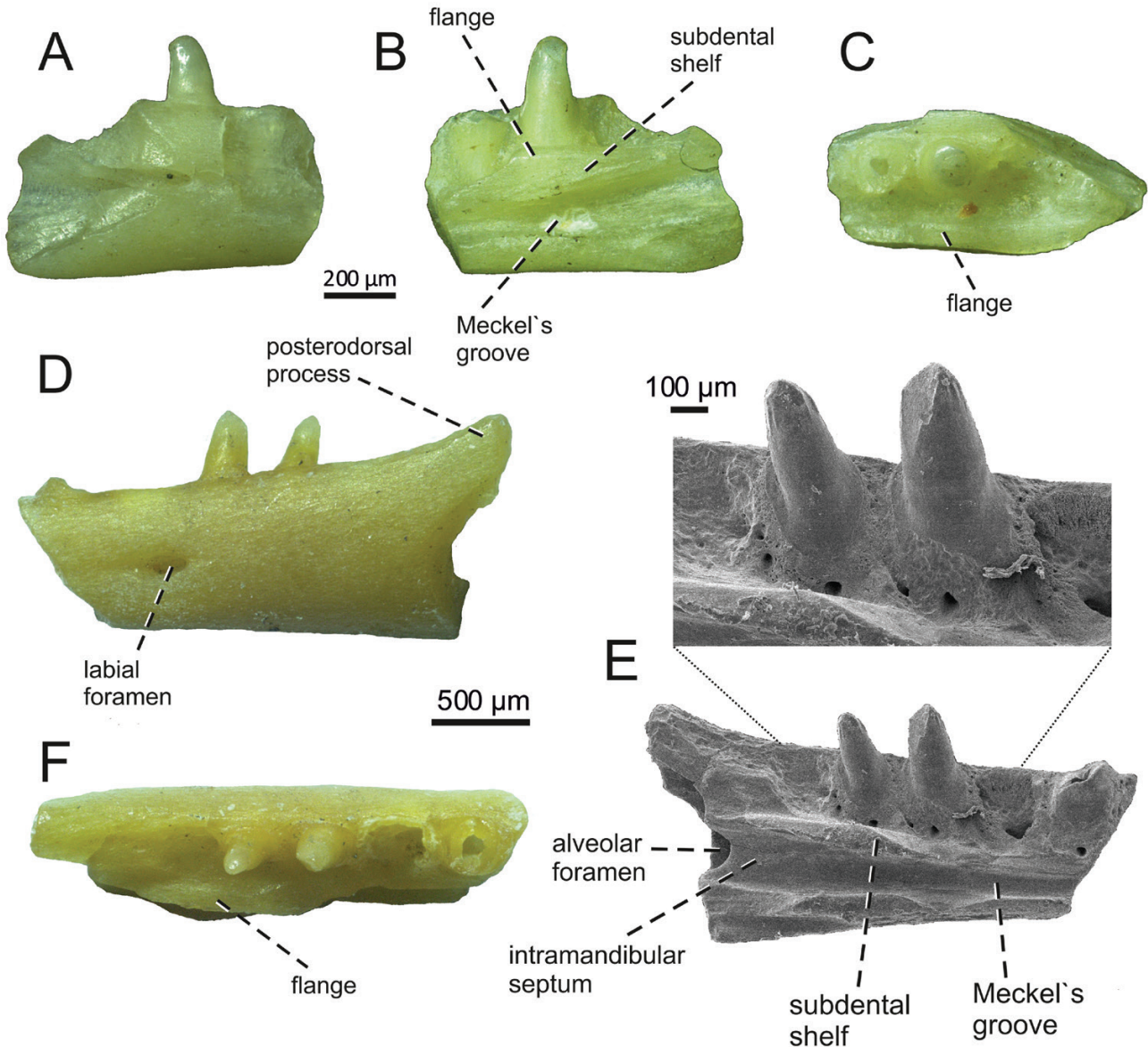


Figure 3. *Hoeckosaurus mongoliensis* from the lower Oligocene (early Rupelian) of Taatsiin Gol left, section TGL-A/2. Right dentary NHMW 2007z0054/0003 in lateral (A), medial (B) and dorsal (C) aspect. Left dentary NHMW 2007z0054/0004 in lateral (D), medial with detail of teeth (E) and dorsal (F) aspects.

conclusions. However, in all the analyses, despite the different topologies in Squamata, *Hoeckosaurus* is consistently recovered as the sister taxon to *Dibamus* (or *Dibamus* + *Anelytropsis*), forming a clade (Fig. 5).

1. In analysis 1, both heuristic and NT searches in TNT produced a single tree (Fig. 5A). This analysis groups Gekkota, Dibamidae and Amphisbaenia (Bremer value 5, relative Bremer 71). *Hoeckosaurus mongoliensis* and *D. leucurus* form a clade (Bremer value 1, relative Bremer 50; see Fig. 5B) that is sister to the Amphisbaenia (Bremer value 5,

relative Bremer 71). Gekkota is not recovered as monophyletic, but the two species included in the analysis are placed at the base of the limbless group. The analysis finds a monophyletic Scincomorpha (Bremer value 1, relative Bremer 20), placing it as sister to Anguimorpha (Bremer value 2, relative Bremer 23; this clade is called Autarchoglossa *sensu* Estes *et al.*, 1988). Iguania are sister to all other squamate clades used in the analysis (Bremer value 6, relative Bremer 40; this clade is called Scleroglossa *sensu* Estes *et al.*, 1988).

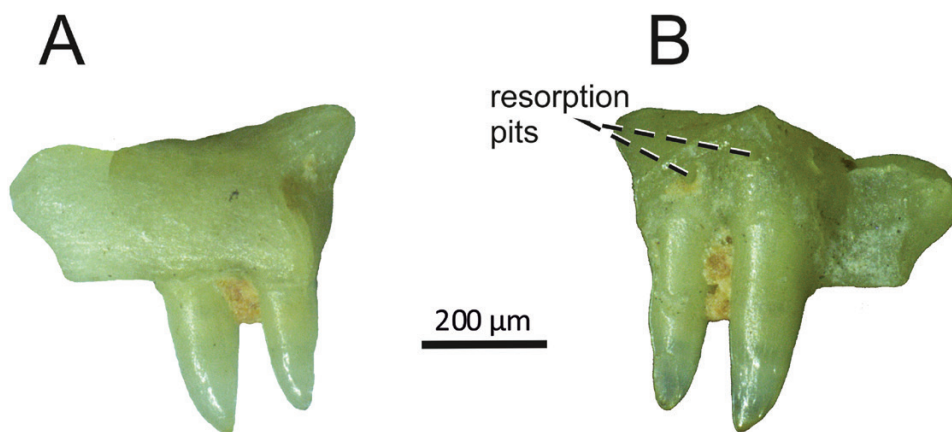


Figure 4. *Hoekosaurus mongoliensis* from the lower Oligocene (Rupelian) of Taatsiin Gol left, section TGL-A/2. Left maxilla NHMW 2007z0054/0002 in lateral (A) and medial (B) aspects.

- In this analysis, the molecular phylogeny of [Pyron *et al.* \(2013\)](#) is used to constrain the ingroup relationships. The constraint tree places *Dibamus* as sister to other squamates, with Scincoidea and Lacertoidea as separate clades and Lacertidae as sister to Amphisbaenia (and *Rhineura* as sister to all other amphisbaenians). The analysis produces a single tree, in which *Dibamus* and *Hoekosaurus* form a clade sister to all other squamates ([Fig. 5C](#)).
- In this analysis, the full [Gauthier *et al.* \(2012\)](#) matrix is used to test the relationship of the Mongolian Oligocene taxon to Squamata. The heuristic analysis in TNT supports the results of the previous analyses. *Hoekosaurus* is found to be sister to *Dibamus* + *Anelytropsis* ([Fig. 5D](#)). This analysis groups limbless squamates, such as amphisbaenians, dibamids, snakes and *Anniella*, in a single clade, as also found by [Gauthier *et al.* \(2012\)](#). It should be noted that this analysis expands on the previous results, because both extant dibamid genera are included. *Hoekosaurus* is placed on the stem of two extant dibamid taxa here.

DISCUSSION

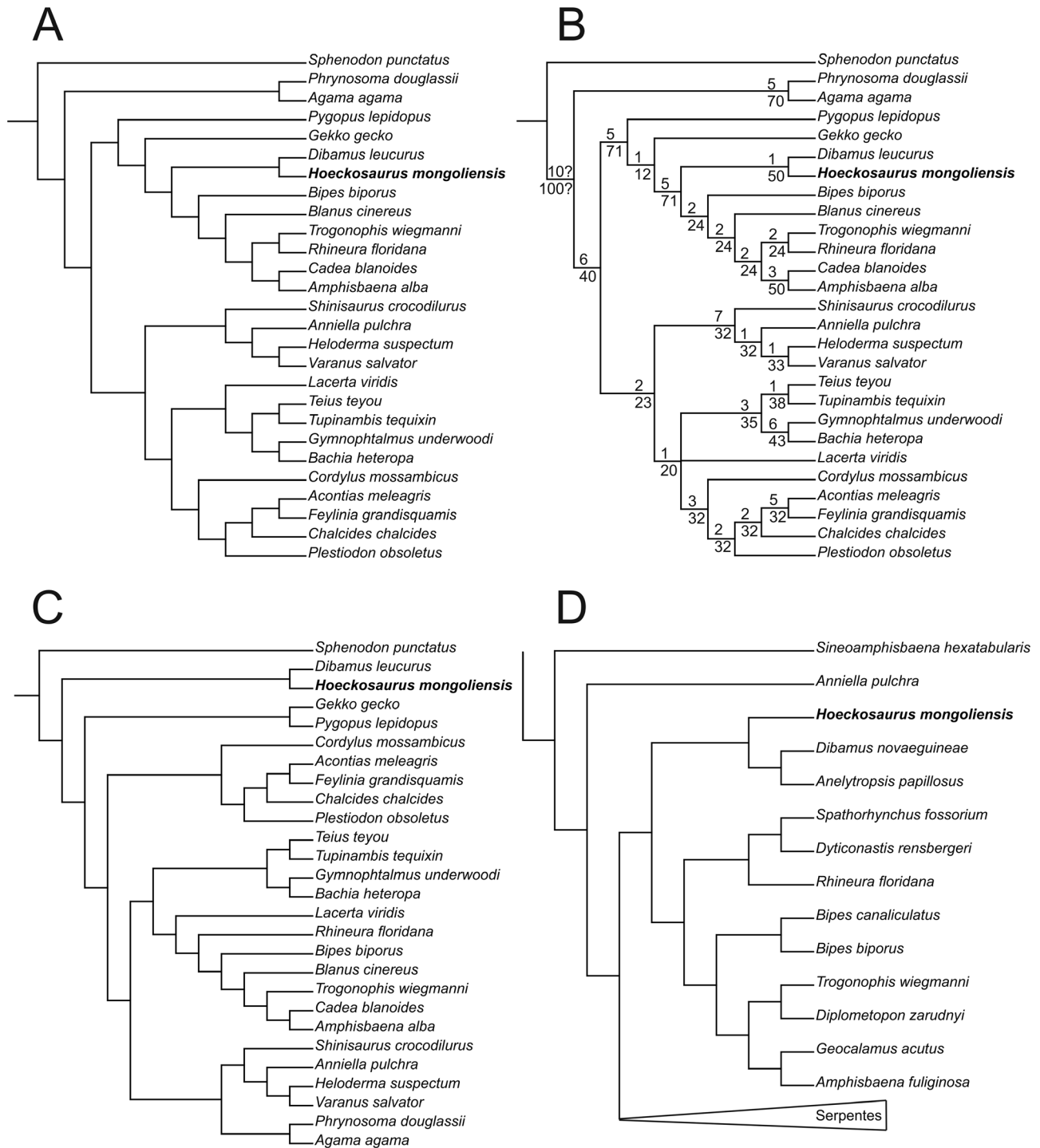
TAXONOMIC ALLOCATION

Previous suggestions

[Alifanov \(2012\)](#) mentioned the dentary figured by [Böhme \(2007: text figures 1, 2a, b; in that paper, attributed to Squamata indet.\)](#) and suggested that it might represent a new arretosaurid genus. In the same year, [Augé \(2012\)](#) suggested a possible relationship to Amphisbaenia, although he noted that the dentary was more delicately built than that of extant amphisbaenians. Indeed, the dentaries described here share the following combination of features with members of the Amphisbaenia clade: (1) an angled symphyseal region (not present in *Rhineura*

or in the Palaeocene clade Polyodontobaenidae; see [Folie *et al.*, 2013](#)); (2) subpleurodont implantation (acrodont in Trogonophiidae); (3) fully open but very narrow Meckel's groove (closed in *Rhineura* and the extinct *Spathorhynchus*, *Oligodontosaurus* or *Archaerhineura*; see [Gilmore, 1942](#); [Gans & Montero, 2008](#); [Longrich *et al.*, 2015](#); [Müller *et al.*, 2016](#)); (4) low number of teeth, compared with high number of teeth in *Arretosaurus* (see [Gilmore, 1943](#)); the presence of ten or fewer teeth is synapomorphic of Amphisbaenia (see [Smith, 2009](#); although not unique to them among squamates, see below in the subchapter *New data and comparison with Dibamidae*) [Note: the amphisbaenian skull is short and robustly built, and the reduced dentary of modern forms bears five to nine teeth (see [Kearney, 2003](#)). Ten or 12 teeth are present in members of the extinct Polyodontobaenidae from the Palaeocene of Belgium and France (see [Folie *et al.*, 2013](#)). Ten teeth are present in *Campinosaurus* and nine in *Anniealexandria* (see [Augé, 1992, 2005, 2012](#); [Smith, 2009](#)). All these taxa represent Palaeocene–earliest Eocene forms.]; (5) intramandibular septum fused to the bone and extending along the entire tooth row (see [Smith, 2009](#)); and (6) tooth crowns unicuspid and pointed, with a basal concavity (see [Smith, 2009](#)).

However, none of those character states is a unique synapomorphy of the clade Amphisbaenia. Based on detailed study of the previously figured dentary, in combination with the new material, allocation to the clade Amphisbaenia cannot be supported. There are at least two character states that do not allow such an allocation of the Mongolian material. These two character states are absent in all extant or extinct amphisbaenians (see below in the subchapter *New data and comparison with Dibamidae*; characters 7 and 9). It is more likely that similar character states are mostly related to convergent evolution owing to the fossorial lifestyle.



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Figure 5. Phylogenetic position of *Hoekosaurus mongoliensis* A, a single parsimonious tree recovered by TNT using NT (New Technology) search (with ratchet) and 1000 iterations. B, tree showing Bremer (above node)/relative Bremer (below node) values at nodes recovered by TNT. C, tree recovered by TNT using constraint based on [Pyron et al. \(2013\)](#). D, the section of strict consensus tree recovered by TNT using the matrix of [Gauthier et al. \(2012\)](#), showing the topology of *Hoekosaurus* within Squamata.

New data and comparison with Dibamidae

The dentary of *Hoeckosaurus* is similar to that of dibamids, as follows: (1) the dentary is long, slender (if its dorsoventral height is compared with its anteroposterior length, the dentary is usually short in amphisbaenians; see Kearney, 2003); (2) the dentary of *Anelytropsis* bears nine or ten functional tooth positions (11 are present in the left dentary of the specimen studied here; see Fig. 6C), and the dentary of *Dibamus* bears eight to ten tooth positions (Rieppel, 1984; Greer, 1985; although 11 can also be present; see Fig. 7); (3) the tooth size more-or-less increases anteriorly (except for the first or second anterior tooth), and this is especially true for *Anelytropsis* (and *D. nicobaricum*), and the same is estimated for *Hoeckosaurus* based on the preserved teeth and tooth bases; (4) subpleurodont implantation; (5) tooth crowns unicuspid and pointed, with a basal concavity; (6) an angled symphyseal region; (7) a strongly developed subdental shelf, with a slight dorsal elevation of the dental shelf lingual to the dentition [see Fig. 2B; this is present in dibamids (see Estes *et al.*, 1988; see also Figs 6, 7), but absent in amphisbaenians (see Estes *et al.*, 1988; Kearney, 2003; see also Fig. 8 in the present paper)]; (8) the intramandibular septum extends posteriorly along the entire tooth row (see Fig. 2B, E; for dibamids see Figs 6D, G, 7G); (9) there is no facet indicating the presence of the anteromedial process of the coronoid (the subdental shelf continues smoothly posteriorly), a state present in all representatives of both dibamid genera (synapomorphy of the clade according to Gauthier *et al.*, 2012), but absent in amphisbaenians; and (10) a long posteroventral process (estimated based on the preserved portion).

It should be noted that the dentaries of extant dibamids show the following differences from *Hoeckosaurus*: (1) absence of a separate splenial (Rieppel, 1984), i.e. the dibamid lower jaw is reduced to three bones; the dentary and the coronoid are present as separate individual elements, and there is a posterior complex consisting of a fused angular, surangular, articular and perhaps (Greer, 1985) the splenial; Gasc (1968: fig. 4) reported a distinct splenial in *D. novaeguineae*, but its presence was not supported by Greer (1985) or by the specimen studied here (Fig. 7D), and none was evident in the two other specimens available to Gasc; (2) the lateral surface of the dentary is pierced by four to seven labial foramina; and (3) Meckel's groove is closed (Rieppel, 1984). This occurs uniformly in extant members of dibamids (both taxa *Dibamus* and *Anelytropsis*; see Greer, 1985; Estes *et al.*, 1988), and this state is in sharp contrast to the early Oligocene material from Mongolia described here. However, Rieppel (1984) mentioned that traces of fusion of Meckel's groove are present in some dentaries

of *Dibamus*, and the same is true for the specimens of *Anelytropsis* and *Dibamus* studied here.

These differences between the Oligocene taxon and extant dibamids could be explained by the limited number of extant surviving taxa that form this clade: *Dibamus* and *Anelytropsis*. Thus, the possible observable morphological disparity is low. In amphisbaenians, a large and successful group of fossorial reptiles, we can also find large morphological disparity at this level (and even larger; see Fig. 8) between members of this clade (e.g. open vs. closed Meckel's groove, pleurodont vs. acrodon dentition, fusion of the postdentary bones vs. their separation; see Kearney, 2003; Gans & Montero, 2008; Smith, 2009; Čerňanský *et al.*, 2015, 2016; Müller *et al.*, 2016).

Moreover, crown striations have not been reported in dibamids, but it should be noted that there is limited detailed knowledge of their dentition. Fine striations on the lingual side of the tooth crowns can be found in some fossil amphisbaenians (see Smith, 2009: fig. 10G; Folie *et al.*, 2013: fig. 2).

COMPARISON WITH OTHER FOSSORIAL SQUAMATES

Given that it is also present in most amphisbaenians, angulation of the dentary symphysis has been associated with fossoriality (see Gans, 1974). The presence of this character in *Hoeckosaurus* suggests an adaptation to this lifestyle [but it should be noted that Gans (1974) already stated that this feature is not present in all amphisbaenians (e.g. *Amphisbaena ridleyi*; Pregill, 1984) and, in contrast, some lizards described as fossorial forms, e.g. some gymnophthalmids, seem to lack this character (see Roscito & Rodrigues, 2010)]. Support for the conclusion of the fossorial lifestyle, although indirect, might also be found in its small size. According to Rieppel (1981), small size (in particular, a small diameter of the head and body) is an important adaptation for burrowing lizards in general (smaller and narrower bodies of animals can expend less energy excavating burrows, an advantage because the energetic cost of burrowing is proportional to the amount of substrate removed; Vleck, 1981). Lizards are most probably limited to small diameters and can increase muscle mass and effective muscle cross-sectional area by increasing body length, not body diameter (see Navas *et al.*, 2004).

Burrowing is an important form of locomotion in squamates (Greer, 1991; Lee, 1998), and the evolution of a serpentiform body plan seems to have occurred frequently, but independently, in squamate lizards (Estes *et al.*, 1988; Lee, 1998). Besides dibamids and amphisbaenians, fossoriality occurs in some skinks, such as *Feylinia* or *Acontias* (for example, see Rieppel, 1981), burrowing gymnophthalmids (see Roscito &

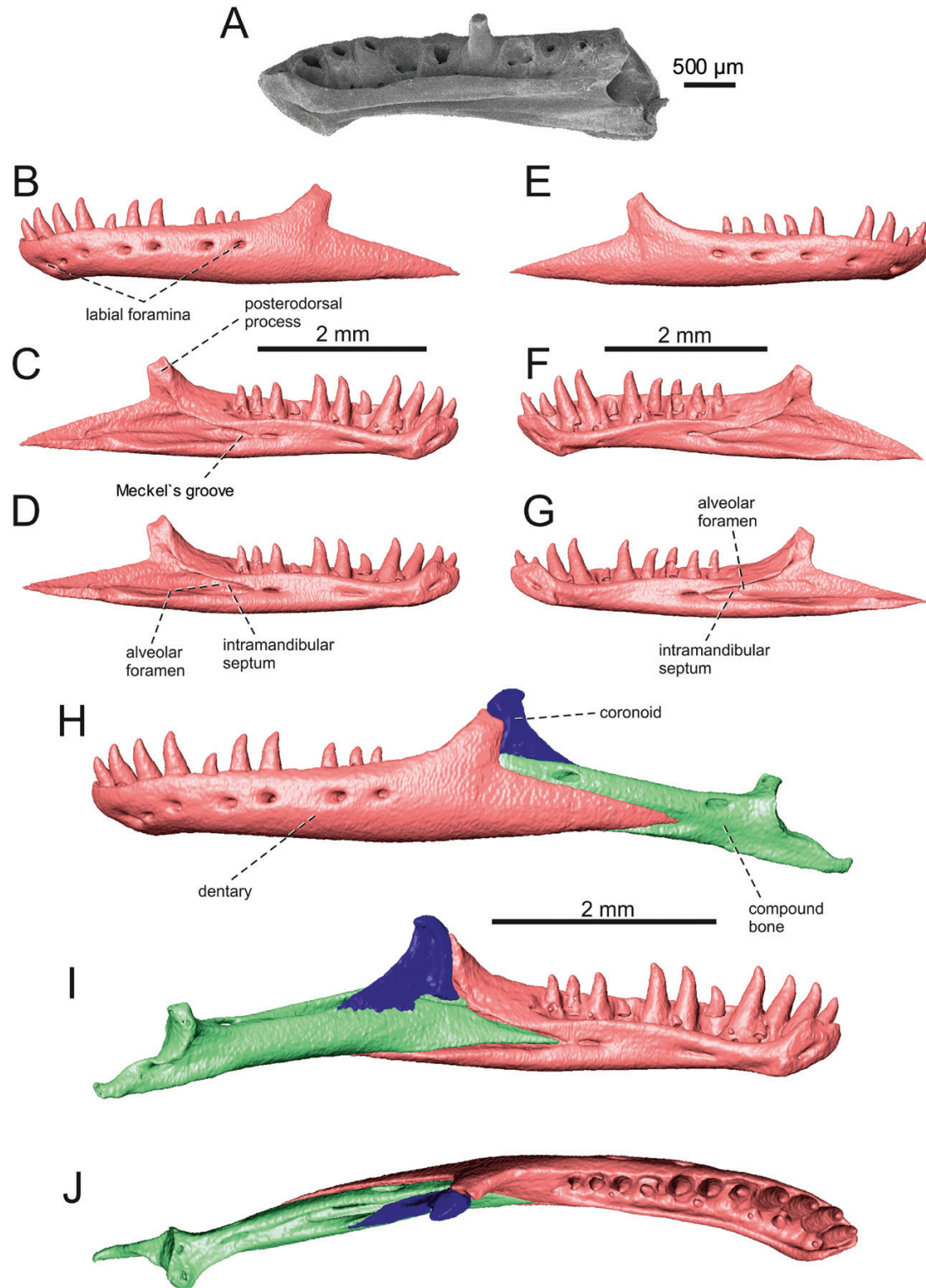


Figure 6. Comparison of *Hoechosaurus mongoliensis* (A; dentary NHMW 2007z0054/0001) with the extant Mexican dibamid *Anelytropsis papillosus* (B–J). A–G, left and right dentaries in medial (A, C, F), lateral (B, E) and ventromedial (D, G) aspects. H–J, the left mandible in lateral (H), medial (I) and dorsal (J) aspects. The pink colour indicates dentary, coronoid is represented by blue and compound bone by green colour.

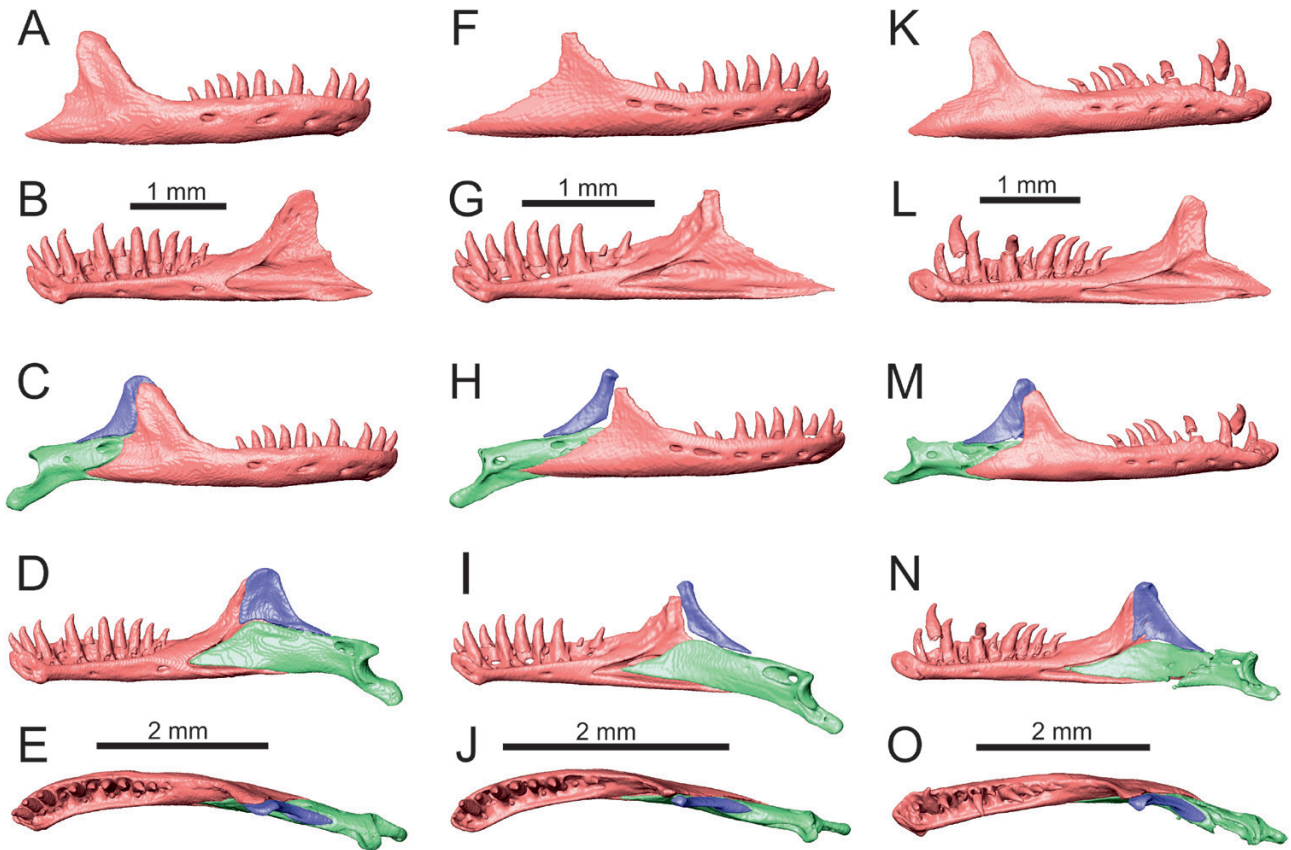


Figure 7. The selected species of extant Asian dibamids: *Dibamus novaeguinae* (A–E), *Dibamus leucurus* (F–J) and *Dibamus nicobaricum* (K–O). Right dentaries in lateral (A, F, K) and medial (B, G, L) aspects. Right mandibles in lateral (C, H, M), medial (D, I, N) and dorsal (E, J, O) aspects. The pink colour indicates dentary, coronoid in represented by blue and compound bone by green colour.

Rodrigues, 2010), blind snakes (see, e.g. Thomas & Thomas, 1978), the fossorial anguimorph *Anniella* (see, e.g. Bezy *et al.*, 1977) and/or the burrowing pygopodid *Aprasia* (see, e.g. Underwood, 1957; Webb & Shine, 1994). All these lineages are often highly convergent owing to their fossorial lifestyle, resulting in many homoplastic characters that obscure phylogenetic relationships. In phylogenetic analyses based only on morphological data, limbless squamates, such as amphisbaenians, dibamids, snakes and (in some cases) some scincids and anguids, are often placed in a single clade (Estes *et al.*, 1988; Conrad, 2008; Gauthier *et al.*, 2012), which is not supported by molecular analyses (Townsend *et al.*, 2004; Vidal & Hedges, 2005; Pyron *et al.*, 2013) or by other aspects of morphology. The taxon deletion experiments of Gauthier *et al.* (2012), in which they excluded all but one of the fossorial taxa from their data set and ran a phylogenetic analysis, deserve a comment here. By doing this for all fossorial taxa, these authors found that most of them group where one would expect them to go: *Anniella* as an anguid, pygopods with the geckos, dibamids as

scincids, etc. Recent molecular analyses using DNA sequencing suggest that amphisbaenians might be a sister group to Lacertidae (Townsend *et al.*, 2004; Vidal & Hedges, 2005), whereas dibamids are sister to all other squamates or to Gekkota (see Introduction).

Dibamus shares with the scincoid Acontinae (Acontidae *sensu* Hedges, 2014) a similar posterior extension of the dentary along the ventral and lateroventral edge of the jaw ramus (Rieppel, 1984). The dentary of *Acontias* bears 12–15 tooth positions (ten in *Acontias percivali* Loveridge, 1935), and Meckel's groove is closed (see Kosma, 2004; Hutchinson & Scanlon, 2009; Fig. 9A–C), but this might reflect the general tendency toward closure of Meckel's groove in scincids (see Greer, 1970; Estes *et al.*, 1988). Although *Feylinia* (Scincidae *sensu* Hedges, 2014) has an open Meckel's groove (Fig. 9D–F), its dentary is peculiar in having a low coronoid process (see Rieppel, 1981); 14 tooth positions are present. Both *Acontias* and *Feylinia* resemble *Hoekosaurus* in the presence of the basal concavity in the tooth crowns (see Kosma, 2004). However, the intramandibular septum of the two

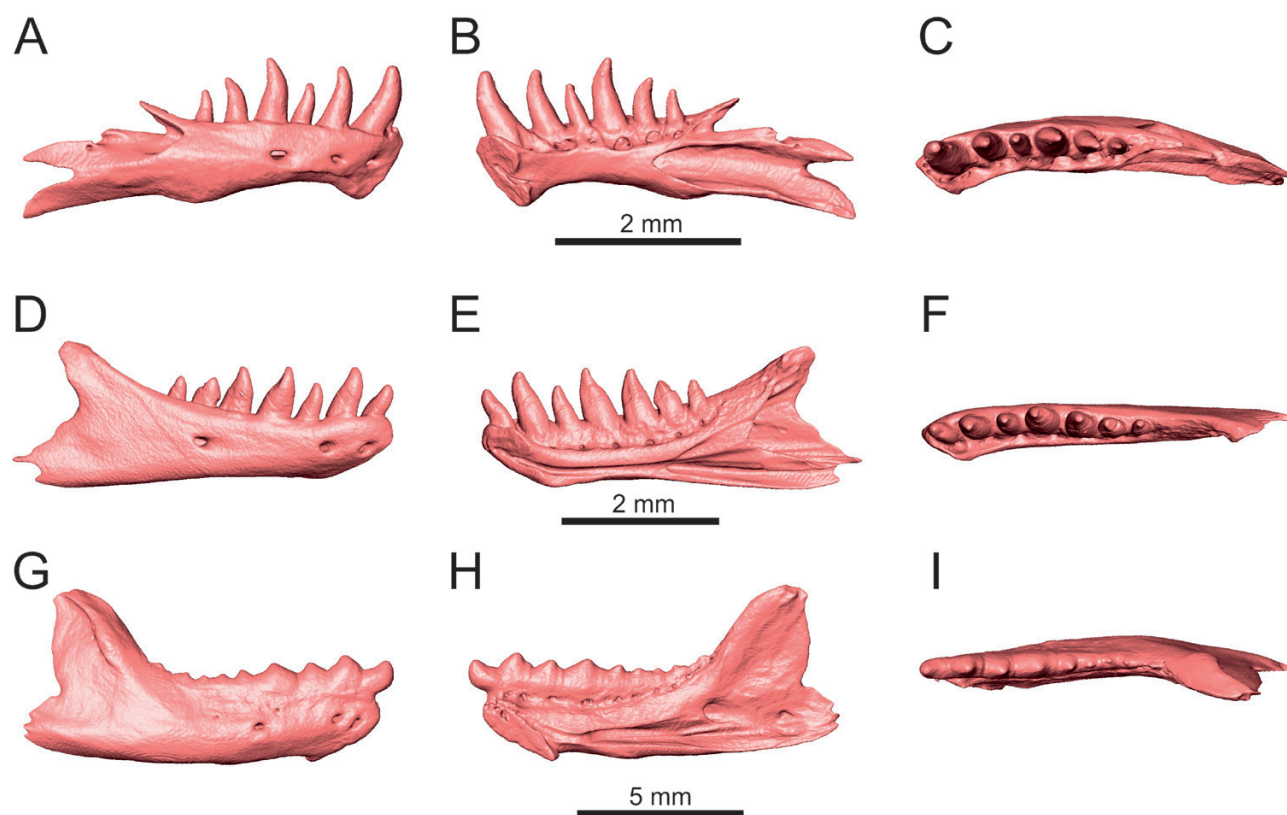


Figure 8. The morphological diversity among selected extant amphisbaenian taxa: *Rhineura floridana* (A–C), *Blanus strauchii* (D–F) and *Trogonophis wiegmanni* (G–I). Right dentaries in lateral (A, D, G), medial (B, E, H) and dorsal (C, F, I) aspects.

extant genera does not reach the end of the tooth row. The same is true for the semi-fossorial limbless skink *O. punctatissimus* (Fig. 9G–I). Moreover, the dentary of this taxon differs from *Hoeckosaurus* in the following features: (1) 14 tooth positions are present; (2) teeth are not recurved, and tooth apices are not pointed; (3) teeth are almost the same size along the tooth row (only slightly increasing in size posteriorly); (4) three well-defined posterior processes; (5) the coronoid process is dorsally elevated, reaching above the level of the largest teeth; and (6) the lateral surface of dentary is pierced by five labial foramina.

The clade Gymnophthalmidae (Estes *et al.*, 1988) encompasses a diversity of small lizards distributed throughout Central and South America (Presh, 1980; Rodrigues *et al.*, 2007). Many of them, e.g. *Nothobachia*, *Scriptosaura* and *Calyptommatus*, are fossorial, with elongated trunks and reduced or lost limbs. Although these forms share several features with *Hoeckosaurus*, such as the open Meckel's groove, presence of the splenial (but both features are primitive, hence not taxonomically useful) and slightly recurved, pointed unicuspid teeth, they can be distinguished from the early Oligocene Mongolian taxon in several aspects (see Tarazona *et al.*, 2008; Roscito & Rodrigues,

2010), as follows: (1) higher tooth number [15 teeth in *Nothobachia ablephara* Rodrigues, 1984 and *Scriptosaura catimbau* Rodrigues & Maranhão Dos Santos, 2008; 13–15 in *Bachia bicolor* (Cope, 1869); 12 in *Calyptommatus nicterus* Rodrigues, 1991]; (2) teeth more-or-less the same size along the entire tooth row; (3) coronoid process of dentary low and short; (4) presence of more than two posterior dentary processes (four in *N. ablephara* and *S. catimbau*); (5) facet for angular does not reach the level of the tooth row; (6) splenial reaches the level of fifth or sixth tooth (counted from posterior); and (7) absence of angled symphyseal region.

The pygopodids, limb-reduced geckos restricted to Australia and New Guinea (Greer, 1989), have a closed Meckel's groove (see Estes *et al.*, 1988). Moreover, the coronoid process of the dentary is absent in *Aprasia* (Fig. 9J–L) and in *Pygopus* (see Rieppel, 1984; Mead *et al.*, 2008). In *Aprasia*, the dentary is markedly curved in dorsal aspect (Fig. 9L). It retains only two (sometimes four) teeth in each ramus, whereas the maxillae are completely edentulous; *Aprasia* has the lowest tooth count among gekkotans (see Daza & Bauer, 2015).

The fossorial anguimorph lizard *Anniella pulchra* is a small (< 20 cm long), worm-like lizard restricted to

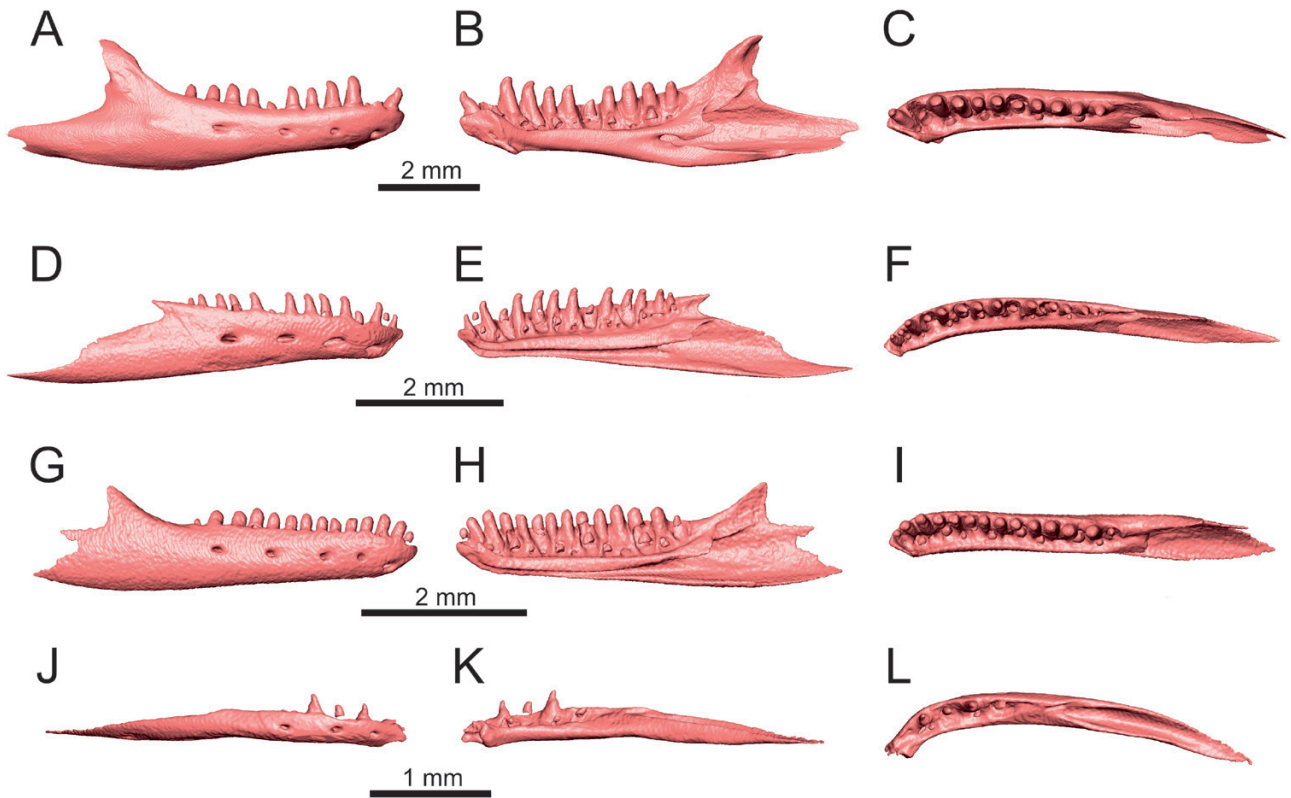


Figure 9. The selected fossorial and semifossorial representatives of Scincoidea and Gekkota: *Acontias meleagris* (A–C), *Feylinia currori* (D–F), *Ophiomorus punctatissimus* (G–I) and *Aprasia pulchella* (J–L). Right dentaries in lateral (A, D, G, J), medial (B, E, H, K) and dorsal (C, F, I, L) aspects.

California and adjacent Baja California Norte, Mexico (e.g. [Wermuth, 1969](#); [Parham & Papenfuss, 2009](#)). The dentary of *Hoekosaurus* differs from that of *Anniella pulchra* (see [Rieppel, 1980](#)) in the following features: (1) six to eight teeth rather than ten; (2) four labial foramina; (3) Meckel's groove opens more ventrally than medially; (4) subdental shelf weakly developed; (5) the presence of a splenial spine in the subdental shelf (the splenial anterior inferior alveolar foramen is located between the splenial and the dentary); (6) teeth increase in size posteriorly, except for the last two teeth; (7) small and short posteroventral process; and (8) long posterodorsal process, reaching dorsally above the level of the largest teeth.

The Scolecophidia, commonly known as blind snakes or thread snakes, are usually considered to be the sister group of other snakes. This clade includes predominantly small and fossorial forms. However, the members of this clade can be distinguished easily from *Hoekosaurus* by their extremely reduced dentary, with few teeth (e.g. five in *Leptotyphlops*) or none (e.g. *Typhlops*). Maxillary teeth are completely absent (see [Parker & Grandison, 1977](#); [Abdeen et al., 1991](#)). The morphological comparisons are in agreement with the results of the phylogenetic analyses that *Hoekosaurus*

mongoliensis cannot be allocated to any of the above-mentioned clades, except for the Dibamidae.

THE POSITION OF THE INTRAMANDIBULAR SEPTUM IN DIBAMIDS

The position of the posterior end of the intramandibular septum is particularly interesting. Its position in dibamids is described here for the first time, and it resembles the condition in modern amphisbaenians ('higher' *sensu* [Smith, 2009](#); Amphisbaenoidea *sensu* [Gauthier et al., 2012](#); a clade excluding Rhineuridae). Amphisbaenian jaws are typically shortened compared with many other squamates (see e.g. [Kearney, 2003](#)), and this shortening will certainly affect other features of the dentary, including the position of the posterior end of the intramandibular septum. However, [Smith \(2009\)](#) suggested that the combination of a reduced tooth row and a short intramandibular septum in *Rhineura floridana* showed that the length of the septum is not directly correlated with the length of the jaw. The dentaries of *Hoekosaurus*, *Dibamus* and *Anelytropis* provide further support for this hypothesis, because they show the opposite condition to *Rhineura*, i.e. the combination of a posteriorly

extended intramandibular septum and a relatively long tooth row. It should be noted that a posteriorly long intramandibular septum can also be found in the mabuyid skink, *Trachylepis laevis* (Boulenger, 1907) [but not in *Trachylepis sulcata* (Peters, 1867) and *Trachylepis gonwouoi* Allen, Tapondjou, Welton & Bauer, 2017]. This species possesses a number of highly modified skull characters that are very likely to be morphological adaptations related to its preference of rocky habitats (see Paluh & Bauer, 2017).

PALAEOBIOGEOGRAPHICAL NOTE

Dibamids have exhibited long-distance (intercontinental) dispersal. According to Townsend *et al.* (2011), the most plausible hypothesis is that they dispersed from Asia to North America (Palaeartic to Nearctic Beringian dispersal) in the Late Palaeocene to Eocene. In fact, support for this dispersal model during the Cenozoic (via Beringia) can be found in many other animals, e.g. the anguine lizard *Ophisaurus* (see Holman, 1970; Macey *et al.*, 2006; Klembara & Rummel, 2018), colubrid and viperid snakes (Burbrink & Lawson, 2007; Wuster *et al.*, 2008; Smith, 2013) and many mammals (e.g. Janis, 1993; Beard, 1998). 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). In any case, if correctly attributed, *Hoeckosaurus* provides the first evidence of dibamids in Asia by the Palaeogene. In several aspects, the *Hoeckosaurus* dentary appears more similar to that of North American representatives of *Anelytropsis* than to Asian *Dibamus*; the subdental shelf of dentary in members of *Dibamus* is more concave (or straight; bowed *sensu* Greer, 1985; only slightly convex in *D. nicobaricum*, Fig. 7L), whereas the *Anelytropsis* dentary is more-or-less convex, and the subdental shelf has a distinct dorsal flange. In fact, the overall morphology of the dentary of *Anelytropsis* in medial aspect strongly resembles that of the dentary of *Hoeckosaurus* (Fig. 6). The only major difference is the closed Meckel's groove in *Anelytropsis* vs. the open one in *Hoeckosaurus*. This character state might have evolved in an Asian ancestor of *Anelytropsis* before its dispersal to North America.

With respect to dibamid biogeography, amphisbaenians deserve a comment here. Amphisbaenians are currently distributed throughout Africa, southernmost Europe, the Middle East, South America, the Caribbean Islands and North America (see, e.g. Gans, 1998; Vidal *et al.*, 2008; Vidal & Hedges, 2009; Longrich *et al.*, 2015). However, there is a complete absence of crown amphisbaenians in East Asia. Although a systematic search of Palaeogene

localities for squamates has not yet been done (see Introduction), there is also no known evidence of amphisbaenians in this region during the Palaeogene. This period represents a particularly important time period for our understanding of the dispersal of reptiles and mammals into Asia. The Turgai Strait became dry land during the Early Oligocene (Rögl, 1999; Hou *et al.*, 2011), forming a terrestrial dispersal corridor between Europe and Asia (Haq *et al.*, 1987). This allowed the migration of many taxa from Europe to Asia (see, e.g. Alifanov, 1993; Čerňanský *et al.*, 2017). According to several authors (Akhmetiev & Beniamovski, 2009; Akhmetiev *et al.*, 2012; Solé *et al.*, 2016) the Turgai Strait was terrestrially passable before the Oligocene, and the Turgai Strait did not act as a barrier as previously thought. The Turgai region most probably allowed the dispersal of land vertebrates affected by sea level conditions and environmental changes (Godinot & Lapparent de Broin, 2003). The underground lifestyle might limit dispersal speed in amphisbaenians (Longrich *et al.*, 2015), but the biogeography of these reptiles clearly shows that this is not as much of a limitation as has been suggested. Nonetheless, there is currently no evidence of the presence of Amphisbaenia in East Asia. Although further studies of Cenozoic fossils from East Asia might yield more precise data, the presence of dibamids in Asia during the Palaeogene might have precluded amphisbaenians (at least some particular lineages) from occupying the same niches there. Today, *Anelytropsis* and *Bipes* also have disjunct distributions in Mexico (see, e.g. Johnson *et al.*, 2017), but it should be noted that amphisbaenians have not excluded Dibamidae completely from North America (although *Anelytropsis* is distributed only in a relatively small area of northeastern Mexico; see Introduction). In any case, this hypothesis needs to be met with caution and should be tested by future studies of new, more complete fossil records from Asia.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website:

Appendix S1. Updated phylogenetic matrices, in TNT file format, used for the phylogenetic analyses in this study (Kearney, 2003; plus newly added characters).

Appendix S2. Character list for phylogenetic analysis (Kearney, 2003; plus newly added characters).

Appendix S3. Updated phylogenetic matrices, in TNT file format, used for the phylogenetic analyses in this study (Gauthier *et al.*, 2012).

Appendix S4. Character list for phylogenetic analysis (Gauthier *et al.*, 2012).