



Daza, J. D., Bauer, A. M., Stanley, E. L., Bolet, A., Dickson, B., & Losos, J. B. (2018). An Enigmatic Miniaturized and Attenuate Whole Lizard from the Mid-Cretaceous Amber of Myanmar. *Breviora*, (563), [563].
<https://doi.org/10.3099/MCZ49.1>

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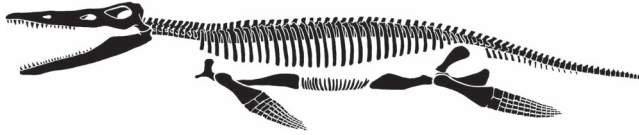
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B R E V I O R A

Museum of Comparative Zoology



US ISSN 0006-9698

CAMBRIDGE, MASS.

1 NOVEMBER 2018

NUMBER 563

AN ENIGMATIC MINIATURIZED AND ATTENUATE WHOLE LIZARD FROM THE MID-CRETACEOUS AMBER OF MYANMAR

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ABSTRACT. We report the discovery of a new genus and species of amber-preserved lizard from the mid-Cretaceous of Myanmar. The fossil is one of the smallest and most complete Cretaceous lizards ever found, preserving both the articulated skeleton and remains of the muscular system and other soft tissues. Despite its completeness, its state of preservation obscures important diagnostic features. We determined its taxonomic allocation using two approaches: we used previously identified autapomorphies of squamates that were observable in the fossil; and we included the fossil in a large squamate morphological data set. The apomorphy-based identification of this specimen, including comparative data on trunk elongation in squamates, suggests its allocation to the stem-group Anguimorpha. Results from the phylogenetic analysis places the fossil in one of four positions: as sister taxon of either *Shinisaurus crocodilurus* or *Parasaniwa wyomingensis*, at the root of Varanoidea, or in a polytomy with Varanoidea and a fossorial group retrieved in a previous assessment of squamate relationships. It is clear that this fossil has many similarities with anguimorph squamates and, if this taxonomic allocation is correct, this fossil would represent the first amber-preserved member of stem Anguimorpha ever recorded, and the smallest known member of that group. It further emphasizes the role of amber inclusions in expanding our understanding of the diversity of Cretaceous lizard communities.

KEY WORDS: burmite; Squamata; osteology; CT scans

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INTRODUCTION

Amber from Myanmar (= burmite) dated to ~ 100 Ma (98.8 ± 0.6 million years; Shi et al., 2012; Xing et al., 2018a, 2018b) has become a rich source of tetrapod fossils in the last decade, yielding frogs, albanerpetontids, turtles, theropod dinosaurs (Xing et al., 2016a, 2016b, 2017, 2018a; Evans, 2016; Matsumoto and Evans, 2018), and a large assembly of squamates including members of several major lizard clades (Gekkota, Scincomorpha, Lacertoidea, Iguania, and Serpentes) (Arnold and Poinar, 2008; Daza et al., 2016; Fontanarroza et al., 2018; Xing et al., 2018b).

Amber preferentially preserves small-bodied taxa that are likely to become entrapped in the sticky resin (Grimaldi, 1996; Poinar et al., 2008; Daza et al., 2016; Xing et al., 2018b). As such, it provides a complement to the rock record, which is biased toward larger, more robust specimens (Kidwell and Flessa, 1995; Kidwell and Holland, 2002). Amber fossils offer a unique opportunity to study fine-scale anatomical detail of specimens, including their soft tissues, which are often in an outstanding state of preservation. Computed tomography (CT) has proved to be a useful method for visualizing these structures (Polcyn et al., 2002; Castañeda et al., 2014; Fernandez et al., 2015; Sherratt et al., 2015; Daza et al., 2016), although in some fossils, such as the one described here, the organic materials have mineralized, increasing their density and reducing the contrast between soft and hard tissues (Friedman et al., 2016).

Burmite fossils provide an especially enlightening view of the early diversification of the major crown squamate clades (stem Gekkota, Scincoidea, Lacertoidea, stem Iguania, and now Anguimorpha), most of which are known or estimated to

have been present by the time these amber deposits were formed (Jones et al., 2013; Zheng and Wiens, 2016). Initial findings suggest that although many modern attributes were already present in many of these lizard clades (e.g., adhesive toe pads and paraphalangeal elements in geckos, multicarinate pectinate scales in skinks, multicuspoid teeth in lacertoideans), burmite lizards also preserve unique character combinations that are not found in closely related living representatives (Arnold and Poinar, 2008; Daza et al., 2016), which suggests that some of these fossils are outside the crown groups (e.g., a stem gekkotan in amber has unfused frontal and indication of a postfrontal and postorbital bone; Daza et al., 2016).

We here describe a new miniature lizard taxon from the amber deposits of northern Myanmar that exhibits a suite of unique morphological traits. Apomorphy-based identification and a phylogenetic analysis confirms that this fossil belongs to the Squamata and more precisely, represents a member of Pan-Anguimorpha. With current evidence, however, it is difficult to determine if it is a stem anguimorph or a member of the crown group.

MATERIALS AND METHODS

The specimen was scanned at Harvard University's Center for Nanoscale Systems using a Nikon Metrology (X-Tek) HMXST225 micro-CT system at 80 kV, 150 μ A, and a voxel size of 6.635 μ m. Tomograms were produced from the raw X-ray data using the Nikon Metrology X-Tek software suite and these tomograms were recompiled, rendered into three-dimensional (3D) volumes, and analyzed using VGStudio Max 3.0 (Volume Graphics, Heidelberg, Germany). Comparative 3D squamate material was gathered from

the University of Florida CT Morpho-source project (bit.ly/UFHerpMorph) and 2D X-ray data produced using a KevexTM PXS10-16W X-ray source and Varian amorphous silicon digital X-Ray detector PaxScanH 4030R at the Smithsonian Institution National Museum of Natural History. The external surface of the lizard and the surrounding amber were converted to stereolithography mesh files and printed at 10× size on an Objet260 Connex2 3D printer at the University of Florida's Nanoscale Research Facility. The mesh files and tomogram series are available to download from Morphosource (STL body doi:10.17602/M2/M30388 and tiff stack doi:10.17602/M2/M48144) and an annotated mesh file can be viewed at Sketchfab (<https://sketchfab.com/models/b224b29a2bda4dd7a0bbd1d0f698cbab>).

The fossil was added to a morphological data set of squamates (Gauthier et al. 2012; Longrich et al., 2012; Martill et al., 2015), of which 84 of 632 characters could be unambiguously scored (Appendix 1). The data set was analyzed in TNT Version 1.5 (Goloboff and Catalano, 2016). Trees were calculated with the command “xmult” until 50 independent hits of the most parsimonious trees were found. Each run of xmult comprised 20 independent Wagner trees with tree bisection and reconnection (TBR), followed by sectorial searches, 100 rounds of ratchet, and tree drifting. Tree fusing was applied after obtaining groups of five trees. Collapsible branches were detected using TBR branch swapping in the resulting trees from the 50 hits until the most parsimonious trees were found. The strict consensus, including this fossil, produced a large polytomy at the base of Anguimorpha; therefore we calculated the consensus tree without the fossil, and indicated the alternative positions in the trimmed consensus.

RESULTS

Systematic paleontology

Squamata Oppel, 1811

?Anguimorpha Fürbringer, 1900

Barlochersaurus winhtini, gen. et sp. nov.

Etymology. The generic name is a combination of the Latin word for lizard and the last name of Mr. Federico Barlocher (owner of the fossil); the specific epithet is a patronym, formed in the genitive singular, honoring the collector of the holotype, Mr. Win Htin.

Holotype. (Figs. 1, 2). Specimen number 8 from the private collection of Federico Barlocher, housed in Lugano, Switzerland. Amber fossils are highly collectable and many are privately held. Deposition in a private collection is consistent with Article 73C of the International Code of Zoological Nomenclature. The specimen will be made available for study to researchers by the owner and, to facilitate study, we are making available 3D printed replicas (10× size) in two publically accessible collections (Florida Museum of Natural History UF-VP-312846 and Museum of Comparative Zoology MCZ R-195109). We also are providing open access to the X-ray computed-tomography (XRCT) data and high-resolution photographs of the specimen on MorphoSource and an annotated interactive surface 3D model on Sketchfab.

Type locality and horizon. The holotype comes from the Hukawng Valley, northern Myanmar (Tanaing, Myitkyina District, Kachin State). Burmese amber deposits are estimated to date close to the Albian–Cenomanian boundary between the Early and Late Cretaceous.

Description. The new fossil is nearly complete, with only small portions of the tail missing (Figs. 1A–C, 2), but the almost uniform density of soft tissues and bone in

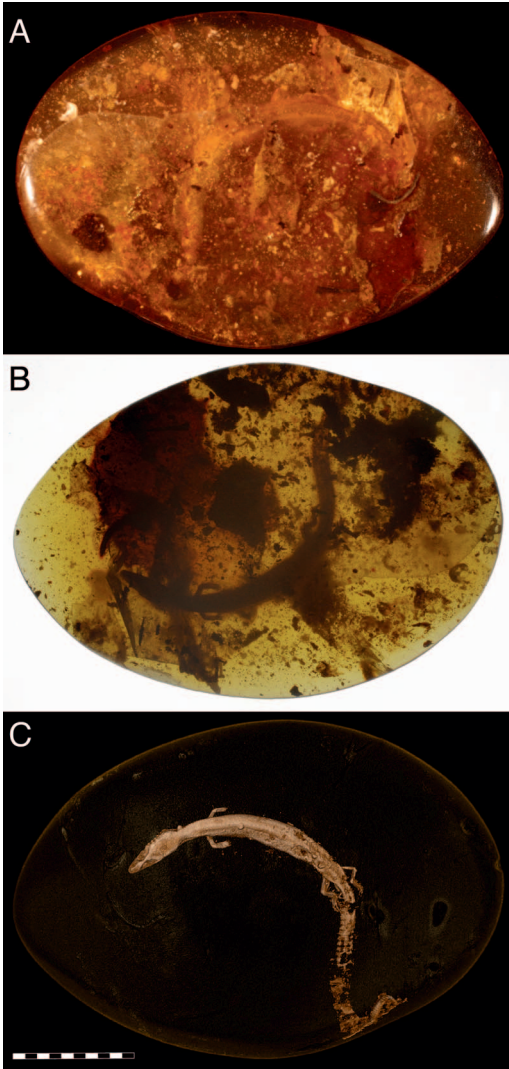


Figure 1. Holotype of *Barlochersaurus winhtini* (Federico Barlocher collection 8) in situ in polished burmite. A, dorsal view, incident light; B, ventral view, transmitted light; C, high-resolution computed tomography specimen showing its dorsal view.

the specimen makes it difficult to distinguish structures in the CT scans. The tomograms show the soft tissues of the fossil to be highly dense, consistent with permineralization.

The body of the specimen is fusiform and the limbs are pentadactyl but small, especially the forelimbs, where the digits of the manus are subequal and parallel oriented. The head and trunk combined are subequal to the tail length. There is a slight constriction in the neck region, following the head (Fig. 2). The tail is broad for nearly all its length, dorsoventrally compressed, and tapers gradually in its last quarter. The digital model derived from XRCT (Figs. 1C, 2, 3) reveals a whole animal (snout-vent length [SVL] 19.1 mm), with a long (4.8 mm), narrow head, short forelimbs (left side 2.3 mm) and digits, hind limbs more than 1.5 times as long as the forelimbs (left side, 3.6 mm), and tail nearly as long as the SVL (18 mm). The body is covered by smooth scales (Fig. 1A, C), which are imbricate on the head and trunk. Little detail of the head scalation is visible, except for the temporal scales, which are arranged in rows of four or five large scutes. In the right postocular region, there are three flattened shields extending laterally from the parietal region; these shields seem to be a fold of skin that has been divided. A maximum of seven longitudinal rows of enlarged, smooth, elongate, oval to hexagonal, juxtaposed to weakly imbricate scales are visible across the dorsum from the nape to the sacrum. Scales are smallest on the well-demarcated neck region and largest in the mid-dorsal line of the posterior half of the body. The rectangular ventral scales of the trunk are larger than the corresponding dorsal scales. In the mid-section of the abdomen, about 15 scales encircle the body. The scales near the tail base are imbricate and mucronate dorsally, and rounded and partially imbricate ventrally. The tail is covered by a series of circumferential whorls of scales, each of which overlaps those of the whorl immediately following. The distal edges of the lateral caudal scales are raised and curved

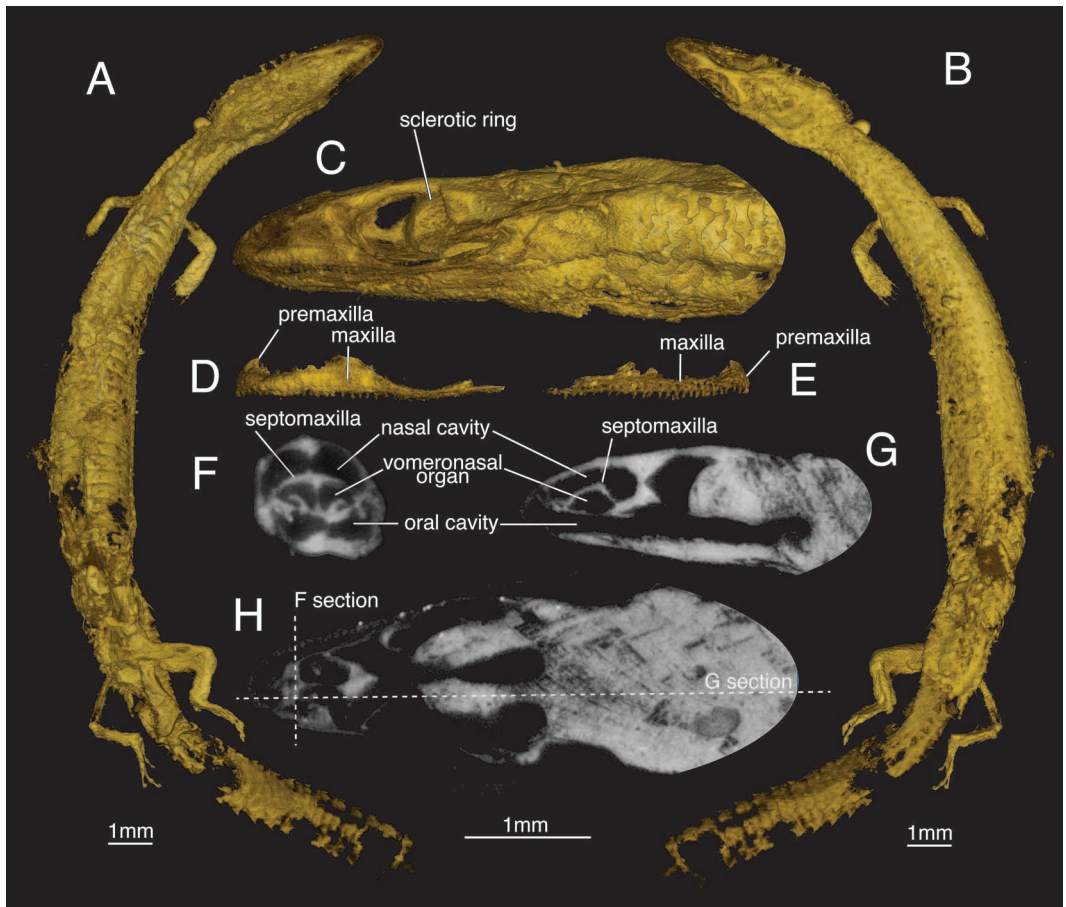


Figure 2. Three-dimensional (3D) reconstruction of specimen number 8 from the Federico Barlocher collection. A, ventral view; B, dorsal view (distal portion of the tail not rendered); C, lateral view of the head; 3D reconstruction of a fragment of the premaxilla (pmax) and left maxilla (max) in D, lateral, and E, medial view; F, transverse section; and G, sagittal section at the level of the vomeronasal area; H, frontal section showing a portion of the vomeronasal and palatal regions.

outward relative to the surface of the tail (Fig. 2A, B), resulting in an apparent series of spines along the margins of the tail as seen in dorsal view. It is unclear if the mode of preservation has resulted in the flattening of such spines elsewhere, or if raised distal scale margins encircled the entire tail in life.

The skull of *Barlochersaurus* is elongated, with an extended and laterally compressed snout (Fig. 2B). In lateral view the head is bullet shaped, with a tall rostrum (Fig. 2C).

The premaxilla has a well-developed and posteriorly tapering internasal process (ascending nasal process). The premaxilla has eight tooth loci; premaxillary teeth are smaller than the anterior maxillary teeth (Fig. 3A). The maxilla has a tall facial process with a steep angle in the narial process (Fig. 2C, D). The osseous nares are large and anteriorly located; the nasal bones are poorly delineated, but appear to be reduced and very thin (Figs. 2B, 3A). It is

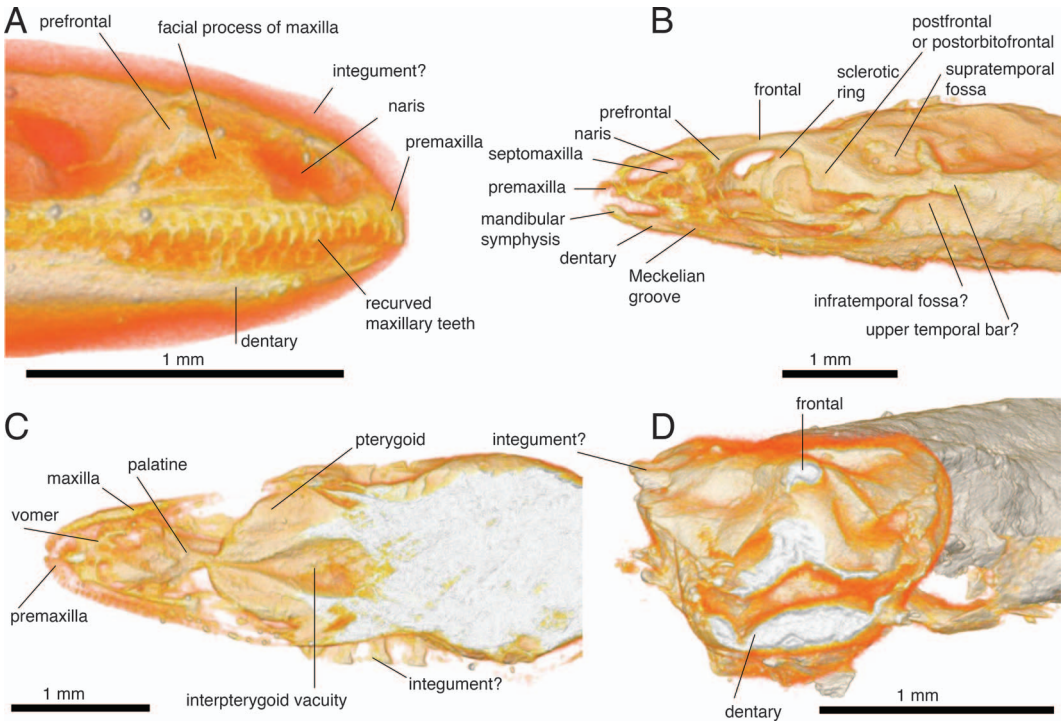


Figure 3. Volume reconstructions using high-resolution computed tomography images of the head of *Barlochersaurus winhtini*. Different color map values were used to dissolve some of the tissue and to reveal details of the skull. A, lateral view of the left side of the snout; B, lateral view of the right side of the head, with a sagittal cut to expose the anatomy of the nasal cavity and vomeronasal organ; C, ventral view of the head with horizontal section to expose the palate and remove the lower jaw; D, anterior view with transverse cut to reveal details of the frontal bone.

possible that the osseous naris might have extended posteriorly toward the frontal, although not as far as in varanids (Conrad et al., 2008). The maxillary tooth row is long (approximately 20 tooth loci), and extends beyond the posterior edge of the orbit (Fig. 2C–E). Teeth are unicuspid and recurved and they have expanded bases, and decrease in size posteriorly. In both the premaxilla and the maxilla, teeth are on the medial side of tooth-bearing element (i.e., pleurodont), and the interdental space is large, more than one tooth position in width (Figs. 2D, E, 3A). There is a prominent septomaxilla that is domed and suggests that it roofs a large cavity for a divided vomeronasal organ

(Figs. 2F, G, 3B). The anterior margin of the septomaxilla is not sutured anteriorly to the maxilla, but contacts the dorsal surface of the maxillary palatal shelf. The vomer is wide and platelike. There is no indication of vomerine, palatine, or pterygoid teeth (Fig. 3C). The tongue is preserved but its anterior tip is not clearly rendered by the XRCT. The pterygoids are fully separated, narrowly so anteriorly and widely posteriorly (Fig. 3C). The circumorbital bones include the frontal (dorsally), prefrontal (anteriorly), maxilla (ventrally), jugal (posteriorly), and a postorbital or postorbitofrontal element in the posterodorsal corner. It is possible the postorbital bar was complete, but this

structure is embedded in the jaw adductor muscles and cannot be resolved (Fig. 2C). The eyes are retracted posteromedially; the orbit is large and the scleral ring is preserved inside of both orbits (Fig. 2C). The eyes are rounded and although the separate scleral ossicles cannot be determined and numbered, the scleral ring indicates the approximate size of the eye and the maximum area occupied by the iris. The frontal is hourglass shaped and extremely slender in the mid-orbital region, and is overlapped anteriorly by the nasals (Fig. 2B). The frontal is a fused element that is open ventrally (not closed beneath the olfactory tracts to form a tubular structure; Fig. 3D). The only bone bounding the orbit dorsally is the frontal, and in the posterolateral corner a single element seems to be present, which might correspond to the postorbitofrontal or post-orbital (Fig. 2C). The frontonasal suture is distinctly narrower than the frontoparietal suture; the latter seems transverse, and might be indicative of mesokinesis, a distinctive trait of squamates (Frazzetta, 1962; Arnold, 1998; Metzger, 2002). There is a depressed area posterior to the frontoparietal suture, but it is unclear if it represents a parietal fontanel or a collapsing of the parietal table. The presence of a parietal foramen could not be confirmed. The skeleton seems to be well ossified, because there is no indication of epiphyseal plates (at least in the individual tomographs), which is indicative of skeletal maturity (Maisano, 2001), but this observation is not conclusive since cartilage might be also permineralized, rendering a continuous mass that includes bones and soft tissue.

The neck (distance between the shoulder and the occiput) is elongate in comparison with most lizards, but less so than in varanids, which have nine cervical vertebrae, one more than most other limbed squamates (Gilmore, 1928; Estes et al., 1988). Elongation of the neck can occur by increasing the number or

size of the cervical vertebrae, or both. In *Varanus* and *Saniwa*, a long neck seems to be a consequence of both, since they have an extra cervical vertebra and longer cervical vertebrae than the anterior dorsal vertebrae (Hoffstetter and Gasc, 1969; Rieppel and Grande, 2007). The trunk region is elongated and shows indication of preserved thoracic ribs, especially in places where there is some degradation of the musculature (Fig. 2A). At least 33 articulated trunk vertebrae are visible in areas where the body walls are degraded, whereas in the cervical and lumbar regions myomere counts suggest 7 to 11 additional segments; the ribs are joined to the synapophyses, and some have a very short proximal tuberculum.

The tail is moderate in length (presumed intact length roughly comparable with head and body length) and somewhat constricted at the base. It expands distally to approximately the width of the trunk posterior to the neck and appears depressed (Fig. 1C). There is no evidence of vertebrae in the majority of the tail.

The limbs are small and pentadactyl with short propodial, epipodial, and autopodial segments and small but well-developed claws. The manus is symmetrical, with digits I and V subequal and much shorter than digits II–IV; digit III is slightly longer than II and IV, which are subequal (Fig. 2B). Pedal digit V is offset from the remaining digits, and digit IV is the longest, followed by III and V, which are subequal; II is considerably shorter, and I is reduced to a nubbin. All pedal digits end in a tall, laterally compressed unguinal phalanx.

Taxonomic allocation. *Barlochersaurus* is identified as a squamate reptile on the basis of the following observable synapomorphies:

1. pleurodont or subpleurodont tooth implantation (Rieppel, 1994; Fig. 2A–E).
2. frontoparietal suture more or less transverse (Estes et al. 1988; Fig. 2B).

3. frontoparietal suture wider than the nasofrontal suture (Rieppel, 1994; Fig. 2B).
 4. gastralia absent (Rieppel, 1994; Fig. 2A).
 5. fused premaxillae (Estes et al., 1988, Gauthier et al., 1988).
 6. septomaxilla contributes to the nasal cavity and roofing of the vomeronasal organ (Estes et al. 1988; Fig. 2F, G).
 7. vomeronasal organ completely separated from the nasal capsule, with potential space for the fungiform body (Gauthier et al., 2012; Fig. 2F, G).
 8. pterygoids separated by a conspicuous interpterygoid vacuity (Estes et al., 1988, Gauthier et al., 2012; Figs. 2H, 3C).
 9. pedal digit V is offset from the remaining digits (Estes et al., 1988).
5. high number (~20) of maxillary tooth loci (e.g., *Saniwa*, Fig. 2D, E) (Rieppel, 1980).
 6. absence of a tubercle on the medial surface of the retroarticular process (Conrad, 2008).

Barlochersaurus differs from some extant varanoids in that the maxillary tooth row does not extend posteriorly below the orbit (Rieppel, 1980; Conrad, 2008; Evans, 2008; Conrad et al., 2011a), and it does not show a notable reduction of tooth loci, which is extreme in helodermatids (Pregill et al., 1986; Conrad et al., 2011b); additionally, platynotans have relatively tall teeth, in contrast to the relatively small (low) teeth of *Barlochersaurus*.

Considering presacral vertebral counts of living and extinct squamates (Hoffstetter and Gasc, 1969), the range of *Barlochersaurus* (34–42) matches only six major groups (Fig. 4; the cordylid *Chamaesaura*, the gerrhosaurid *Tetradactylus*, some skinks [e.g., *Amphiglossus*, *Ctenotus*, *Chalcides*], two groups of fossil marine/aquatic reptiles traditionally allocated to the Anguimorpha [mosasaurs and dolichosaurs], and some extant anguimorph families [Diploglossidae, Helodermatidae, Lanthanotidae]). Using this character in combination with other observed features (see below), we favor its identification as a stem-anguimorph lizard. Features present in some anguimorph groups supporting this interpretation are:

1. more than 26 presacral vertebrae (Estes et al., 1988).
2. lateral border of frontals strongly constricted between the orbits (e.g., Xenosauridae, Fig. 2B).
3. tooth crowns recurved (Rieppel, 1994) (Fig. 2D, E).
4. external nares elongated posteriorly (platynotans, Fig. 2B, C).

Phylogenetic position (Fig. 5). Results from the phylogenetic analysis places the fossil in one of four positions: as sister taxon of either *Shinisaurus crocodilurus* or *Parasaniwa wyomingensis*, at the root of Varanoidea, or at a polytomy with Varanoidea and a previously retrieved artificial fossorial group (Gauthier et al., 2012), including most limb-reduced lineages except pygopods and *Pseudopus apodus*. The amount of missing data might explain the rogue behavior of this taxon; nonetheless it does support affinities with the Anguimorpha (*sensu* Gauthier et al., 2012). Although in our analyses the Mosasauroidae was not recovered near snakes (Pythonomorpha), we also discuss the similarities of *Barlochersaurus* with some mosasauroids based on selected shared characters.

Diagnosis. A small lizard (SVL 19.1 mm) with a long tail and small limbs. Limbs short and pentadactyl, body attenuate and fusiform with head–trunk length and tail length subequal, head covered by large scutes. Manual digits short, subequal, and parallel oriented. Hind limbs and digits on the pes longer than those of forelimb. Cervical region (shoulder–occiput distance) elongate (a common phenomenon in attenuate squa-

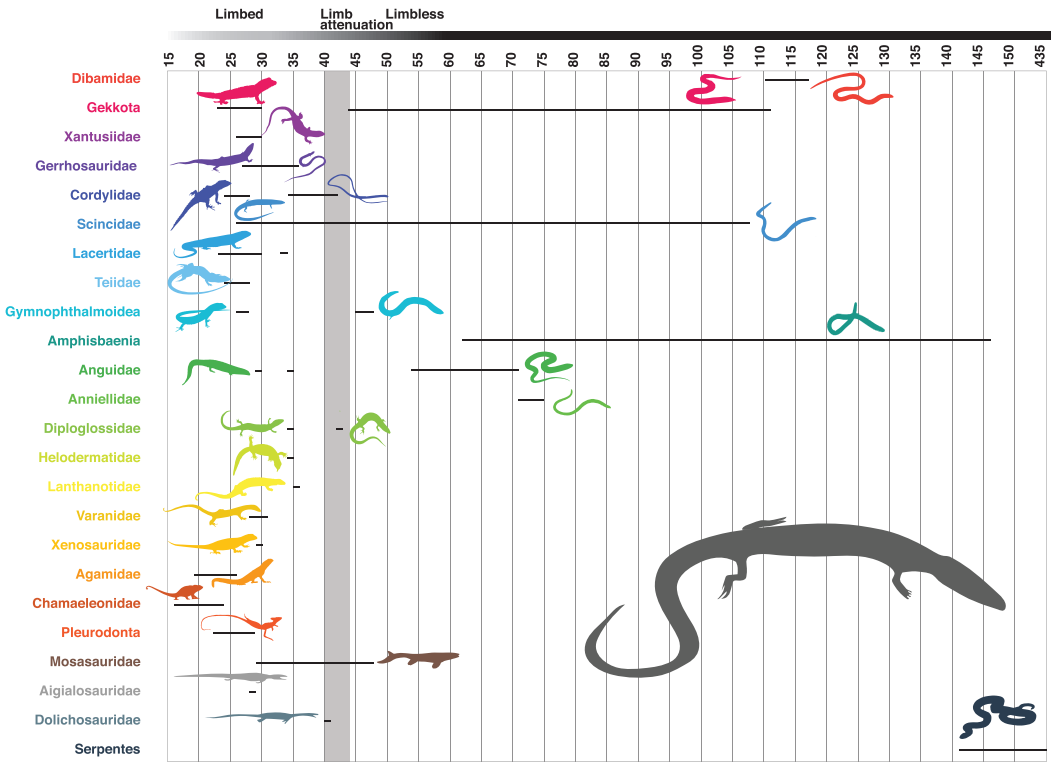


Figure 4. Presacral vertebra counts of squamates. The gray bar indicates the estimated range for *Barlochersaurus*. The limbed-to-limbless transition is well documented by Scincidae; at approximately 40 presacral vertebrae, limbs become strongly reduced in size, and limb loss is evident in forms with 50 presacral vertebrae or more. Silhouette of reconstructed *Barlochersaurus* in life in gray.

mates [Caldwell, 2000]). It differs from many Cretaceous fossil anguimorphs (Estes, 1983; Borsuk-Bialynicka, 1984) in having a very narrow frontal at the interorbital region (but see the larger form *Paravaranus*). *Barlochersaurus* is much smaller than the Lower Cretaceous lizard *Jucaraseps* (estimated SVL 27 mm [Bolet and Evans, 2012]) and, although both forms have increased presacral counts, *Barlochersaurus* has a higher estimated number (42 ± 2 , based on countable vertebrae in the trunk and estimation based on myomeres in the cervical and lumbar regions), as well as more highly reduced limbs and digits and a narrower head, especially across the snout.

DISCUSSION

Among reptiles, 24 presacral vertebrae seems to be the plesiomorphic number, but among squamate clades this number has increased in multiple lineages (Hoffstetter and Gasc, 1969; Tschopp, 2016), especially in groups with reduced or lost limbs (Fig. 4); chameleons are the only group where there is a marked tendency toward reduction (Estes et al. 1988; Hoffstetter and Gasc, 1969; Fig. 4). The number of vertebrae becomes extreme in limbless squamates, but when limbs are present but reduced, vertebral counts are intermediate (Hoffstetter and Gasc, 1969). An increased number of vertebrae in limb-reduced lizards is a feature that has evolved

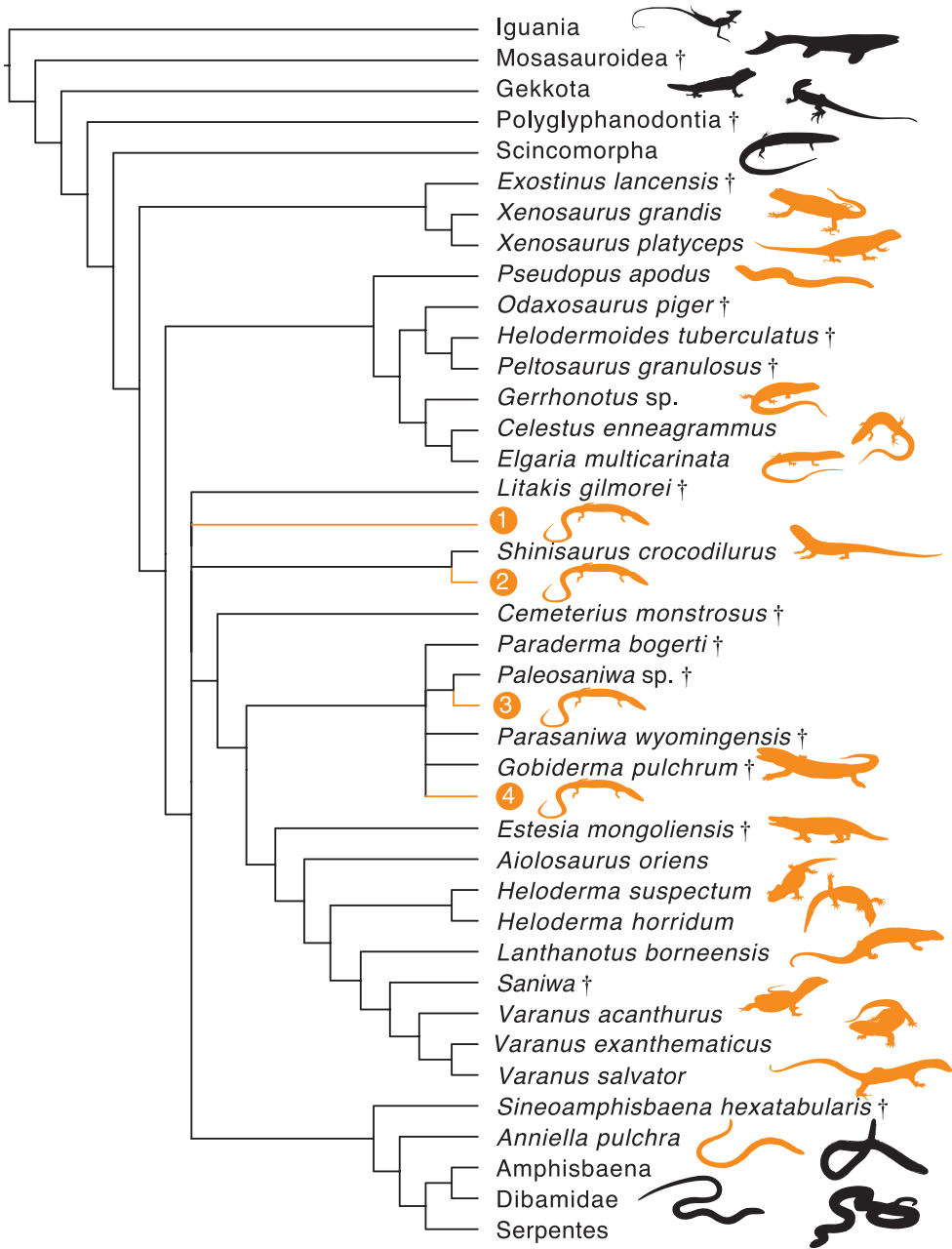


Figure 5. Alternative phylogenetic position of *Barlochersaurus winhtini* among squamate reptiles. The tree is a strict consensus of 1,200 most parsimonious trees calculated without *Barlochersaurus winhtini* and the four different retrieved positions of the fossil indicated *a posteriori*. Silhouettes in orange indicate all the traditional anguimorph groups. Daggers indicate fossil taxa.

repeatedly among the clade Bifurcata (Fig. 3). Within Bifurcata, skinks have proved to be most predisposed to attenuation, with multiple lineages independently evolving both limb reduction and increased number of vertebrae (ranging from 26 to 107 presacral vertebrae; Hoffstetter and Gasc, 1969; Gauthier et al., 2012).

The body plan of *Barlochersaurus* resembles that of many skinks and anguimorphs, with a long trunk, and small but not structurally reduced limbs (Fig. 2). *Barlochersaurus* cannot be unambiguously allocated within Bifurcata, but it shares many synapomorphies with anguimorph lizards and three of four positions in our phylogenetic analysis support this placement. In contrast, other candidate groups, such as skinks, lack the elongated neck, possibly posteriorly extending osseous naris and highly constricted frontal bone exhibited by this fossil.

The earliest widely accepted anguimorph is the Late Jurassic *Dorsetisaurus* (148 Ma, Estes, 1983). However, if we regard snakes as the sister clade of Anguimorpha (Jones et al., 2013), anguimorphs must be at least as old as the Middle Jurassic putative snake *Eophis* (167 Ma; Caldwell et al., 2015). Several Early Cretaceous fossils have been identified as anguimorphs (Evans and Manabe, 1999; Evans and Wang, 2005; Fernandez et al., 2015). *Dorsetisaurus* is also recorded from the Early Cretaceous, and only a few other forms have been suggested to represent potential anguimorphs in the first half of the Cretaceous. For example, *Meyasaurus* (Conrad, 2008; Richter, 1994) is one, but its relationship to the anguimorph stem has been considered tentative by others (Evans and Bolet, 2016). A diversity of more definitive anguimorphs, including varanoids (*Paraderma*, Pregill et al., 1986) and members also attributed to Monstersauria (*Gobiderma* and *Estesia*, Conrad et al., 2011a,

2011b), are known from the Late Cretaceous.

Early and Late Cretaceous squamate faunas frequently contain forms with morphological adaptations to an aquatic environment, probably related to the development of shallow seas (associated with a rise of the sea level) and to high sea-surface temperatures (Rage, 2013) and the favorable conditions for fossilization that these conditions provide. These include “aigialosaurs,” “dolichosaurs,” and closely related forms, all considered nonmosasaurid pythonomorphs (Caldwell, 2000; Rage and Néraudeau, 2004; Simões et al., 2017). Although these forms resemble *Barlochersaurus* in having elongated bodies and attenuated limbs, they are readily distinguishable on the basis of their evident adaptations to an aquatic lifestyle (including pachyostosis, paddlelike limb, and very long necks, among others). Of these groups, *Barlochersaurus* is most similar to aigialosaurs in having moderately elongated necks and a frontal bone roofing most of the orbit, but it lacks many distinctive features of aigialosaurs, such as moderately large size, well-developed limbs and fingers, pterygoid teeth, procoelous trunk vertebrae with condyles exposed ventrally instead of being completely covered by the following centrum (Dutchak and Caldwell, 2009), and compressed caudal vertebrae with elongate, posteriorly angled neural and hemal spines (Carroll and deBraga, 1992).

Moreover, the paleoenvironment of the locality and the entrapment in amber, as well as the small size of the specimen, are incompatible with an interpretation of *Barlochersaurus* as an aquatic pythonomorph. Nonetheless, even if *Barlochersaurus* was a terrestrial lizard, it cannot be ruled out that it might belong to a group sister to aquatic pythonomorphs. Besides this aquatic radiation, which would ultimately give rise to the large mosasaurs, many of the main extant

groups of terrestrial anguimorphs were already known in the Late Cretaceous (Simões et al., 2017).

Most Jurassic and Cretaceous taxa that have previously been assigned to Anguimorpha fall into one of the following categories:

1. forms that share a suite of characters with crown anguimorphs, but that present a unique combination of characters, possibly suggesting that they are stem members of the group.
2. members of an aquatic radiation (i.e., mosasauroides, considered by some to be anguimorphs [Lee, 1997; Conrad et al. 2011a] contra Gauthier et al., 2012) that are easily identifiable on the basis of adaptations to an aquatic lifestyle.
3. forms identifiable as members of the particular clades within Anguimorpha, including Late Cretaceous varanoids from Asia (Borsuk-Bialynicka, 1984) and Europe (Houssaye et al., 2013); North-American anguils, xenosaurs, and platynotans (Longrich et al., 2012); and a putative xenosaur from Europe (Pérez-García et al., 2016).

Of the three options, *Barlochersaurus* belongs to the first group.

Difficulties in identifying Cretaceous lizards are not restricted to anguimorphs. The phylogenetic position of many Early Cretaceous forms is highly unstable despite being based on multiple complete and well-preserved specimens (e.g. *Scandensia*, *Meyasaurus*, *Dalinghosaurus*; Evans and Wang, 2005; Bolet and Evans, 2010, 2011). This is perhaps not surprising given the present conflict between molecular and morphological trees that suggest problems with morphological characters related to homoplasy (Losos et al., 2012) as revealed by the lumping of all reduced limbed taxa (except pygopods) into a single, although obviously

polyphyletic, fossorial group (Gauthier et al., 2012).

In our phylogenetic analysis, the position of *Barlochersaurus* is unstable, presumably due to the high number of missing characters. The removal of such rogue taxa generally improves overall tree node stability (Reeder et al., 2015). Despite the ambiguity of its affinities, we find the combination of anguimorph synapomorphies present in *Barlochersaurus* compelling evidence of its probable relationships.

The rarity of amber-embedded anguimorphs is not surprising; amber is typically a preservation filter that entraps predominantly small organisms (Arnold and Poinar, 2008; Daza et al., 2016; Fontanarroza et al., 2018), whereas extant anguimorphs are typically large bodied (mean maximum SVL = 249 mm; Meiri, 2008). Among extant lizards they are rivaled only by the largest iguanians (to 750 mm SVL; Meiri, 2008) and include the largest living lizard (*Varanus komodoensis*, maximum SVL 1.54 m; Meiri, 2008) and extinct forms of even larger size (e.g., *V. priscus*, with an estimated precaudal length of 2.1 m and the marine mosasauroids reaching a total length of 17 m; Benton, 2014; Grigoriev, 2014). The squamate lineages thus far found in amber include iguanians, stem gekkotans, and lacertoides (Arnold and Poinar, 2008; Daza et al., 2016; Fontanarroza et al., 2018), groups today represented by numerous small and miniaturized species (Rieppel, 1984; Feldman et al., 2016). If *Barlochersaurus* is an anguimorph, it is exceptional for its tiny size and indeed is one of the smallest known species of squamate reptiles. It is only slightly larger in body length (19.1 mm SVL) than the smallest sphaerodactyl geckos (*Sphaerodactylus ariasae*, 14.1–17.9 SVL) (Hedges and Thomas, 2001) and extant dwarf chameleons (*Brookesia minima*, 15–

21.8 SVL) (Glaw et al., 2012), but is more attenuate than either.

If *Barlochersaurus* is an adult, it would be the smallest known lizard of anguimorph affinities. Even if *Barlochersaurus* is a juvenile, it is substantially smaller than the neonates or hatchlings of the smallest living species of anguimorphs, including smaller species of *Celestus* (Henderson and Powell, 2009) and *Gerrhonotus parvus* (based on maximum egg dimensions of 13.57×7.36 mm [Banda-Leal et al., 2014]).

Among fossil forms, the combination of a high vertebral count, attenuate limbs, and a very small size had been achieved earlier by the apparently unrelated genus *Jucaraseps* (31 presacral vertebrae, 27 mm SVL) and, to a lesser degree, *Hoyalacerta* (27 or 28 presacral vertebrae, 34 mm of SVL) from the Barremian of Spain (Evans and Barbadillo, 1999; Bolet and Evans, 2012). The fact that *Jucaraseps*, *Hoyalacerta*, and *Barlochersaurus* are only known from the corresponding type localities and from a single specimen each highlights the extremely low potential for preservation of such small and gracile forms, even in localities with exceptional preservation.

Jucaraseps has reduced limbs with unusually long feet and has been inferred to have had a surface-dwelling lifestyle based on the assumption that such a small lizard would have lacked the ability to generate the force needed by a limb-based burrower, an inference that is supported by the condition in modern burrowers, which usually also have shorter tails (Camp, 1923; Bolet and Evans, 2012).

Barlochersaurus likewise lacks features such as compact skull bones, a closed braincase, reduced dentition, and rounded snouts, which are convergently shared by fossorial taxa such as thread snakes (List, 1966), blind snakes (Rieppel et al., 2009), burrowing pygopods (Daza and Bauer,

2015), and amphisbaenians (Montero and Gans, 2008), suggesting that it was not a head-first burrower. Attenuate bodies are also seen in surface-active grass swimmers (Camp, 1923; Wiens and Slingsluff, 2001), but in such forms tails are typically much longer than SVL (e.g., *Chamaesaura*, Fig. 6D). *Barlochersaurus* is most similar in build to some extant anguimorph diploglossids such as *Diploglossus* and *Celestus* (Fig 6H, I) and to many scincid lizards (Fig. 6). These lizard groups occupy a variety of habitats, from terrestrial to semifossorial, and it is possible that *Barlochersaurus* might have lived in leaf litter or a loose soil substrate, a microenvironment compatible with the specimen's entrapment in amber. Squamates dwelling in these microhabitats typically move by "swimming" through the substrate instead of using their limbs to dig or pull themselves forward; these species may use lateral undulation to move at high speeds on the surface, but use typical tetrapod locomotion when moving more slowly and deliberately (Vitt et al., 2005; Siler et al., 2010).

Remarkable fossil finds over the past several decades have vastly expanded our understanding of the evolutionary history of squamates. Even in the context of this new body of knowledge, the insights coming from recent discoveries in burmite are extraordinary for the comprehensive window into a mid-Cretaceous lizard fauna with representatives from most major lizard clades. The discovery of *Barlochersaurus* extends the range of squamates known to occur in this assemblage, which is the most taxonomically diverse of any amber deposit in the world. In terms of major clades represented, the burmite fauna includes forms apparently closely related to Iguania, Gekkota, Scincoidae, Lacertoidea, and now, Anguimorpha, thus encompassing most of the major extant lizard clades.

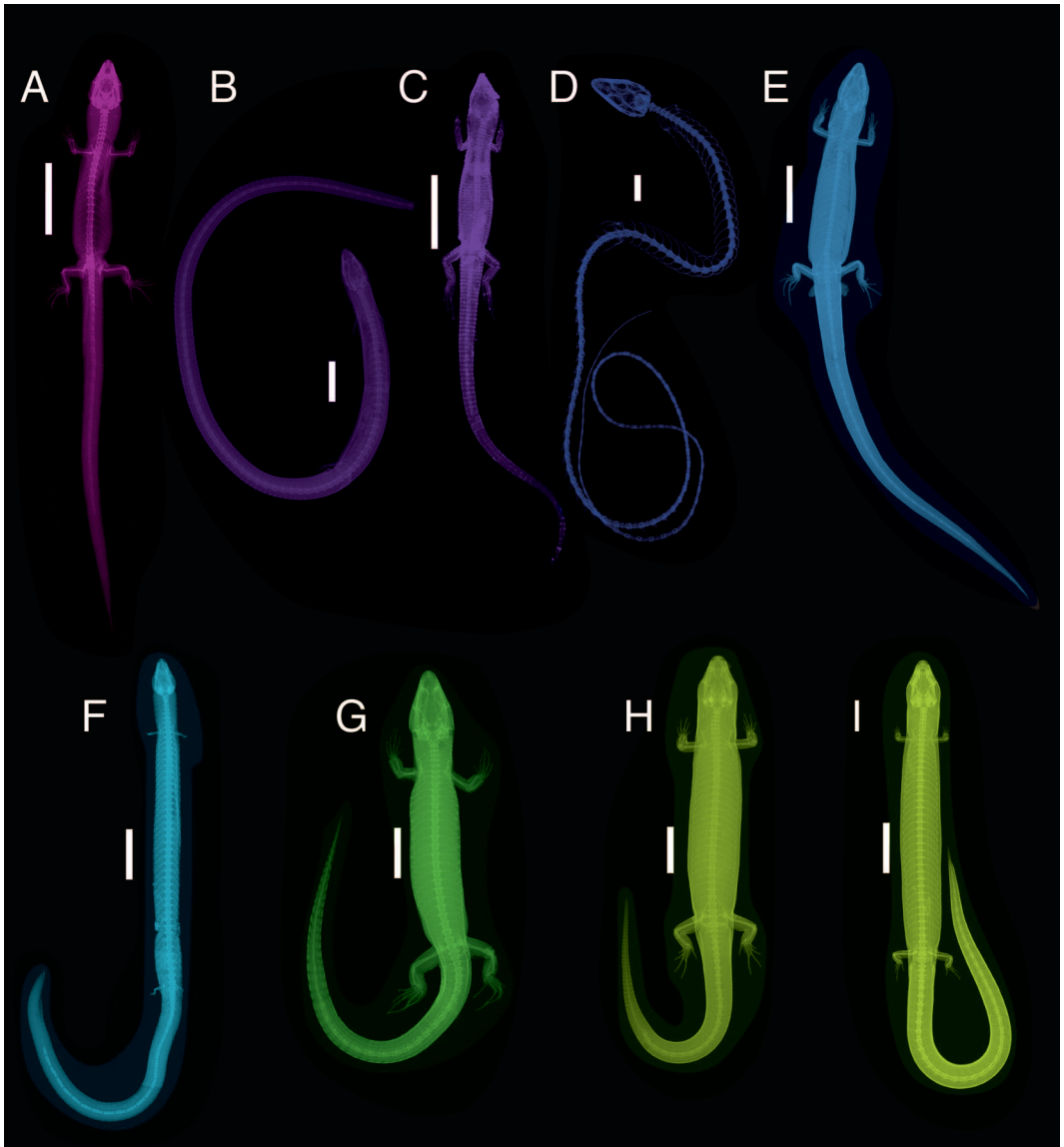


Figure 6. Sample of living squamates with reduced limbs and elongated bodies. A, *Cricosaura typica* (Xantusiidae, USNM 305441); B, *Tetradactylus tetradactylus* (Gerrhosauridae, USNM 162430); C, *Cordylosaurus subtessellatus* (Gerrhosauridae, USNM 184912); D, *Chamaesaura anguina* MCZ R21429 (Cordylidae); E, *Scincella lateralis* (Scincidae, USNM 581688); F, *Bachia flavescens* (Gymnophthalmidae, USNM 566427); G, *Mesaspis moreletii* (Anguidae, USNM 217592); H, *Diploglossus bilobatus* (Diploglossidae, USNM_347178); I, *Celestus sepsoides* (Diploglossidae USNM 259984). Scale bar equals 10 mm.

ACKNOWLEDGMENTS

We thank F. Barlocher for providing access to the specimen. Linda Ford established a connection between the owner of the fossil and the authors. Joseph Martinez took high-resolution photographs of the specimen. We thank Maria Camila Vallejo, Elizabeth Glynne, and Cristian Hernández for assistance with the digital X-rays. We also thank Rayna Bell, Kevin de Queiroz, Kenneth Tighe, Addison Wynn, and Steve Gotte for facilitating access to the Smithsonian Institution National Museum of Natural History Amphibian and Reptiles Collection. Kevin de Queiroz also provided comments and criticisms that improved the quality of this paper. Alan E. Greer kindly provided access to an extensive data set of skink vertebral data from Table 37 of his unpublished manuscript “The Biology of Scincid Lizards.” We thank J. Salvador Arias from the INSUE (Instituto Superior de Entomología “Dr. Abraham Willink”), and Instituto Miguel Lillo for his assistance with the phylogenetic analysis.

J.D.D. received funding from National Science Foundation (NSF) DEB 1657648 and the Biological Sciences Program at Sam Houston State University. A.M.B. received funding from NSF DEB 1555968 and 1556585 and the Gerald M. Lemole Endowed Chair Funds. A.B. is a Newton International Fellow (NF160464) funded by the Royal Society.

APPENDIX 1

Character scores for *Barlochersaurus winhtini*. Data are compatible with the data set of Martill et al. (2015).

Barlochersaurus
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