A small venomous reptile from the Late Triassic (Norian) of the southwestern United States (#100155)

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A small venomous reptile from the Late Triassic (Norian) of the southwestern United States

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Reptile feeding strategies encompass a wide variety of diets and accompanying diversity in methods for subduing prey. One such strategy, the use of venom for prey capture, is found in living reptile clades like helodermatid (beaded) lizards and some groups of snakes, and venom secreting glands are also present in some monitor lizards and iguanians. The fossil record of some of these groups shows strong evidence for venom use, and this feeding strategy has also been hypothesized for a variety of extinct reptiles (e.g., archosauromorphs, anguimorphs, and a sphenodontian). However, evidence of systems for venom delivery in extinct groups and its evolutionary origins has been scarce, especially when based on more than isolated teeth. Here, we describe a potentially venomous new reptile, *Microzemiotes sonselaensis* gen. et sp. nov., from a partial left dentary recovered from the Sonsela Member of the Chinle Formation (middle Norian, Upper Triassic) of northeastern Arizona, USA. The three dentary teeth have apices that are distally reclined relative to their bases and the tip of the posteriormost tooth curves mesially. The teeth show subthecodont implantation and are interspaced by empty sockets that terminate dorsally to the Meckelian canal, which is dorsoventrally expanded posteriorly. Replacement tooth sockets are positioned lingulodistally to the active teeth as in varanid-like replacement. We identify this new specimen as a diapsid reptile based on its monocuspid teeth that lack carinae and serrations. A more exclusive phylogenetic position within Diapsida is not well supported and remains uncertain. Several features of this new taxon, such as an intramandibular septum, are shared with some anguimorph squamates, however, these likely evolved independently. The teeth of the new taxon are distinctively marked by superficial grooves that extend the length of the crown on the labial and lingual sides, as seen in the teeth of living beaded lizards. If these grooves are functionally similar to those of beaded lizards, which use the grooves to deliver venom, this new taxon represents the oldest known reptile where venom-conducting teeth are preserved within a jaw. The teeth of the new species are ~10x smaller than those of the only other known Late Triassic hypothesized venomous reptile, *Uatchitodon*, supporting venom use across multiple body size classes. This new species represents the third Late Triassic reptile species to possibly have used envenomation as a feeding (and/or defensive) strategy, adding to the small number of venomous reptiles known from the Mesozoic Era.

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Abstract

Reptile feeding strategies encompass a wide variety of diets and accompanying diversity in methods for subduing prey. One such strategy, the use of venom for prey capture, is found in living reptile clades like helodermatid (beaded) lizards and some groups of snakes, and venom secreting glands are also present in some monitor lizards and iguanians. The fossil record of some of these groups shows strong evidence for venom use, and this feeding strategy has also been hypothesized for a variety of extinct reptiles (e.g., archosauromorphs, anguimorphs, and a sphenodontian). However, evidence of systems for venom delivery in extinct groups and its evolutionary origins has been scarce, especially when based on more than isolated teeth. Here, we describe a potentially venomous new reptile, *Microzemiotes sonselaensis* gen. et sp. nov., from a partial left dentary recovered from the Sonsela Member of the Chinle Formation (middle Norian, Upper Triassic) of northeastern Arizona, USA. The three dentary teeth have apices that are distally reclined relative to their bases and the tip of the posteriormost tooth curves mesially. The teeth show subthecodont implantation and are interspaced by empty sockets that terminate dorsally to the Meckelia³n canal, which is dorsoventrally expanded posteriorly. Replacement tooth sockets are positioned lingulodistally to the active teeth as in varanid-like replacement. We identify this new specimen as a diapsid reptile based on its monocuspid teeth that lack carinae and serrations. A more exclusive phylogenetic position within Diapsida is not well supported and remains uncertain. Several features of this new taxon, such as an intramandibular septum, are shared with some anguimorph squamates, however, these likely evolved independently. The teeth of the new taxon are distinctively marked by superficial grooves that extend the length of the crown on the labial and lingual sides, as seen in the teeth of living beaded lizards. If these grooves are functionally similar to those of beaded lizards, which use the grooves to deliver venom, this new taxon represents the oldest known reptile where venom-conducting teeth are preserved within a jaw. The teeth of the new species are ~10x smaller than those of the only other known Late Triassic hypothesized venomous reptile, *Uatchitodon*, supporting venom use across multiple body size classes. This new species represents the third Late Triassic reptile species to possibly have used envenomation as a feeding (and/or defensive) strategy, adding to the small number of venomous reptiles known from the Mesozoic Era.

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Introduction

Though the oldest diapsids appear in the fossil record as early as the Carboniferous Period (Reisz & Müller, 2004), it is not until the Triassic Period that these animals became pervasive in the fossil record and evolved a diversity of body sizes, bauplans, and feeding ecologies (e.g., Brusatte et al., 2010; Turner & Nesbitt, 2013; Pritchard, 2015; Zanno et al., 2015). New clades diversified as diapsid ecologies expanded, including archosauromorphs and lepidosauromorphs. As diapsids radiated in the aftermath of the end-Permian mass extinction, diverse feeding strategies evolved, including the use of venom to subdue prey.

A number of diapsids have shown evidence of venom production, including two Triassic archosauromorphs (Mitchell et al., 2010; Sues, 1991), a Jurassic sphenodontian (Reynoso, 2005), living beaded lizards and some varanids and iguanians, 2,500 species of living snakes, and close fossil relatives of these living groups (Fry et al., 2006). Within these groups venom is used both for predation and defense, with venoms that are primarily used defensively having an increased ability to cause pain to deter predators, and venoms for predation that decrease motor function to prevent escape for prey capture and relocation (i.e., having lethal neurological or coagulant effects; Saviola et al., 2013 Koludarov et al., 2014; Schendel et al., 2019). A variety of physical methods are utilized for venom delivery in Reptilia**,** including through saliva in lizards lacking grooved teeth (e.g., varanid squamates; Fry et al., 2009), grooved teeth as seen in the archosauromorph †*Uatchitodon kroehleri*, opisthoglyphous colubrid snakes, †*Sphenovipera jimmysjoyi* (Reynoso, 2005) and helodermatid lizards (Koludarov et al., 2014; Mitchell et al., 2010; Sues, 1991), and injection via a tube within the tooth as seen in the archosauromorph †*Uatchitodon schneideri* and front fanged snakes like viperids (Mitchell et al., 2010). Venom use is most common among snakes, and the hollow anterior fang mechanism for venom delivery has been largely conserved since its first appearance in the fossil record ~23 million years ago (Kuch et al., 2006). The presence of venom in extant lizards and snakes has given rise to the Toxicofera Hypothesis, which proposes that venom is ancestral to the clade Toxicofera that includes all squamates to the exclusion of lacertoids, scincoids, gekkotans, and dibamids (Fry et al., 2006; Fry et al., 2009; Reeder et al., 2015). However, this topic has been hotly debated and is contradicted by anatomical data and homology in non-toxin molecular sequences (Hargreaves et al., 2015). Osteological correlates for venom in vertebrates typically include deeply grooved teeth for venom delivery, which are often the longest teeth in the jaw, sometimes with an apical opening connecting to a venom canal within the tooth, and a cavity or fossa (typically within the maxilla) that may hold space for a venom duct, though this is not present in all venom-producing animals (Benoit et al., 2017; Mitchell et al., 2010).

Within the fossil record, evidence of venom in early reptiles is exceedingly scarce and is often only hypothesized from isolated teeth such as in *Uatchitodon* (Mitchell et al., 2010; Sues, 1991, 1996). The oldest record of a structure for envenomation is seen in the Permian therapsid *Euchambersia mirabilis* (NHMUK R5696; Benoit et al., 2017), which possessed strongly ridged incisiform dentition with deep grooves and a deep maxillary fossa to house a hypothesized venom gland~~)~~. The dromaeosaur *Sinornithosaurus* has also been proposed as a venom-producing archosaur, the only suggested instance of venom production in archosauromorphs besides *Uatchitodon* (Gong et al., 2010). However, a reevaluation of specimens of *Sinornithosaurus* demonstrated its grooved teeth are dissimilar to grooves seen in living venomous species, and the proposed correlated for venom delivery are instead misinterpretations of anatomy and taphonomy (Gianechini et al., 2011).

Here we describe unique venom-delivering teeth within a partial left dentary (DMNH PAL 2018-05-0017) representing a new genus and species of Late Triassic (Norian) reptile from the Sonsela Member of the Chinle Formation in northern Arizona, U.S.A. This specimen represents the earliest evidence of venomous teeth preserved within a jaw since the discovery of *Euchambersia* and demonstrates an uncommon feeding strategy in a Late Triassic community.

Materials & Methods

Computed Tomographic (CT) Scanning Parameters and Segmentation— We analyzed DMNH PAL 2018-05-0017 using X-ray microcomputed tomography (µCT-scanning) at the Shared Materials Instrumentation Facility at Duke University using a Nikon XTH 225 ST scanner. Permission for collection and study of this specimen was given by the Perot Museum of Nature and Science. The specimen was scanned at 185 kV and 76 µA with a 0.125 mm copper filter with 2,200 projections for each segment at a 0.01430282 mm voxel size. Reconstructions were created and analyzed using Mimics Innovation Suite 20. These data are available at Morphosource.org under Project 000607596. A 3D surface model was generated from these data using MeshLab 2022.02.

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Institutional Abbreviations— **BMRP**, Burpee Museum of Natural History, Rockford, Illinois, U.S.A.; **BP**, Bernard Price Institute, Johannesburg, South Africa; **BRSMG**, The Bristol City Museum, Bristol, U.K.; **CM**, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A.; **DMNH**, Denver Museum of Natural History, Denver, Colorado, U.S.A; **FMNH**, Field Museum of Natural History, Chicago, Illinois, USA; **IRScNB**, Institute Royal des Sciences Naturelles de Belgique, Brussels, Belgium; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **LACM**, Natural History Museum of Los Angeles County, Los Angeles, California, U.S.A.; **MNA**, Museum of Northern Arizona, Flagstaff, Arizona, U.S.A.; **NCSM**, North Carolina State Museum of Natural Sciences, Raleigh, North Carolina, U.S.A.; **NHMUK**, Natural History Museum of the United Kingdom, London, U.K.; **NMC**, Canadian Museum of Nature, Ottawa, Canada; **OMNH**, Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma, U.S.A.; **PEFO**, Petrified Forest National Park, Arizona, U.S.A; **PIMUZ**, Paläontologischen Institut ~~und Museum~~ der Universität, Zürich, Switzerland; **ROMVP**, Royal Ontario Museum, Ontario, Canada; **SAMA**, South Australian Museum, Adelaide, South Australia; **UCMP**, University of California Museum of Paleontology, Berkeley, California, U.S.A; **UCMZ**, University of Cambridge Museum of Zoology, Cambridge, U.K.;

USNM, National Museum of Natural History, Smithsonian Institution, Department of Vertebrate Zoology, Washington D.C., U.S.A; **USTL**, University of Sciences and Techniques of Languedoc, Montpellier, France.

SYSTEMATIC PALEONTOLOGY

DIAPSIDA Osborn 1903 sensu Gauthier et al., 1988

MICROZEMIOTES SONSELAENSIS, gen. et sp. nov.

Fig. 1

Type Species – *Microzemiotes sonselaensis*

Etymology – The genus name *Microzemiotes* is derived from the Greek 'micro' = small, and 'zemiotes' = punisher. The species epithet *sonselaensis* recognizes the Sonsela Member of the Chinle Formation, which produced this specimen.

Holotype – DMNH PAL 2018-05-0017, a partial left dentary with three preserved teeth, partially deformed on the lingual side.

Diagnosis – This species is diagnosed by the following combination of anatomical traits (potential autapomorphy denoted with an *): ankylosed subthecodont dentition (sensu Zaher & Rieppel 1999); posterior dentary teeth are inclined distally from perpendicular to the mesial tooth edge; posterior dentary teeth are oval in coronal cross-section (longer in the mesial-distal direction) with no carinae or serrations; replacement of teeth occurring in pits located linguo-distally to the active teeth, a taller (1.0 mm) labial wall and slightly lower (0.9 mm) lingual wall; intramandibular septum; a rounded, incomplete, and ventrally-free intramandibular septum at the posteroventral portion of the dentary* (sensu Estes, 1964) projecting from the labial wall; lingual and labial grooves extending from the base of the tooth to the tip of the crown.

Locality, Horizon, and Age– *M. sonselaensis* was recovered from the 'Green Layer' site, which is ~2–4 m of interbedded green and white laminated sandstone matrix (grain size ~0.5 mm) within the lower part of the Jim Camp Wash beds (*sensu* Martz & Parker, 2010) of the Sonsela Member of the Chinle Formation southeast of Petrified Forest National Park, Arizona (exact locality information on file at the Perot Museum of Nature and Science). The age of the locality is ~217.7 Ma–213.870 ± 0.078 Ma (Kligman et al., 2020; Stocker et al., 2019) based on local stratigraphic correlation with dated localities within Petrified Forest National Park, Arizona. Other vertebrate taxa present at the Green Layer Site include chondrichthyans (e.g., *Reticulodus*), sarcopterygians (coelacanths and lungfish), and actinopterygians; tetrapods include salientians (Stocker et al., 2019), the allokotosaur *Trilophosaurus phasmalophos* (e.g., DMNH PAL 2018-05-0012 and DMNH PAL 2018-05-0013; Kligman et al., 2020), leptosuchomorph phytosaurs, *Revueltosaurus callenderi* (e.g., DMNH PAL 2018-05-0129), and aetosaurians (e.g., DMNH PAL 2018-05-0014; Mellett et al., 2023). The presence of non-pseudopalatine leptosuchomorph phytosaurs and stratigraphic correlations with locality PFV 089 at Petrified Forest National Park suggest that the site occurs in the Revueltian estimated holochronozone (Kligman et al., 2020; Martz & Parker, 2017).

Taphonomy– The specimen was transported within a fluvial system and is preserved in a fine-grained sandstone with clasts of larger grains. Two of the in-situ teeth demonstrate an abrupt narrowing on the lingual side (0.2 mm basal from the tooth apex) inconsistent with our understanding of carnivorous teeth, which are generally conical, evenly tapering, and recurved (Henderson, 1998; Jones, 2008; Presch, 1974). Analysis using SEM shows this decrease in angle is the product of minute loss of fossil material (Fig. 2. B, C). The enamel from the tooth apex could have been lost due to wear via occlusion and feeding use in life, or from fluvial transport processes prior to fossilization. The latter explanation is very unlikely because if degradation from fluvial transport occurred, it would be expected to cause damage to other parts of the jaw besides the tooth apices. We interpret the empty sockets as products of both biological and taphonomic processes; newly erupted replacement teeth in these alveoli were likely to have not been ankylosed and were therefore more susceptible to displacement, as in silesaurid dinosauriformes (Mestriner et al., 2022). The same is likely true for the replacement teeth developing in the dentary, which are marked by small cavities distolingual to the three parent teeth but lack in-situ replacements. The thin lingual wall (0.05 mm in cross section) is deformed at each of its three contact points with the teeth, where compaction following burial caused lateral compression of the wall both into the empty sockets and across these hard in-situ teeth, resulting in breakage.

Nomenclatural acts— This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank Life Science Identifiers (LSIDs) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix zoobank.org/. The LSIDs for this publication are as follows: xxxxxxxxxx.

Description

Dentary

The holotype of *Microzemiotes sonselaensis* (DMNH PAL 2018-05-0017) consists of a partial left dentary with three well preserved teeth (Fig. 1) that was deformed by lateral compression on the lingual surface. The dentary is broken and missing bone anterior to the first tooth position (counting alveoli from anterior to posterior). The preserved portion is 6 mm long anteroposteriorly and 1 mm deep dorsoventrally (measured from CT data in Mimics v.20), with teeth rising ~0.8 mm above the lateral wall, which is perforated with a foramen. The posterior process of the dentary extends 1.33 mm beyond the distal edge of the terminal tooth socket and narrows dorsoventrally to a point. The termination is dorsally inflected 4° above the dorsal surface of the tooth-bearing portion of the dentary, creating a concave effect. The overall anatomy of the dentary is markedly similar to those of early diverging archosauromorphs: the dorsally inflected posterior taper of the dentary is also seen in *Youngina capensis* (BP/1/2871) but unlike *Youngina capensis* (BP/1/2871) it does not bifurcate into posterolateral and posteromedial processes (Hunt et al., 2023). A posteriorly tapering dentary is also present in tanystropheids including *Tanystropheus hydroides* (PIMUZ T 2790) and *Tanystropheus longobardicus* (PIMUZ T 3901), *Prolacerta broomi* (UCMZ 2003.41R), Permian varanopids such as *Mesenosaurus efremovi* (ROMVP 85456), *Varanops brevirostris* (FMNH UC 64), and *Aerosaurus wellesi* (UCMP 40096) and parareptiles such as *Feeserpeton oklahomensis* (OMNH 73541), *Colobomycter pholeter* (BMNRP 2008.3.1), and *Carbonodraco lundi* (CM 41714) (Campione & Reisz, 2010; Hunt et al., 2023; Macdougall et al., 2017; MacDougall, Winge, et al., 2019; Maho et al., 2019; Mann et al., 2019; Nosotti, 2007; Sobral, 2023; Spiekman et al., 2020; Langston & Reisz, 1981). The tapered posterior part of the dentary also occurs in some squamate groups, most notably in scincoids (Hutchinson et al., 2012). However, this is almost always accompanied by ventral projections of the dentary in those taxa (e.g. subdental shelf, angular process, surangular process) that extend posteriorly to or nearly to the end of the coronoid process forming a V or W shape, which is absent in *Microzemiotes sonselaensis*. No sockets are present on this posterior portion in *Microzemiotes sonselaensis*, and a shallow, curved facet is present on the ventral edge of the lateral surface, most likely articulating with the surangular as seen in archosauromorphs *Youngina capensis* (BP/1/2871) and *Prolacerta broomi* (UCMZ 2003.41R) which seem to have homologous arrangements of mandibular anatomy (Hunt et al., 2023; Sobral, 2023). The lateral surface of the dentary of *Microzemiotes sonselaensis* is convex, as the ventral half curves laterally beneath the tooth bearing dorsal surface. The ventral edge of the lateral wall of the dentary of *Microzemiotes sonselaensis* is medially inflected to form the floor of the Meckelian canal. There is a concave ridge on the medial surface of this ventral edge of the dentary that we interpret as an articular surface for the splenial as in *Youngina capensis* (BP/1/2871; Hunt et al., 2023). The Meckelian canal is prominent and is lingually open for the preserved length (presumed to be enclosed by the splenial in life) and widens dorsoventrally in the posterior direction, as is the condition in many amniotes. The anatomy of the anterior portion of the dentary and symphysis is unknown.

The Meckelian canal is incompletely divided by a ~~C-shaped~~ intramandibular septum, which forms a round C-shaped edge projecting posteriorly from between the lateral and lingual walls of the dentary (Fig. 1. B, C) that connects to the medial surface of the lateral wall of the dentary ventral to the two posteriormost teeth, creating brief separation of the alveolar cavity from the Meckelian canal. In *Microzemiotes sonselaenisis*, the intramandibular septum projects from the medial surface of the lateral wall (Fig. 3. A3) rather than extending from the ventral surface of the lingual wall to lower on the medial surface of the lateral wall, as is the condition in anguid lizards and snakes (Lee & Scanlon, 2001). Amongst Triassic reptiles, a similar posteriorly projecting intramandibular septum is only known from the kuehneosaurid-like Carnian diapsid *Idiosaura virginiensis* (Kligman et al., in review), however differences in tooth attachment and neurovascular morphology suggest that this similarity is likely convergent.

Dentition

The dentary preserves eight tooth positions including three pits for replacement teeth located distolingually to the fully erupted teeth. The three teeth present, in sockets three, five, and seven identified from the anterior (Fig. 1. F, G, Fig. 3) are conical in sagittal cross section and oval (mesiodistally longer) in coronal cross section. The posterior dentary teeth do not erupt perpendicular to the dentary but are inclined distally 20–24° from perpendicular toward the mesial tooth edge. The third tooth (posteriormost) is recurved mesially. Though mesially curving teeth are scarcely documented, they are not entirely unheard of in the distal teeth in some reptilian groups that show more typical distally recurved teeth or straight teeth in the rest of the jaw (e.g., the dinosaur *Camarasaurus*, SMA 0002 and the diapsid *Maiothisavros dianeae* (ROMVP 87366) (Mooney et al., 2022; Wiersma & Sander, 2017). Thus, this single tooth may not indicate mesial curvature for the rest of the more anterior teeth. The teeth of *Microzemiotes sonselaensis* lack carinae or serrations but possess deep labial and lingual grooves that span from just dorsal to the connection to the dentary up to the apex of the crown on the labial side and up to 0.1–0.2 mm away from the tooth apex where original fossil material is missing on the lingual side (Fig. 2).

The teeth in *Microzemiotes sonselaensis* exhibit subthecodont implantation, inset in sockets extending 60% of the dorsoventral depth of the dentary measured from the lateral side, underlain by the Meckelian canal (Fig1. B, C; Fig. 3A). The labial wall is slightly higher than the lingual wall, as seen in *Youngina capensis*, which also exhibits subthecodont dentition (Hunt et al., 2023). The sockets lacking in-situ teeth are incomplete ventrally and open directly into the Meckelian canal, which is uncommonly described in taxa with subthecodont implantation but has been noted in mosasaurs such as *Clidastes propython* (FMNH PR 164, PR 4; Rieppel & Kearney, 2005). The roots of the teeth of DMNH PAL 2018-05-0017 are 0.4–0.5 mm long measured apicobasally, covered medially by the lingual wall. The teeth roots are completely surrounded by ankylosing tissue (Fig 3. B3, B4) as in other ankylothecodont taxa like azendohsaurids and silesaurids (e.g., Mestriner, 2021).

Microzemiotes sonselaensis shows an alternate method of tooth replacement, with the three in-situ teeth interspaced with empty sockets, and alveoli for replacement teeth are positioned distolingually to active teeth (Bertin et al., 2018; Fig. 3. B). The alternate replacement method is noted in a variety of groups including archosauromorphs *Youngina capensis* and *Prolacerta broomi* Triassic sauropterygians like *Nothosaurus* and *Simosaurus*, and in many modern lizard groups (Gow, 1974; Neenan et al., 2014).

Discussion

Proposed taxonomy

We attribute this new taxon to the sauropsid group Diapsida on the basis of a combination of character states defined most recently by Ford & Benson (2019): teeth, marginal dentition, cutting edges (carinae) on the mesial and distal surfaces: absent ([character] 8– [state] 0); teeth, serrations on crown of marginal teeth: absent (9–0); teeth, multiple apical cusps on marginal dentition: absent (11–0). The posteriorly tapering and dorsally inflected shape of the dentary seen in *Microzemiotes sonselaensis* is also present in early-diverging diapsids from the Permian (*Youngina*, varanopids, and parareptiles), though no varanopids are known to have persisted into the Triassic Period and the only Triassic parareptiles are the procolophonids, which have not yet been documented from the Sonsela Member of the Chinle Formation (MacDougall et al., 2019). It should be noted that a recent phylogenetic hypothesis using extensive morphological characters recovered varanopids as early diverging diapsids rather than synapsids (Ford & Benson, 2020). Subthecodont dentition is shared among these taxa and *Microzemiotes sonselaensis*, a condition also seen in mosasaurs and non-therapsid synapsids, and may be the plesiomorphic condition for Diapsida (Caldwell, 2007; Evans et al., 2009; Liu et al., 2016; Sues & Kligman, 2020).

Within Diapsida, the phylogenetic placement of *Microzemiotes sonselaensis* is ambiguous given the limited number of observable character states in the only known specimen that are apomorphic of various clades. However, *Microzemiotes sonselaensis* does share anatomy that among living groups is only found in some lizards. The presence of an intramandibular septum with a free posteroventral margin, as noted in *Microzemiotes sonselaensis,* has been described as an unambiguous synapomorphy for extant anguids within Squamata, whereas archosauromorphs and non-squamate lepidosauromorphs lack this feature (Estes et al., 1988; Conrad et al., 2011). The extension of the intramandibular septum posterior to the posteriormost teeth would characterize the septum as being 'well developed' (Estes et al., 1988), a character state that is considered a synapomorphy of anguimorphs and convergent in some iguanians (Lee & Scanlon, 2001). However, the intramandibular septum in *Microzemiotes sonselaensis* differs from those seen in most anguimorphs in two key ways: 1) the ventral margin is not coossified to the body of the dentary; and 2) the anterior edge terminates under the second tooth from the posterior end, poorly separating the alveolar foramen from the Meckelian canal. These differences demonstrate that convergence of this structure is more likely than homology with anguimorphs. It is notable that the posterior projection of the intramandibular septum forms a C shape, which although independently evolved, is also seen in the intramandibular septum of some anguid lizards such as the Pleistocene *Ragesaurus medasensis* (USTL MED-121; Bailon & Auge, 2012) and those of agamid lizards, particularly *Uromastyx aegyptia* (SAMA R48106) (Hutchinson et al., 2012). The intramandibular septum also has a somewhat enigmatic nature as a character due to challenges preparing specimens to reveal the fragile septum leading to inconsistent descriptions of the character relative to variable jaw anatomy. The intramandibular septum of the Triassic diapsid *Idiosaura virginiensis* suggests that this anatomy likely evolved multiple times in Triassic diapsids (Kligman et al., in review).

M. sonselaensis shares several distinctive characters with the tooth morphotype named *Uatchitodon*, including recurved, labiolingually compressed teeth, and venom grooves (specifically *Uatchitodon kroehleri,* USNM542518; Mitchell et. al., 2010).

Evidence of venom in *Microzemiotes sonselaensis*

The teeth of *Microzemiotes sonselaensis* possess a suite of osteological correlates that indicate that it may have utilized envenomation as a feeding or defense strategy, and what follows is a discussion on the evidence to support this hypothesis. The grooves on the lateral surfaces of all three teeth present in the dentary of *Microzemiotes sonselaensis* extend from contact with the dorsal surface of the dentary to the tips of the teeth and are only absent where surface enamel was lost due to breakage (Fig. 2. C). We rule out the possibility that these grooves are the product of wear based on inspection of SEM photos (Fig. 2) that show the tooth enamel to be fully intact across the grooves and that the shape of the grooves remains constant across the lingual and labial sides and across the three preserved teeth. The presence of deep grooves extending from the base to the tip of the tooth in a non-mammalian amniote is strongly indicative of the presence of an envenomation system (Mitchell et al., 2010). The continuation of the groove from the base to the tip of the tooth is consistent with the venom delivery structure present in helodermatid lizards, which use a combination of capillary action and a sharp cutting surface to inject venom into prey through a sustained bite (Koludarov et al., 2014). The teeth of *Microzemiotes sonselaensis* are similar to the conical, curved, and deeply grooved teeth of the extant venom-producing Gila monster (*Heloderma suspectum*), which are characterized by deep surficial venom grooves and lack interior venom canals with apical openings, though the teeth of the Gila monster have a single groove on each tooth rather than grooves on both the labial and lingual surfaces. Both *M. sonselaensis* and *H. suspectum* have a less complex condition for venom delivery, which is observed in helodermatids, *Uatchitodon kroehleri*, and living snakes' early stage fangs that lack internal tubes (Mitchell et al., 2010). Among these animals, the location of the venom gland varies. In helodermatids, the venom gland is located anterolaterally to the dentary and venom is secreted to the bases of the grooved dentary teeth through ducts; the maxillary teeth are also grooved but do not have connected ducts (Fry et al., 2006; Mackessy, 2022). In venomous snakes (colubrids, elapids, and viperids) the gland, or group of glands, is located subdermally ventral to the eye (Mackessy, 2022; Schendel et al., 2019). The location of the venom gland is unknown for *Uatchitodon kroehleri* and *Uatchitodon schneideri*, which are only represented by teeth (Mitchell et al., 2010). We suggest the position for a venom gland for *Microzemiotes sonselaensis* would be anterolateral to the dentary with ducts leading to the bases of the grooved teeth, as is the condition in helodermatids, to supply venom slowly for a sustained bite.

Regardless of delivery method, venom can function to disable prey or to defend against attacking predators. In helodermatids, venom is hypothesized to function both defensively and for predation, whereas in viperous snakes it is used primarily for predation (Saviola et al., 2013; Koludarov et al., 2014; Schendel et al., 2019). If the venom delivery system in *Microzemiotes sonselaensis* was functionally similar to that of helodermatids as suggested by shared anatomy, it would follow that venom delivery was more passive compared to taxa that inject venom via interior tubes (e.g., vipers and possibly *Uatchitodon schneideri*), and an individual would need to grasp its target for some amount of time (e.g., up to one hour in helodermatids) in order inflict significant damage (Koludarov et al., 2014). However, though the method of delivery may be inferred from fossil evidence, the active chemical components of the venom itself cannot be assessed without soft tissue and/or biomolecules and so the biochemical mechanism of venom in *Microzemiotes sonselaensis* remains unknown.

Implications for venomous reptiles in the Late Triassic

Prior to the discovery of DMNH PAL 2018-05-0017, anatomy consistent with a venom apparatus was observed in only two other Triassic taxa, *Uatchitodon kroehleri* and *Uatchitodon schneideri*, both from Late Triassic (Carnian and Norian, respectively) deposits of North America. Occurrences of *Uatchitodon schneideri* in western North America include the following: UCMP A269/MNA loc. 207 (the *Placerias* Quarry; PFV 396 (Coprolite Layer; Parker et al., 2021); and PFV 456 (Thunderstorm Ridge; Kligman, 2023). The *Placerias* Quarry has a maximum depositional age of 219.39 ± 0.16 Ma (Ramezani et al., 2014), whereas the Green Layer has an estimated age of ~217.7 Ma to 213.870 ± 0.078 Ma (Kligman et al., 2020; Stocker et al., 2019) (Fig. 4). The ages of these localities and fauna present indicate that the two species are separated by the Adamanian-Revueltian Boundary, a time of significant faunal turnover (Parker & Martz, 2011). *Uatchitodon schneideri* is present in the Adamanian teilzone whereas *Microzemiotes sonselaensis* is present in the Revueltian teilzone (Martz & Parker, 2017). However, with minimal distance and time separating these specimens, the co-occurrence of *Uatchitodon schneideri* and *Microzemiotes sonselaensis* cannot be ruled out. Both species of *Uatchitodon* are described only from isolated teeth and have been thought to represent carnivorous archosauromorphs based on the presence of compound denticles (i.e., serrations, or denticles with subdivided or irregular cutting edges) and thecodont implantation based on a single specimen possessing a root, USNM 448624 (Sues, 1991, 1996). Serrated teeth have evolved many times throughout the fossil record but are only recognized in one group of venom-producing reptiles, the varanids, including *Varanus komodoensis* and the extinct *Varanus priscus* that both possess ziphodont teeth with structures for venom delivery. Functionally, ziphodont teeth allow for slicing of prey tissue, suggesting this was part of the feeding ecology of *Uatchitodon*. The absence of ziphodonty in *Microzemiotes sonselaensis* suggests that unlike *Uatchitodon*, it was using its teeth for piercing prey tissue only, not slicing. *Microzemiotes sonselaensis* and both species of *Uatchitodon* are characterized by conical, sharp teeth with both labial and lingual grooves, a character that has not been recognized in living reptilian venom users. Coronal cross sections of the teeth (Fig. 3. B2, B3) of *Microzemiotes sonselaensis* are similar to those of *Uatchitodon kroehleri* and *Uatchitodon schneideri* in that the pulp cavity is compressed at the center of the tooth in the labio-lingual direction (Mitchell et al., 2010). In the teeth of *Uatchitodon schniederi* and some specimens of *Uatchitodon kroehleri*, the pulp cavity is so compressed it is divided, which is not seen in any of the teeth of *Microzemiotes sonselaensis* (Mitchell et al., 2010). The addition of *Microzemiotes sonselaensis* to the recognized venom producing taxa of the Late Triassic indicates that venom was likely utilized by taxa with some variation of tooth morphology.

One specimen of *Uatchitodon schneideri* (MNA V3680; Mitchell et al., 2010; Sues, 1996) recovered in northeastern Arizona consists of an isolated tooth that measures ~6.5 mm from base to tip, longer than the entire preserved length of the dentary in *Microzemiotes sonselaensis*, which holds teeth measuring no more than 0.8 mm from base to tip (size comparison in Fig. 4). Some of the smallest extant vertebrate venom producers are among the opisthoglyphous (i.e., rear-fanged) members of the colubrid family, which use venom in a similar method to helodermatids using grooved fangs in the posterior region of the maxilla and venomous saliva to deliver a sustained bite (Fry et al., 2009). Snakes benefit from venom use in the ability to subdue large prey that they can consume using flexible hemimandibles and a ligamentous mandibular symphysis. Small mammalian venom users, such as the short tailed shrew (7–10 cm long), lack this ability and have been noted to use venom for the immobilization of prey (insects and mice) for ease of consumption or for delayed feeding (Martin, 1981; Schendel et al., 2019; Tomasi, 1978). The diminutive size of the preserved length of the dentary in *Microzemiotes sonselaensis* suggests that this animal was a very small predator and likely had even smaller prey – potentially insects and similarly small vertebrates. Wear from feeding during life at the tooth apices suggests that it may have fed on harder-shelled invertebrates. We demonstrate here that *Microzemiotes sonselaensis* was a much smaller predator than *Uatchitodon,* supporting venom use among different size classes of predators in the Late Triassic, though whether the small size of *Microzemiotes sonselaensis* is due to ontogeny remains ambiguous.

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Figure 1

Left Dentary (partial) of *Microzemiotes sonselaensis* holotype DMNH PAL 2018-05-0017.

(A) Photograph of *Microzemiotes sonselaensis* holotype DMNH PAL 2018-05-0017, (B, C) three-dimensional render and line drawing of the dentary in lingual view, (D,E) labial view, and (F,G) dorsal view. Scale bar equals 1mm, arrow points anterior. Abbreviations**:** im, intramandibular; mec, Meckelian canal; fac, facet; f, foramen; sa, surangular; vg, venom groove.

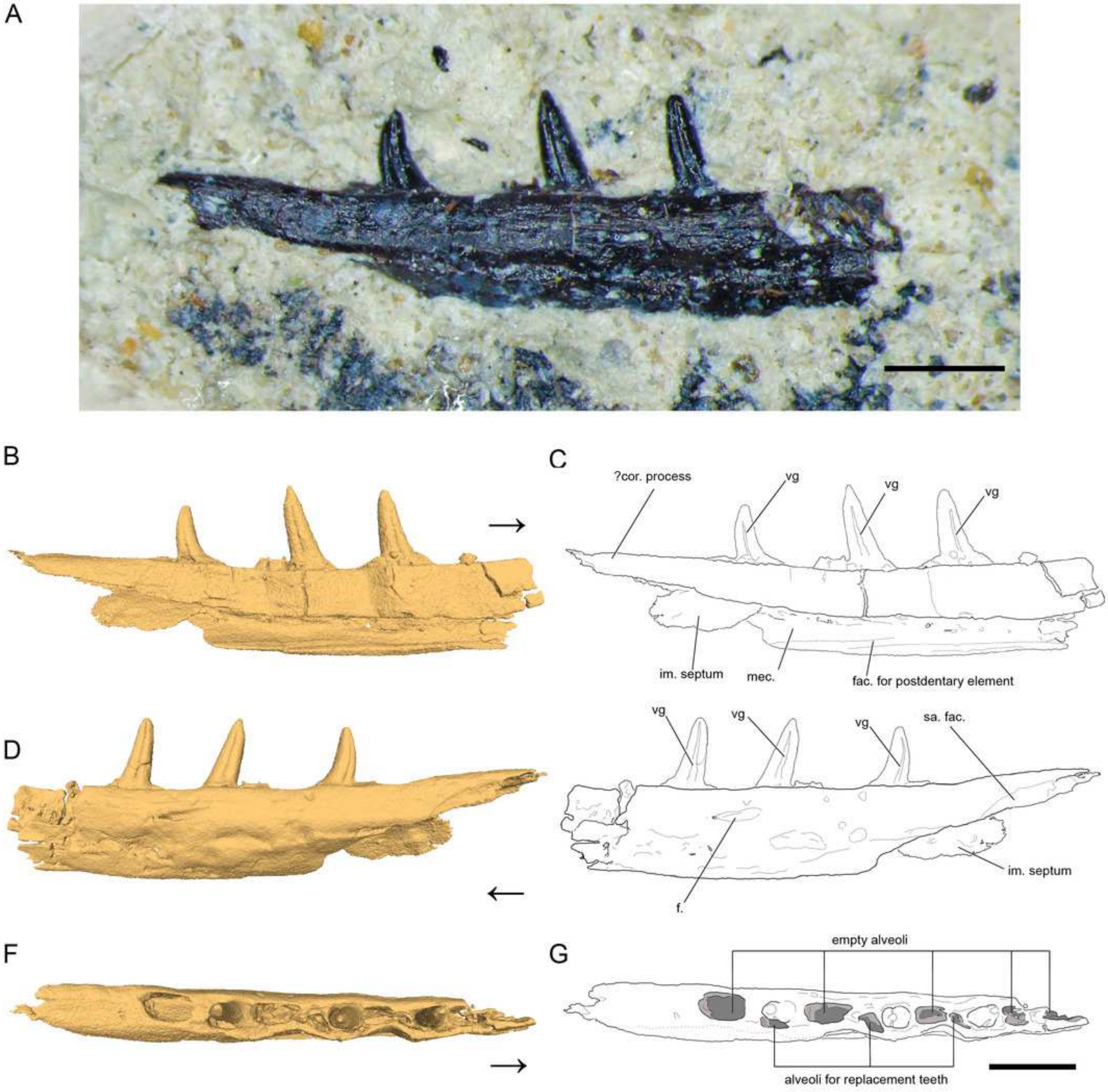

A
B
C
?cor. process
vg
vg
vg
im. septum
mec.
fac. for postdentary element
D
vg
vg
vg
sa. fac.
im. septum
f.
F
G
empty alveoli
alveoli for replacement teeth

Figure 2

SEM photographs of *Microzemiotes sonselaensis* holotype, DMNH PAL 2018-05-0017, grooved teeth (lingual view).

Teeth labelled A, B, C from posterior to anterior. Scale bar equals 1mm, arrow points anterior.

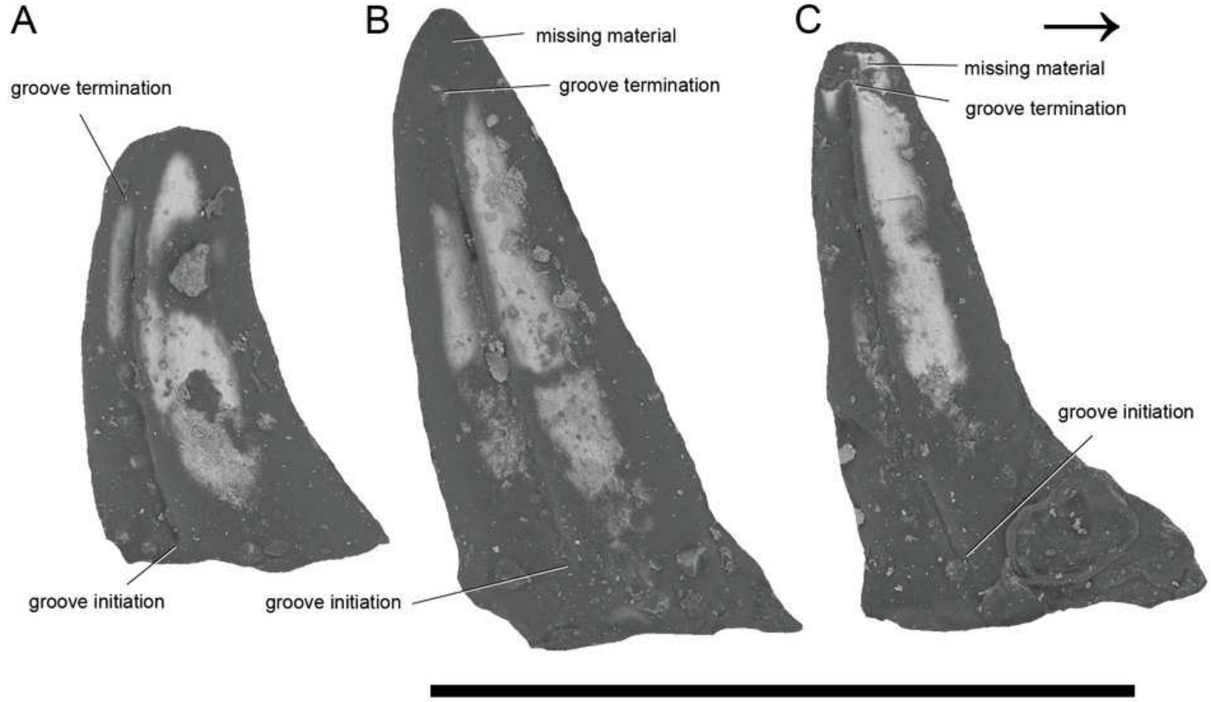


Figure 3

3D surface rendering of the dentary of *Microzemiotes sonselaensis* holotype DMNH PAL 2018-05-0017 in lingual view and CT cross sections.

(A1–A3) Series of coronal sections and (B1-B4) series of axial sections of the CT reconstructions (slices) showing internal anatomy. Abbreviations: **at**, ankylosing tissue; **iac**, inferior alveolar canal; **im**, intramandibular; **mec**, Meckelian canal; **tr**, tooth root; **pc**, pulp cavity **vg**, venom groove. Scale bar equals 1mm, arrows indicate labial direction.

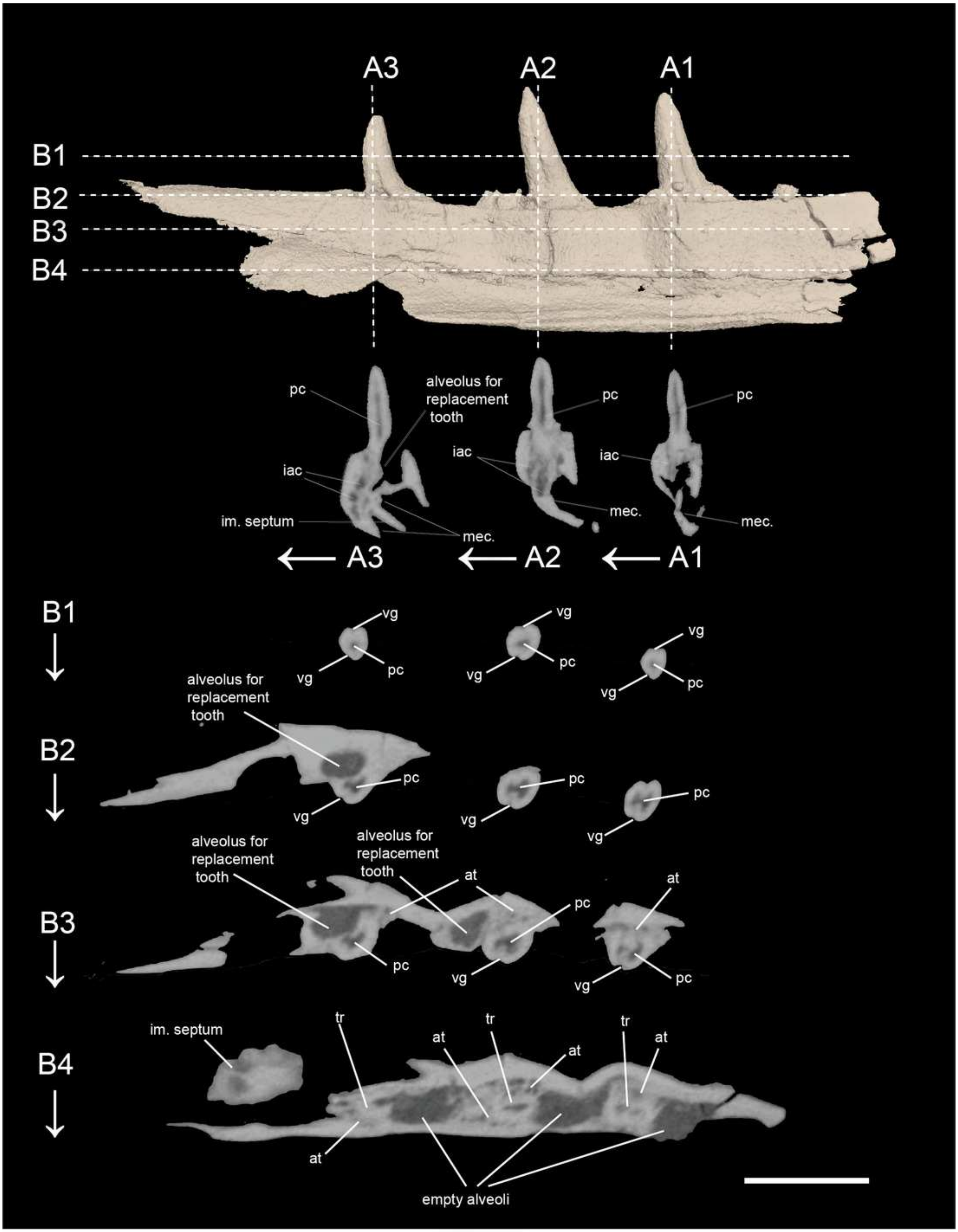
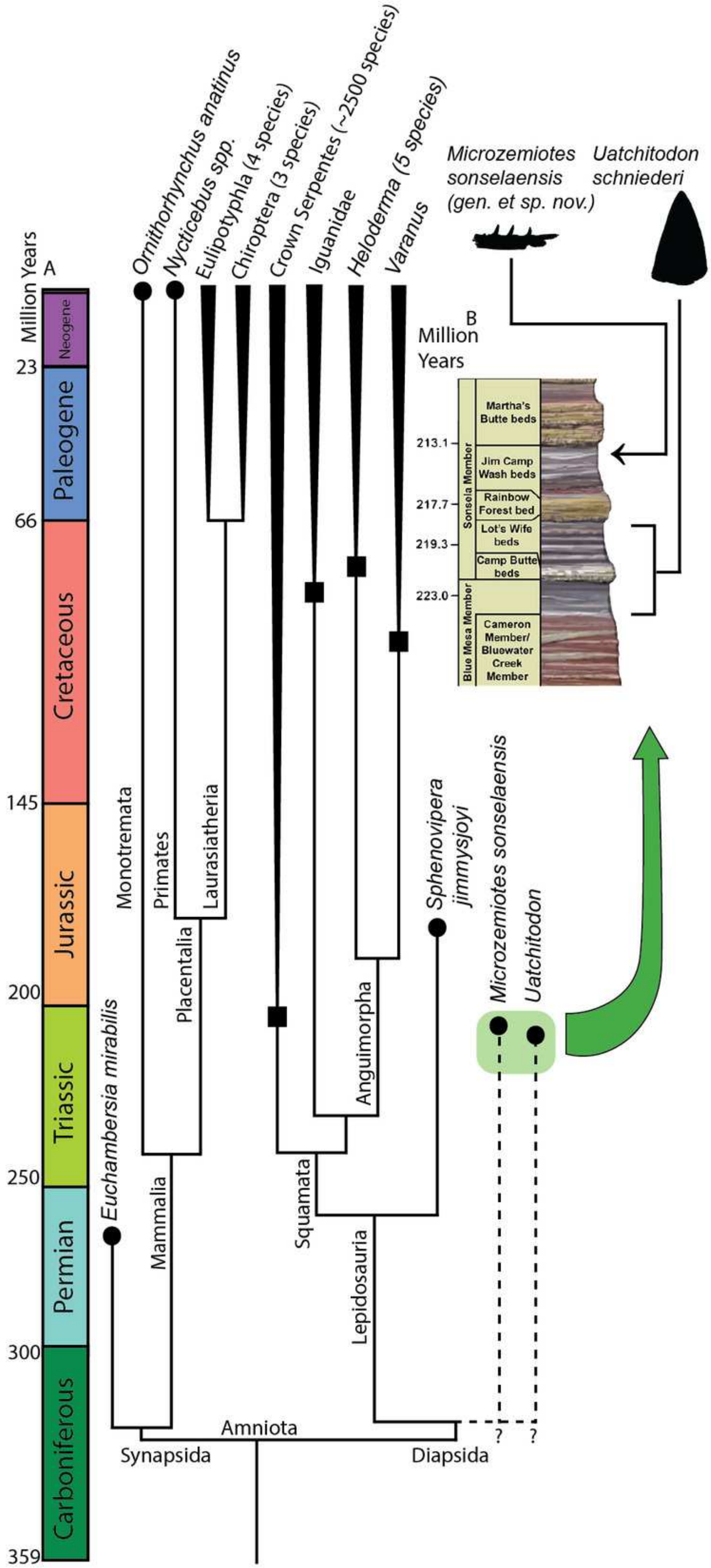

A3
A2
A1
B1
B2
B3
B4
pc
alveolus for replacement tooth
iac
im. septum
mec.
pc
iac
mec.
pc
iac
mec.
A3
A2
A1
B1
vg
vg
pc
vg
vg
pc
vg
vg
pc
alveolus for replacement tooth
B2
pc
vg
pc
vg
pc
vg
alveolus for replacement tooth
alveolus for replacement tooth
at
at
B3
pc
pc
vg
vg
pc
im. septum
tr
tr
tr
at
at
at
B4
at
empty alveoli

Figure 4

Phylogenetic tree of venom producing taxa and stratigraphic context.

A: Phylogenetic tree of venom producing vertebrate taxa modified from Ford & Benson, 2020; Rougier et al., 2021; Upham et al., 2019. B: Stratigraphic context of occurrences of *Microzemiotes sonselaensis* in the Green Layer Locality and *Uatchitodon schneideri Placerias* Quarry (Sues, 1996; Mitchell et al., 2010) ; PFV 396 (Coprolite Layer; Parker et al., 2021) ; and PFV 456 (Kligman, 2023) in the Chinle Formation in Arizona, USA. Outlines of *M. sonselaensis* and *U. schneideri* (modified from Sues, 1996) are scaled to one another. Stratigraphic column modified from the National Park Service.


A
Million Years
Neogene
Paleogene
Cretaceous
Jurassic
Triassic
Permian
Carboniferous
23
66
145
200
250
300
359
Ornithorhynchus anatinus
Nycticebus spp.
Eulipotyphla (4 species)
Chiroptera (3 species)
Crown Serpentes (~2500 species)
Iguanidae
Heloderma (5 species)
Varanus
Monotremata
Primates
Laurasiatheria
Placentalia
Mammalia
Euchambersia mirabilis
Sphenovipera jimmysjoyi
Anguimorpha
Squamata
Lepidosauria
Microzemiotes sonselaensis
Uatchitodon
Amniota
Synapsida
Diapsida
?
?
Microzemiotes sonselaensis (gen. et sp. nov.)
Uatchitodon schniederi
B
Million Years
Martha's Butte beds
Jim Camp Wash beds
Rainbow Forest bed
Lot's Wife beds
Camp Butte beds
Cameron Member/ Bluewater Creek Member
Sonsela Member
Blue Mesa Member
213.1
217.7
219.3
223.0