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New sphenodontian (Reptilia: Lepidosauria) from a novel Late Triassic paleobiota in western North America sheds light on the earliest radiation of herbivorous lepidosaurs

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Abstract.—Herbivory is a common ecological function among extant lepidosaurs, but little is known about the origin of this feeding strategy within Lepidosauria. Here we describe a sphenodontian (Lepidosauria) from the Late Triassic of western North America, *Trullidens purgatorii* n. gen. n. sp., that reveals new aspects of the earliest radiation of herbivorous lepidosaurs. This taxon is represented by an isolated lower jaw with robust structure bearing transversely widened dentition and extensive wear facets, suggesting a masticatory apparatus specialized for herbivory. An unusual 'incisor-like' tooth is present at the anterior end of the jaw; a unique feature among lepidosaurs, this tooth is convergent with the incisors of extant rodents and lagomorphs. Phylogenetic analyses support the placement of this taxon within opisthodontian sphenodontians, a group sharing derived cranio-dental morphologies specialized for herbivory. The new taxon was recovered in a recently discovered and unnamed series of Upper Triassic strata in southeastern Colorado, USA, exposed in Canyons incised by the Purgatoire River and its tributaries. These strata comprise a dominantly red-bed sequence of conglomerates, sandstones, and siltstones deposited in a fluvio-lacustrine setting, preserving a Late Triassic biota of invertebrate and vertebrate ichnofossils, plant macrofossils, bony fish, temnospondyl amphibians, and reptiles. We use aetosaur osteoderms as biostratigraphic links to the nearby Chinle Formation of Arizona, USA, establishing a middle Norian age for these strata. The presence of an opisthodontian from western equatorial Pangaea in the Norian Stage reveals a near-global radiation of this clade across the Pangaean supercontinent during the Late Triassic.

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Introduction

Knowledge of lepidosaurian (lizards, snakes, amphisbaenians, and tuatara) origins in the Triassic is largely based on fossils from Europe and South America (e.g., Fraser and Benton, 1989; Jones et al., 2013; Whiteside et al., 2017; Simões et al., 2018; Hsiou et al., 2019; Romo de Vivar et al., 2020). The record of this clade in the Upper Triassic rocks of western North America is comparatively incomplete. This is surprising because of the extensive paleontological research on Upper Triassic strata in the Chinle and Dockum basins, and is likely a result of biases towards collection of large-bodied tetrapod taxa such as metoposaurids, aetosaurs, phytosaurs, and dinosaurs (Kligman et al., 2017, 2018; Stocker et al., 2019). Triassic-aged lepidosaurs are reported from at least 12 localities in western North America, suggesting they were common elements of these ecosystems, but occurrences are almost entirely comprised of highly fragmentary dentigerous material that severely limits understanding of their diversity, biogeography, and ecology (Murry, 1987a, b; Murry and Long, 1989; Kirby, 1991; Kaye and Padian, 1994; Polcyn et al., 2002; Heckert, 2004; Heckert et al., 2008; Martz et al., 2013; Britt et al., 2016; Lucas et al., 2016).

Here we describe *Trullidens purgatorii* n. gen. n. sp. (DMNH EPV.135990), a sphenodontian rhynchocephalian from Upper Triassic strata of the Purgatoire River valley, southeastern Colorado. *Trullidens purgatorii* n. gen. n. sp. is the first lepidosaur from the Triassic of western North America with sufficient morphological information to analyze phylogenetic relationships, revealing its inclusion within Opisthodontia (Lepidosauria: Sphenodontia). This is the earliest record of this clade from North America and one of the earliest records globally. The new taxon possesses a masticatory apparatus specialized for herbivory similar to that in other opisthodontians from the Triassic of Europe and South America, including *Sphenotitan leyesi* Martinez et al., 2013 and *Fraserosphenodon latidens* (Fraser, 1993) (Martinez et al., 2013; Herrera-Flores et al., 2018). The lower jaw bears an elongate 'incisor-like' tooth, a morphology unique among lepidosaurs, indicative of a novel ecological function within this clade. The occurrence of this taxon in the Late Triassic of North America demonstrates that opisthodontians were a globally distributed clade of small-bodied herbivores with an unknown biogeographic and evolutionary history prior to the Late Triassic.

The stratigraphic context of *Trullidens purgatorii* n. gen. n. sp. is in a poorly known sequence of Upper Triassic red beds originally mentioned by Stanton (1905), and recently re-discovered and re-interpreted (Schumacher, 2002; Heckert et al., 2012). The sequence is poorly known due to limited exposure and difficult accessibility. The strata represent a fluvio-lacustrine depositional setting and preserve a fossil biota typical of the Late Triassic of western North America (Heckert et al., 2012). The geographic isolation of these rocks from other Upper Triassic sequences in western North America renders exact stratigraphic and geochronologic correlation difficult, but limited biochronologic evidence suggests a middle Norian age. The unique fossil biota of these rocks, including *Trullidens purgatorii* n. gen. n. sp. and early sauropodomorph trackways (McClure et al., 2021), suggests biogeographic heterogeneity and endemism between Upper Triassic basins in western North America (Small and Martz, 2013; Martz and Small, 2019).

Geological setting

The specimens discussed herein are from Upper Triassic rocks exposed in a limited area of canyonlands along the main canyon of the Purgatoire River and several tributary canyons in Las Animas County, Colorado (Fig. 1.1). These rocks are mostly red in color, and consist of fluvial sandstones and conglomerates, floodplain mudstones, and paleosols (Fig. 1.2). A distinctive bed of vertebrate bone-bearing, lenticular, limestone-pebble conglomerate is present as the basal unit of the Upper Triassic sequence directly overlying the top of the Jelm Formation (Heckert et al., 2012). These rocks are exposed as cliffs and benches along the Purgatoire River and its side canyons. The Upper Triassic rocks unconformably overlie aeolianites of the Middle Triassic Red Draw Member of the Jelm Formation and are unconformably overlain by gypsiferous beds of the Middle Jurassic Ralston Creek Formation (de Albuquerque, 1988; Heckert et al., 2012).

The Upper Triassic sediments are likely derived from the Ancestral Front Range, which was located to the west in south-central Colorado in the Late Triassic (Dubiel, 1994). The Ancestral Front Range may have separated this depositional sequence of Upper Triassic strata exposed in the Purgatoire River canyonlands from the Chinle Formation in Arizona and Utah, as well as other Triassic basins in Western Colorado and Wyoming (e.g., Eagle Basin and Popo Agie Formation; Dubiel, 1994). The presence of abundant conglomerate beds and lenticular sandstone bodies in these strata indicate deposition in a high-energy fluvial setting, possibly suggesting a closer proximity to the Ancestral Front Range source area than the nearest exposures of Upper Triassic rocks in Union County, New Mexico and neighboring Oklahoma, where strata are dominated by finer-grained sediments deposited in a lower-energy setting (Stovall and Savage, 1939). Heckert et al. (2012) proposed that these rocks may be a geographic outlier of the Chinle Formation. Further investigation is needed to develop a clearer understanding of the depositional connection of the Purgatoire canyonlands deposits to the Chinle Formation.

The Upper Triassic rocks of the Purgatoire canyonlands include a diverse fossil biota of invertebrates, plants, and vertebrates. Invertebrate trace fossils attributed to *Scoyenia* are common on sandstone bedding planes, particularly in the lower half of the strata. Vertebrate ichnofossils include locally abundant vertical burrows, possibly constructed by dipnoans

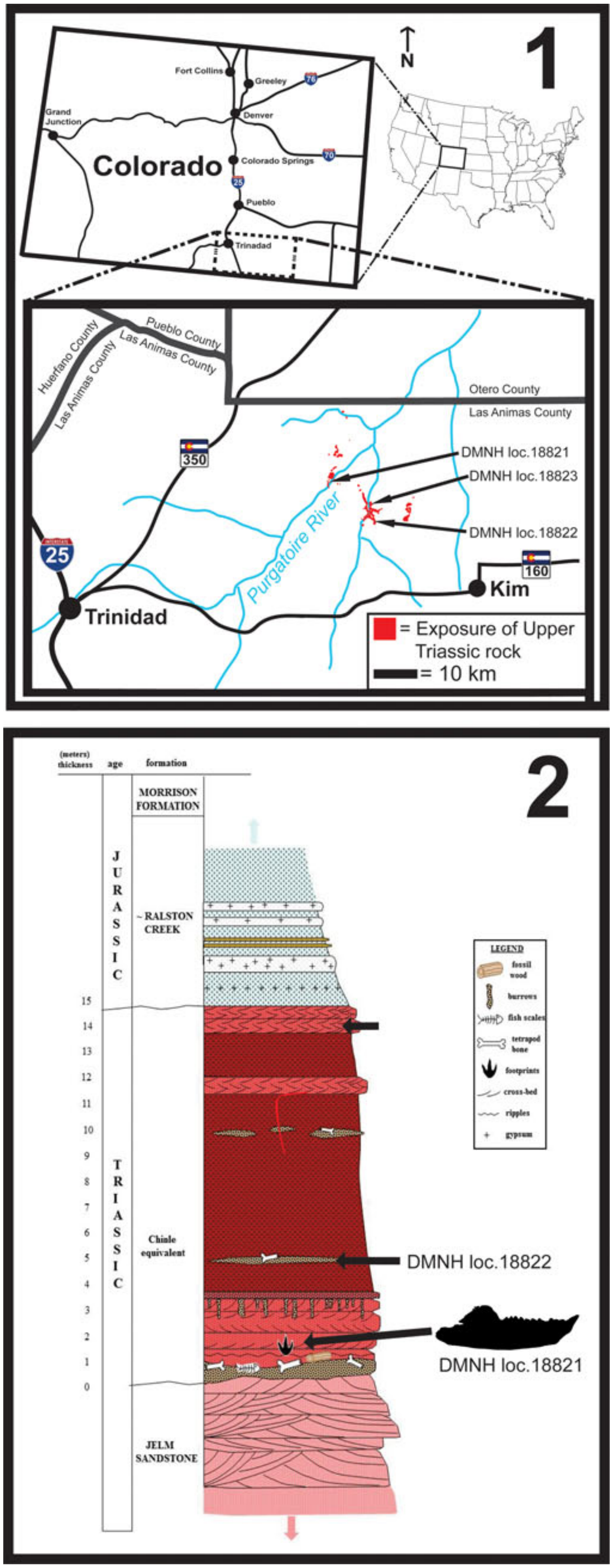

Figure 1. Geographic (**1**) and stratigraphic (**2**) locations of the holotype specimen of *Trullidens purgatorii* n. gen. n. sp. (DMNH EPV.135990; DMNH loc. 18821), and aetosaur osteoderms used for biostratigraphic correlation, including *Paratypothorax* sp. (DMNH EPV.135991; DMNH loc. 18822) and Aetosauria indet. (DMNH EPV.135992; DMNH loc. 18823).

Figure 2. (**1**) DMNH EPV.135991, *Paratypothorax* sp. right lateral osteoderm in ventral view; (**2**) DMNH EPV.135992, Aetosauria indet., right dorsal paramedian osteoderm in dorsal view. Scale bars = 1 cm.

(or other vertebrates), and a vertebrate trackway from a large tetrapod with likely sauropodomorph affinities (McClure et al., 2021). During field work conducted in 2019, plant macrofossils, paleoniscoid fish, and abundant phytosaur and aetosaur material were collected, further supporting a Late Triassic age for these strata, as reported by Heckert et al. (2012).

Two aetosaur osteoderms collected in 2019 allow for biostratigraphic correlation with the Chinle Formation. DMNH EPV.125991 is a right lateral dorsal osteoderm of a paratypothoracine aetosaur (Parker, 2007) that we refer to *Paratypothorax* sp. (Fig. 2.1) based on the following synapomorphies: (1) dorsal and lateral flanges that connect to form a laterally projected horn, (2) presence of radial grooves radiating longitudinally from an acute horn, and (3) a reduced dorsal flange (Long and Ballew, 1985; Hunt and Lucas, 1992; Parker, 2007). Occurrences of aetosaur fossils referable to *Paratypothorax* in the Chinle Formation are limited to within the Sonsela Member (‘upper subbiozone’ of the Adamanian holochronozone and the Revueltian holochronozone; Parker and Martz, 2010; Martz and Parker, 2017). The lowest documented stratigraphic occurrence of *Paratypothorax* is in the Lot’s Wife Beds of the Sonsela Member at the *Placerias* Quarry (MNA 207-2) where the taxon is represented by lateral and paramedian osteoderms (MNA V3202; Parker, 2005). The *Placerias* Quarry is isotopically dated to 219.317 ± 0.080 Ma (Ramezani et al., 2014). The highest documented stratigraphic occurrence of *Paratypothorax* in the Chinle Formation is a partial carapace (PEFO 3004) from the Crystal Forest Buttes locality (PFV 173) in the Martha’s Butte Beds of the Sonsela Member (Parker and Martz, 2010), a locality bracketed by isotopic ages of 209.926 ± 0.26 and 212.81 ± 1.25 Ma (Ramezani et al., 2011; Kent et al., 2018). DMNH EPV.125991 was collected from a lens of limestone pebble conglomerate ∼5 m above the base of the Upper Triassic Sequence in the Picket Wire Canyonlands (DMNH loc. 18822; Fig. 1.2).

The second aetosaur specimen, DMNH EPV.135992 (Fig. 2.2), is a right dorsal paramedian osteoderm similar to those of *Stenomyti huangae* Small and Martz, 2013 (DMNH EPV.60708) of the Eagle Basin in Colorado and *Aetosaurus ferratus* Fraas, 1877 of Germany and Italy, based on the small size of the osteoderm, presence of weak radiating grooves on its dorsal surface, a weak dorsal eminence that does not reach the anterior bar, and a 5:2.7 length to width ratio (Schoch, 2007; Small and Martz, 2013). DMNH EPV.135992 was collected from a lens of limestone pebble conglomerate, one meter below the contact of Upper Triassic rocks with the overlying Ralston Creek Formation (DMNH loc. 18823; Fig. 1.2). The occurrence of *Stenomyti huangae* in the Eagle Basin is biostratigraphically correlated to the Revueltian holochronozone (sensu Martz and Parker, 2017) of the Chinle Formation based on the presence of the procolophonid *Libognathus sheddi* Small, 1997, the aetosaur *Rioarribosuchus chamaensis* Lucas, Hunt, and Spielmann, 2006, and the lagerpetid *Dromomeron romeri* Irmis et al., 2007 (Small and Martz, 2013; Martz and Small, 2019). Therefore DMNH EPV.135992 adds a second, though tentative, biostratigraphic link to the Revueltian holochronozone.

Given these biostratigraphic correlations, we assign the vertebrate assemblage of the Upper Triassic strata from the Purgatoire River valley to the upper subzone of the Adamanian holochronozone and the Revueltian holochronozone with geochronologic bounds of ca. 219 to ca. 209 Ma (middle Norian). The basal conglomerates of these strata were tentatively correlated to the Cobert Canyon Bed from the base of the Chinle Formation in far western Oklahoma and northeast New Mexico or the Gartra Formation of Wyoming, which are of uncertain Late Triassic age (Heckert et al., 2012).

DMNH EPV.135990 (*Trullidens purgatorii* n. gen. n. sp.) was found embedded in the matrix of a red-brown colored limestone pebble conglomerate bed with sand-sized matrix that was exposed on the banks of the Purgatoire River (DMNH loc. 18821; Fig. 1.2; 37°27'53.67"N, 103°45'43.11W GCS). The sub-rounded imbricated limestone rip-up clasts of up to 7 cm are matrix-supported. Other vertebrate material is common in this horizon, mainly consisting of bone fragments up to 5 cm in length that are too worn or incomplete for identification. A stratigraphically equivalent sandstone bed at the same locality preserves a large sized trackway assigned to a sauropodomorph dinosaur (McClure et al., 2021).

Material and methods

Field and lab methods.—DMNH EPV.135990 was collected by hand and trimmed of excess rock matrix using a battery powered rotary tool with a diamond blade. The specimen was subsequently scanned using x-ray microcomputed microtomography (μCT scanning) at the Duke Shared Materials Instrumentation Facility on a Nikon XTH 225 ST High Resolution X-ray Computed Tomography Scanner using the following parameters: source voltage (kV) = 173, source current (μA) = 81, image pixel size (μm) = 17.42. Digital three-dimensional models were generated in Materialize Mimics 20.0 and imaged in Meshlab 2016.

Phylogenetic methods.—Evolutionary relationships of DMNH EPV.135990 were tested using a recent rhynchocephalian dataset (analysis 2 dataset of Hsiou et al., 2019). We added DMNH EPV.135990 to this dataset and performed a parsimony analysis using TNT v. 1.5 (Goloboff et al., 2008) under the following parameters: new technology search option with four rounds of tree fusing, 10 rounds of drifting, and 200 ratcheting iterations. Seven resulting most parsimonious trees were found with 253 steps each (consistency index = 0.423; retention index = 0.695). The most parsimonious trees were summarized in a maximum parsimony 50% majority rule consensus tree using traditional tree bisection and reconnection branch swapping. A Bayesian inference analysis was performed in MrBayes 3.2.6 (Ronquist et al., 2012) under the Mkv evolutionary model. The analyses used two independent runs with four Markov chains each, sampling every 1000 generations with a total of 10 million generations. The burn in fraction was set to 25% and rate variation across characters was sampled from a gamma distribution. A 50% majority rule consensus tree was produced to summarize this analysis. A time-scaled tree was produced in the package *strap* (Bell and Lloyd, 2015) using the consensus tree topology from the parsimony analysis and the temporal ranges of rhynchocephalians used in this analysis. Temporal range data are derived from the supplementary information of Hsiou et al. (2019) and incorporates new temporal range data for *Trullidens purgatorii* n. gen. n. sp., and revisions of temporal range data for *Brachyrhinodon taylori* Huene, 1910. Method summary and data sets used in phylogenetic analyses are available in the supplemental data file.

Anatomical terminology.—Terms describing tooth generations in rhynchocephalians (i.e., additional, successional, hatchling) follow the terminology of Robinson (1976) and Apesteguía et al. (2012). Herein, teeth in each of the dental generations are numbered sequentially anterior to posterior (the anterior-most tooth in each generation is tooth one, and numbers increase posteriorly).

Repositories and institutional abbreviations.—University of Aberdeen Paleontology Collection (AUP), Aberdeen, UK; Denver Museum of Natural History Vertebrate Paleontology Collection (DMNH EPV), Denver, USA; Field Museum of Natural History (FMNH), Chicago, USA; Museu Municipal Aristides Carlos Rodrigues (MMACR), Rio Grande do Sul Province, Brazil; Museum of Northern Arizona (MNA), Flagstaff, USA; Museo Carlos Ameghino, Cipolletti, (MPCA) Rio Negro Province, Argentina; Petrified Forest National Park (PEFO), Petrified Forest, USA; Division of Paleontology of the Museo de Ciencias Naturales, Universidad Nacional de San Juan (PVSJ), San Juan, Argentina; Virginia Museum of National History (VMNH), Virginia, USA.

Systematic paleontology

Lepidosauria Haeckel, 1866
Rhynchocephalia Günther, 1867
Sphenodontia Williston, 1925
Opisthodontia Apesteguía and Novas, 2003
Trullidens new genus

Type species.—*Trullidens purgatorii* n. gen. n. sp. (by monotypy).

Diagnosis.—As for type species.

Occurrence.—DMNH loc. 18821, a fossiliferous horizon in the Upper Triassic rocks of the Purgatoire River valley, J.E. Canyon Ranch, Las Animas County, Colorado, USA (Fig. 1). Estimated middle Norian age, estimated Revueltian holochronozone (sensu Martz and Parker, 2017). Detailed locality information is on file from DMNH and available to qualified researchers.

Etymology.—Named for the Latin word for trowel, ‘*trulla*’ for its trowel-like anterior-most mandibular tooth, and the Latin word ‘*dens*’ for tooth.

Remarks.—*Trullidens* n. gen. is referred to Sphenodontia Williston, 1925 based on acrodont implantation of the entire dental series in the hypodigm, where the teeth are attached to the dorsal crest of the dentary, lacking a bony wall on their labial and lingual sides. Unlike the dentition in some parareptiles, which has been described as ‘acrodont,’ the teeth in *Trullidens* n. gen. and other sphenodontians are not replaced, and instead new teeth are added at the posterior position in the jaw (Jenkins et al., 2017). Erection of this new genus is warranted given the distinct characteristics of the current hypodigm, which includes a series of features unique among sphenodontian taxa (detailed below in the species diagnosis section), particularly the elongate anterior-most tooth.

Trullidens purgatorii new species
Figures 3, 4

Holotype.—DMNH EPV.135990, a complete right dentary.

Diagnosis.—Sphenodontian rhynchocephalian with a robust dentary differing from all known sphenodontians in possessing the following unique combination of autapomorphic features in the lower jaw: an antero-dorsally projecting, elongate ‘incisor-like’ tooth extending anteriorly and dorsally beyond the mandibular symphysis; in occlusal view, the long axis of the ‘incisor-like’ tooth is medial to and

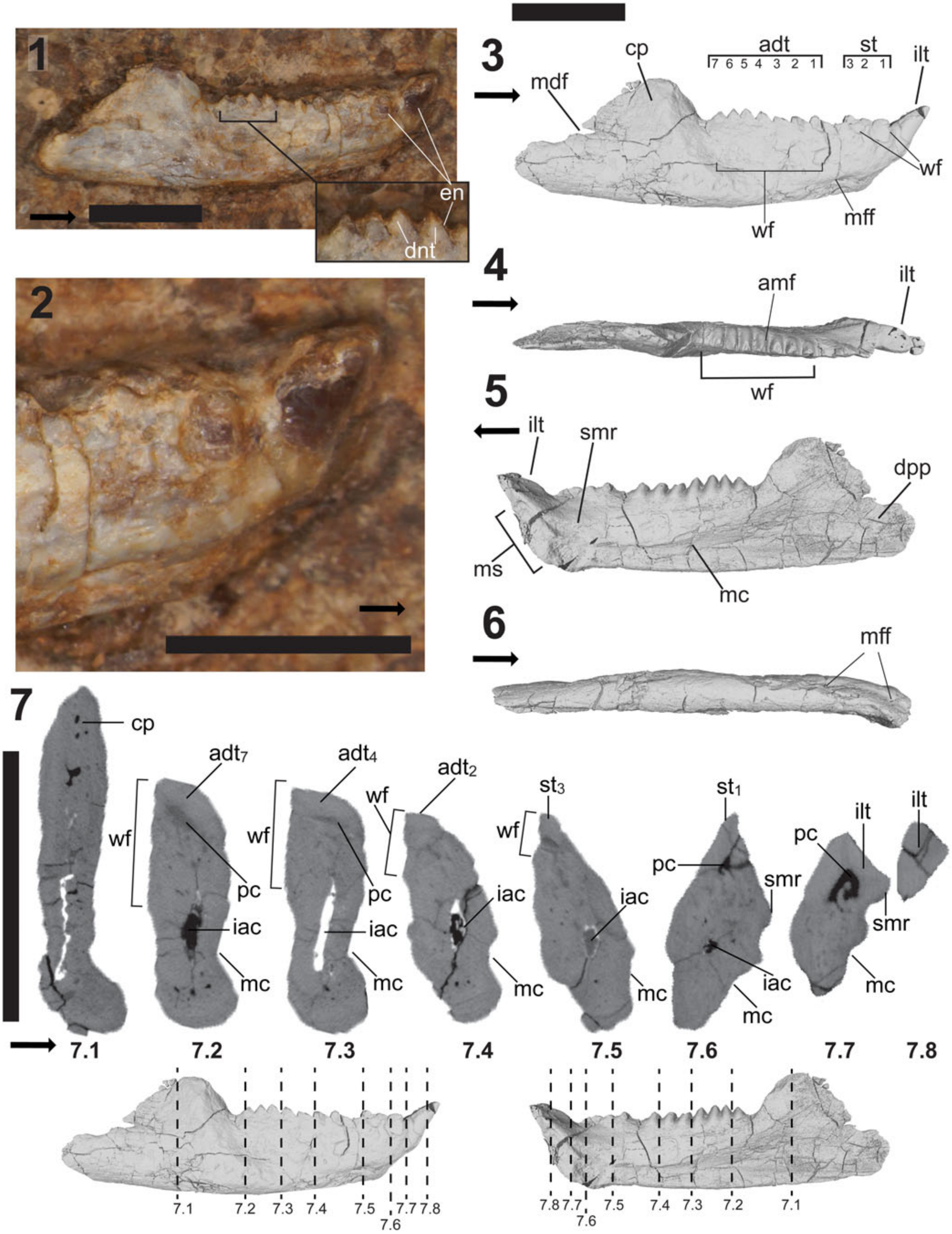
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Figure 3. DMNH EPV.135990, holotypic right dentary of *Trullidens purgatorii* n. gen. n. sp. (**1**) Labeled photograph of lateral surface of jaw embedded in rock matrix; (**2**) magnified photograph of the anterior end of the jaw in lateral view; (**3–6**), labeled images of 3D reconstruction of jaw in; (**3**) lateral view; (**4**) dorsal view; (**5**) medial view; (**6**) ventral view. Coronal μCT cross sections of DMNH EPV.135990 (**7**), locations of cross section indicated by dashed lines labeled **7.1**–**7.8**; dashed lines correspond to μCT cross sections with the corresponding label (**7.1–7.8**). Abbreviations: adt, additional teeth; amf, anteromedial flange; cp, coronoid process; dpp, dentary posterior process; dnt, dentine; en, enamel; iac, inferior alveolar canal; ilt, 'incisor-like' tooth; mdf, mandibular foramen; mc; Meckelian canal; mff, mental foramina; ms, mandibular symphysis; pc, pulp cavity; smr, supra-Meckelian ridge; st, successional teeth; wf, wear facet. Numbers indicate tooth position in each dental generation. Arrows indicate anterior direction (**1–6**) and medial direction (**7**). Scale bars = 5 mm.

parallel to the rest of the dentition; a continuous wear surface on the labial side of the dentary from the apex of the additional teeth towards the ventrolateral surface of the dentary, occupying 70% of the dorsoventral depth of the jaw (formed by occlusion with the lingual surface of the maxillary dentition); a U-shaped wear facet on the lateral surface of the second and third successional

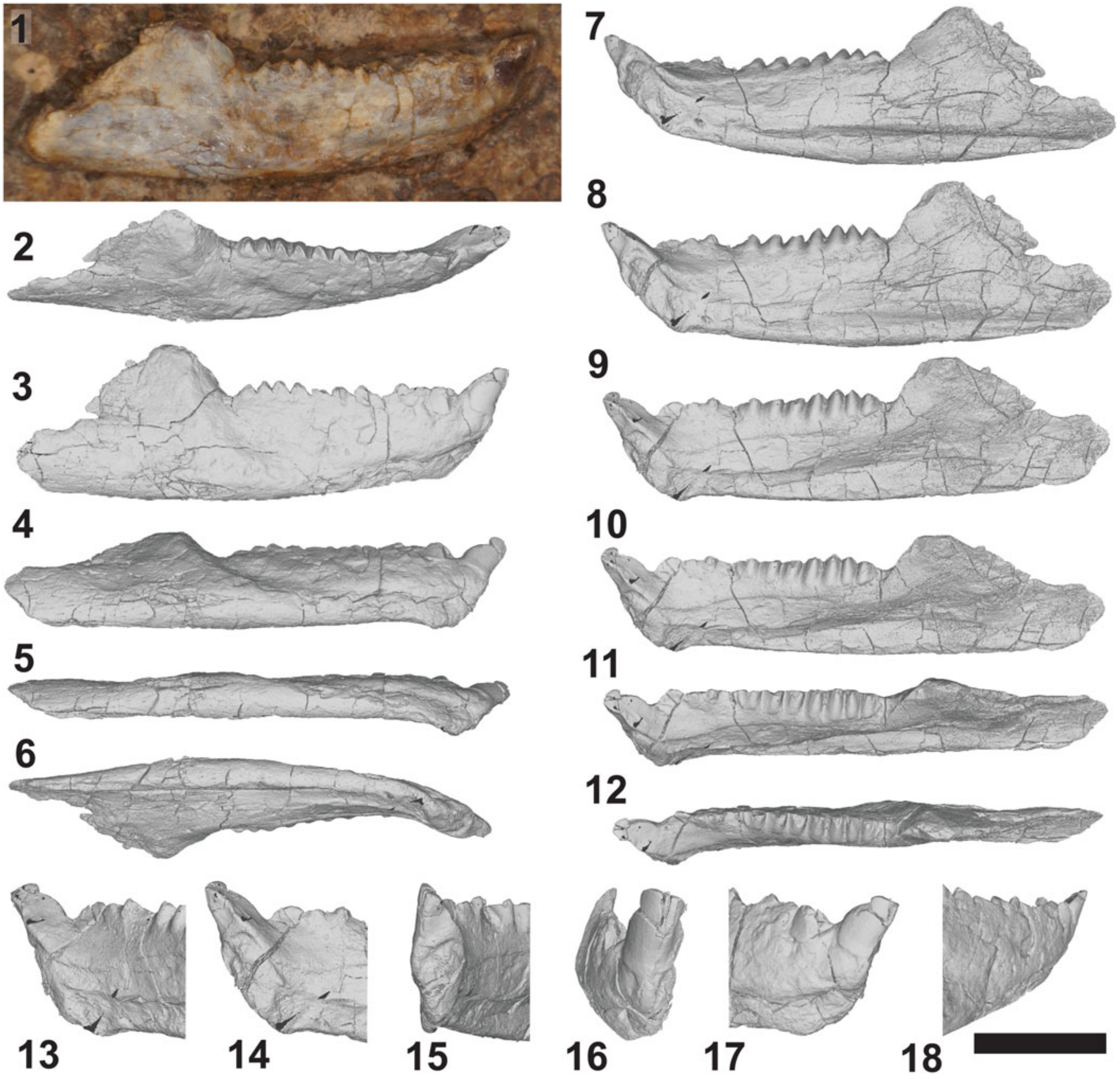

Figure 4. DMNH EPV.135990, holotypic right dentary of *Trullidens purgatorii* n. gen. n. sp. (**1**) Photograph of lateral surface of jaw. Images of 3D reconstruction of jaw (**2–12**), in: dorsolateral (**2**), lateral (**3**), ventrolateral (**4**), ventral (**5**), ventromedial (**6**, **7**), medial (**8**), dorsomedial (**9–11**), and dorsal (**12**) views. 3D reconstructions of anterior end of the jaw showing 'incisor-like' tooth (**13–18**), in: posteromedial (**13**), medial (**14**), anteromedial (**15**), anterior (**16**), lateral (**17**), and posterolateral (**18**) views. Scale bar = 5 mm.

teeth and a ventrally pointing triangular wear facet on the lateral side of the jaw between the first succession tooth and the ‘incisor-like’ tooth.

Description.—Holotype dentary DMNH EPV.135990 is a complete right dentary (Figs. 3, 4) with an anteroposterior length of 1.81 cm. Although DMNH EPV.135990 was found and collected in situ from the outcrop at DMNH Loc. 18821 with its lateral side exposed, there is no apparent damage to the specimen from weathering. Shallow incised concavities on the lateral side of the dentary are similar to wear surfaces found in other rhynchocephalians, and are interpreted to be formed by occlusion of the lingual surface of the maxillary dentition on the labial surface of the dentary during mastication.

Dentary.—In mediolateral view, the precoronoid dentary is an elongate anteriorly tapering rectangle with an anterior end inflected anterodorsally at a 45° angle. The jaw is mediolaterally thick with a maximum length-to-width ratio of 0.1. The anterior half of the lower jaw is medially curved towards the symphysis in dorsoventral view. The dorsoventral depth and mediolateral thickness of the dentary are similar to those of other opisthodontians, including *Sphenotitan leyesi*, *Opisthias rarus* Gilmore, 1909, and *Fraserosphenodon latidens* (Martinez et al., 2013; Herrera-Flores et al., 2018). The anteroposterior length of the jaw is 1.81 cm, shorter than other opisthodontians with complete dentaries such as *Opisthias rarus* and *Priosphenodon avelasi* Apesteguía and Novas, 2003 that range from 2–4 cm in length, and much smaller than *Sphenotitan leyesi* that can reach over 6 cm in length.

In mediolateral view, the coronoid process rises posterodorsally from the dorsal crest of the precoronoid dentary at a 60° angle to an overall dorsoventral height of 140% greater than the height of the posterior-most tooth. The thin bone at the anterodorsal corner of the coronoid process is broken, but the posterodorsal corner is squared off. The dorsoventrally tall, trapezoidal, robust coronoid process differs from the dorsoventrally low, triangular coronoid process in other opisthodontians where this feature is preserved (e.g., *Priosphenodon avelasi* Apesteguía and Novas, 2003). An anteriorly directed notch in the posterior margin of the coronoid forms the anterior margin of the mandibular foramen (Fig. 3.3). In mediolateral view, the ventral margin of the dentary is almost straight with a slight anterior and posterior parabolic curve. The posterior process of the jaw is short and deep, occupying 15% of the total jaw length. The posterior margin is rounded and mostly complete, and there are no clear facets for the attachment of the postdentary bones.

The Meckelian groove extends from a point ventral to the coronoid process to the mandibular symphysis (Fig. 3.5). It is mediolaterally shallow and dorsoventrally tall, occupying 40% of the dorsoventral depth of the jaw ventral to the posterior-most additional tooth, and tapering anteriorly to a minimum height where it meets the mandibular symphysis where it occupies 12% of the dorsoventral depth of the jaw. As it approaches the symphysis the groove shallows in its mediolateral depth, a similar morphology to that of clevosaurs such as *Clevosaurus hudsoni* Swinton, 1939 (Fraser, 1988) as well as opisthodontians including *Sphenotitan leyesi* (PVSJ 887; Martinez et al., 2013), *Toxolophosaurus cloudi* Olson, 1960 (Throckmorton et al., 1981), and *Kaikaifilusaurus calvoi* Simón and Kellner, 2003. The mandibular symphysis points anteromedially and rises slightly from the surrounding bone surface to form an oval shape with its long axis oriented tilted anterodorsally at a 45° angle. It occupies 83% of the dorsoventral depth of the anterior surface of the jaw (excluding the height of the ‘incisor-like’ tooth). The mandibular symphysis is dorsoventrally tall as in other opisthodontians and forms an extensive surface (e.g., *Sphenotitan leyesi*, *Kaikaifilusaurus calvoi*). On the medial surface of the dentary between the ventral margin of the teeth and the dorsal margin of the Meckelian canal is a ridge that is subparallel with the Meckelian canal, extending from the base of the 7th additional tooth to the mandibular symphysis (‘supra-Meckelian ridge’ in Fig. 3.5). A similar ridge is present in the dentary of *Sphenotitan leyesi* (PVSJ 887; Martinez et al., 2013).

The lateral side of the dentary is marked by an extensive wear facet formed by occlusion from the lingual surface of the maxillary dentition (Fig. 3.3, 3.4, 3.7). It occupies 63% of the length of the dentigerous region of the jaw, from the posterior-most additional tooth to the anterior-most additional tooth. This wear surface extends down 70% of the dorsoventral depth of the jaw at its deepest ventral to the 5th additional tooth. The presence of a similar extensive wear facet on the labial side of the dentary teeth is shared with *Pelecymala robustus* Fraser, 1986, several opisthodontians, including *Fraserosphenodon latidens* (Fraser, 1993; Herrera-Flores et al., 2018), and *Sphenotitan leyesi* (Martinez et al., 2013). Two small wear facets occupy the lateral surface of the dentary below the successional teeth. A ventrally pointed, U-shaped wear facet occupies the labial side of the second and third successional teeth and the bone just below it (Fig. 3.3). A ventrally pointed triangular wear facet occupies the mesiolabial side of the first successional tooth and the dentary bone between that tooth and the ‘incisor-like’ tooth (Fig. 3.3). Two mental foramina are present on the ventrolateral side of the jaw, ventral to the first successional tooth and the gap between the successional and additional teeth (Figs. 3.3, 3.6).

Dentition.—All teeth have acrodont implantation, and 11 teeth occupy the dentigerous region of the jaw. Three dental generations of teeth are present in anterior to posterior sequence (sensu Robinson, 1976): a single large ‘incisor-like’ tooth at the anterior end of the jaw, three successional teeth just posterior to the ‘incisor-like’ tooth, and seven labiolingually broadened additional teeth with extensive labial wear.

The ‘incisor-like’ tooth is wedge-shaped with a flat dorsal surface with sharp edges where it meets the rounded surface formed by the medial, ventral, and lateral sides of the tooth (Figs. 3.1–3.4, 3.7.8, 4.13–4.18). It is the only tooth in the jaw that lacks wear on its labial side, and therefore is the only tooth with extensive enamel on its labial side. Although mostly obscured by rock matrix, the apical surface of this tooth is enamel-less, exposing a flat dentine surface that meets the enamel-covered labial side at an acute angle (Figs. 3.2, 4.13–4.18). The lingual side of this tooth is a flat-planar surface forming a dorsal extension of the symphyseal surface, such that left and right ‘incisor-like’ teeth would form a single chisel-like spur in life. It is unclear whether enamel is present on the lingual side of this tooth because it is covered in rock matrix, and the µCT data lacks resolution to differentiate enamel from dentine (Fig. 3.7.7, 3.7.8), but the aforementioned symphyseal structure of the lingual surface may indicate the absence of enamel on this surface. When included in the dorsoventral depth of the anterior end of the jaw, this tooth is 45% of the total depth and projects anterodorsally beyond the end of the dentary bone. The 'incisor-like' morphology of this tooth is unique among lepidosaurs, with exception of the Norian-aged sphenodontian *Clevosaurus hadroprodon* Hsiou et al., 2019 (MMACR PV-027-T), which bears an anterodorsally projecting tooth at the anterior-most position in the dentary. In *Clevosaurus hadroprodon* this tooth is less elongate than in *Trullidens purgatorii* n. gen. n. sp. Opisthodontian sphenodontians bear an anterodorsally projecting mandibular spur, exemplified in *Sphenotitan leyesi* (PVSJ 887), *Priosphenodon avelasi*, (MPCA 300; Apesteguía and Novas, 2003), and *Toxolophosaurus cloudi* (FMNH UR 619; Throckmorton et al., 1981), although this spur is formed by edentulous bone of the dentary and not an enamel-bearing tooth. Within Rhynchocephalia, successional teeth in the anterior of the lower jaw that are substantially larger than adjacent teeth are referred to as 'caniniform' (Apesteguía et al., 2012) and are present in many taxa, including *Theretairus antiquus* Simpson, 1926, *Sphenovipera jimmysjoyi* Reynoso, 2005, *Sphenocondor gracilis* Apesteguía, Gómez, and Rougier, 2012, and *Sphenodon punctatus* (Gray, 1842) (Jones, 2009). The anterior-most tooth in *Trullidens purgatorii* n. gen. n. sp. and *Clevosaurus hadroprodon* differs substantially from the aforementioned taxa with true caniniform teeth because of its anterior-most position, the robust chisel-like shape, and its anterodorsally projection beyond the anterior margin of the dentary.

Posterior to the 'incisor-like' tooth are three labiolingually compressed successional teeth with a triangular shape and rounded apices in lateral view. All three teeth are closely spaced with no gaps between them (Fig. 3.3). The apical margin of each tooth forms a continuous acute ridge extending from the anterior-most to posterior-most tooth. The first successional tooth has a small amount of enamel on its labial side (Fig. 3.2), but the enamel is not present where the triangular wear facet cuts the anterior surface of the tooth. This tooth resembles the second anterior-most tooth in the dentary of *Fraserosphenodon latidens* (AUP 1192; Herrera-Flores et al., 2018). The second and third successional teeth are worn on their labial sides by the U-shaped wear facet (Fig. 3.3, 3.7.5).

No hatchling teeth are present between the successional and additional generations, suggesting a later stage in ontogeny for this individual. A gap separates the third successional tooth from the first additional tooth. The additional teeth all share a similar morphology, forming labiolingually widened rectangular outlines in occlusal view (Fig. 3.4). The labiolingual width of these teeth reduces anteriorly and posteriorly, with the third tooth being the widest. The teeth are closely spaced with no gaps between teeth. The teeth have anteromedially oriented flanges extending down the medial surface of the jaw (Fig. 3.4). The overall shape of each tooth is a loaf with a rounded apex that becomes more acute in the labial direction. Enamel covers the surface of each tooth except for the labial side. Wear from the lingual surface of the maxillary dentition has produced a vertical wear facet and exposes cross sections of the internal tissues of the teeth showing enamel and dentine layers (Fig. 3.1). The shape and size of these teeth resemble the posterior dentition of *Fraserosphenodon latidens* (Fraser, 1993; Herrera-Flores et al., 2018), and *Sphenotitan leyesi* (Martinez et al., 2013).

The resolution of the µCT scans prohibits differentiation of dental and mandibular tissue types (e.g., enamel, dentine, attachment tissue), but some features of the internal structure are apparent (Fig. 3.7). A sheet-like vascular bed (pulp cavity) floors the base of each additional tooth ('pulp cavity' in Fig. 3.7.2, 3.7.3). This resembles the structure of the sheet-like vascular beds in the eilenodontine opisthodontian *Priosphenodon avelasi* (LeBlanc et al., 2020), and in both *Trullidens purgatorii* n. gen. n. sp. and *Priosphenodon avelasi* these vascular beds progressively decrease in size anteriorly and are absent in the oldest anterior-most additional teeth (Fig. 3.7.4). In lateral view, the wear surface on the labial side of the additional tooth series exposes the internal dental structure (Fig. 3.1), revealing two features: (1) the enamel layer is ∼0.2 mm thick; and (2) the distal side of each tooth overlaps the basal 1/2–1/3 of the posteriorly adjacent tooth (shown best in additional teeth four and five, Fig. 3.1). In *Priosphendon avelasi*, the enamel layer on the additional teeth reaches a thickness of 0.6 mm (LeBlanc et al., 2020), significantly thicker than the 0.2 mm thickness in *Trullidens purgatorii* n. gen. n. sp., however the dentary of *Priosphendon avelasi* is about twice the size in *Trullidens purgatorii* n. gen. n. sp. The additional teeth of *Priosphendon avelasi* and *Trullidens purgatorii* n. gen. n. sp. overlap and anchor to the enamel surface of the immediately adjacent posterior tooth, which is a feature also apparent in *Fraserosphenodon latidens* and *Pelecymala robustus* (Fraser, 1986; Herrera-Flores et al., 2018).

Etymology.—Named 'purgatorii' for the type locality on the bank of the Purgatoire River.

Remarks.—The taphonomic setting of the bone-bearing unit (DMNH loc. 18821) that produced the holotype of *Trullidens purgatorii* n. gen. n. sp. (DMNH EPV.135990) makes discovery of additional material referable to this taxon unlikely. All vertebrate bone found in the limestone pebble conglomerate at DMNH loc. 18821 is highly worn, with the exception of DMNH EPV.135990. Although more material of this taxon is unlikely to be found at the holotypic locality, its presence indicates the future possibility of finding additional opisthodontian sphenodontian material from other Upper Triassic strata in western North America.

Results

Phylogenetic analyses.—Both parsimony and Bayesian-inference phylogenetic analyses recover *Trullidens purgatorii* n. gen. n. sp. within the stem-based definition of Opisthodontia, lending strong support for its inclusion within this clade (Fig. 5.1, 5.2). All most-parsimonious trees (MPT's) recovered *Trullidens purgatorii* n. gen. n. sp. in a sister group relationship with *Sphenotitan leyesi* (Fig. 5.1), with the presence of a small

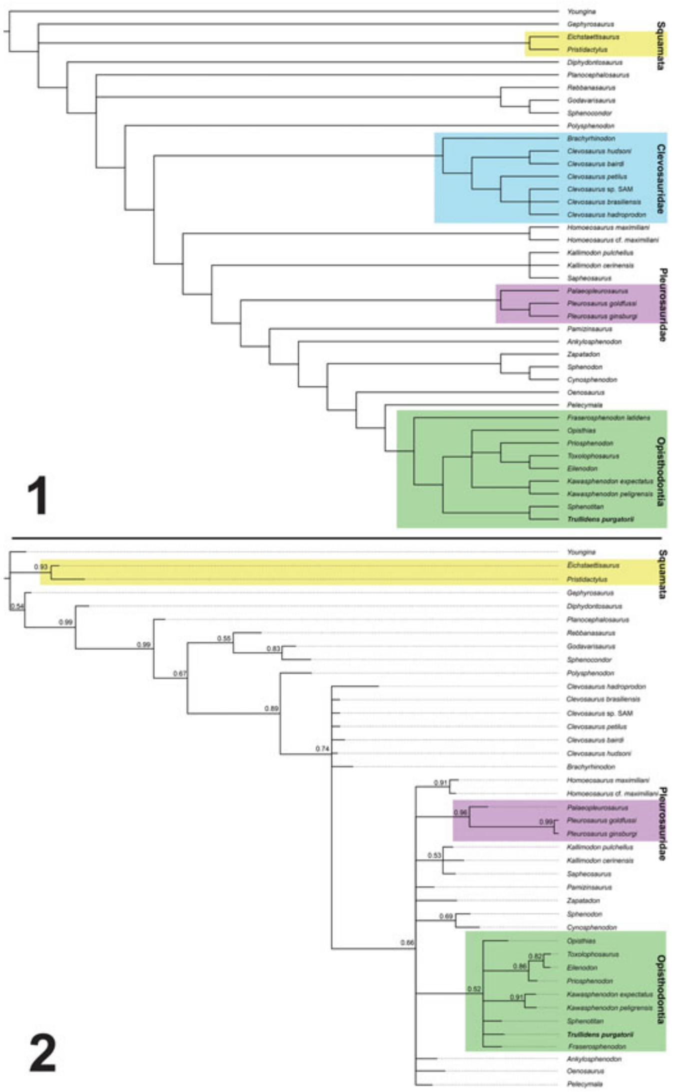

Figure 5. Phylogenetic analyses supporting the position of *Trullidens purgatorii* n. gen. n. sp. within Opisthodontia using two optimality criteria. (**1**) 50% majority rule consensus tree, CI = 0.423, RI = 0.695; (**2**) 50% majority rule consensus tree from trees produced by Bayesian-inference analysis (clade credibility values in decimal proportions labeled on nodes).

mandibular foramen as a synapomorphy of this clade (Character 37.0). All MPTs recovered *Oenosaurus muehlheimensis* Rauhut et al., 2012 as the earliest-diverging opisthodontian, with the clade *Oenosaurus muehlheimensis* + Opisthodontia sharing the following synapomorphies: an antorbital region length relative to skull length of one fourth or less (Character 1.2), a short central region between the two pterygoid rami (Character 25.0), and a well-developed and rounded Mentonian process of the mandibular symphysis (Character 33.3). The clade *Pelecymala robustus* + Opisthodontia (excluding *Oenosaurus muehlheimensis*) share marginal teeth with rectangular (wider than long) cross sections as a synapomorphy (Character 47.3). The clade *Fraserosphenodon latidens* + Opisthodontia (excluding *Pelecymala robustus* and *Oenosaurus muehlheimensis*) share the following synapomorphies: a maxilla excluded from the margin of the external naris by the posterodorsal process of the premaxilla (Character 7.1), and anteromedial flanges present in at least one mandibular tooth (Character 57.1). In all MPTs, *Trullidens purgatorii* n. gen. n. sp. + *Sphenotitan leyesi* are recovered in a sister relationship to the clade of derived opisthodontians including *Opisthias rarus*, *Kawasphenodon peligrensis* Apesteguía, Gómez, and Rougier, 2014, *Kawasphenodon expectatus* Apesteguía, 2005, *Priosphenodon avelasi*, *Eilenodon robustus*, and *Toxolophosaurus cloudi*, sharing the following synapomorphies: a well-developed, anterodorsally projected symphyseal spur (Character 36.1), and extensive posteromedial flanges on posterior maxillary teeth (Character 50.2). In the consensus tree the polytomy including *Opisthias rarus*, *Kawasphenodon peligrensis*, *Kawasphenodon expectatus*, *Priosphenodon avelasi*, *Eilenodon robustus*, and *Toxolophosaurus cloudi* shares enamel ornamentation of a few striae and wide grooves on additional mandibular teeth (Character 58.2).

In the Bayesian analysis, Opisthodontia was recovered as a polytomy including *Opisthias rarus*, *Sphenotitan leyesi*, *Trullidens purgatorii* n. gen. n. sp., *Fraserosphenodon latidens*, the sister taxa *Kawasphenodon expectatus* and *Kawasphenodon peligrensis*, and a clade including *Priosphenodon avelasi*, *Eilenodon robustus*, and *Toxolophosaurus cloudi*. *Fraserosphenodon latidens* was recovered within a monophyletic Opisthodontia, strengthening support for its inclusion within this clade (previous Bayesian analyses recovered *Fraserosphenodon latidens* outside Opisthodontia; Herrera-Flores et al., 2018).

The timing of rhynchocephalian evolution was assessed using the parsimony analysis tree topology and taxon temporal range data to produce a time-scaled phylogeny of Rhynchocephalia (Fig. 6). This analysis demonstrates the presence of two opisthodontian taxa (*Trullidens purgatorii* n. gen. n. sp. and *Sphenotitan leyesi*) by the Norian and estimates the origin of Opisthodontian rhynchocephalians to have occurred sometime prior to the Norian.

Discussion

Evolutionary implications.—Our findings suggest that in the Triassic opisthodontian sphenodontians were one of the first monophyletic lepidosaur sub-clades united by shared derived craniodental morphologies to achieve taxonomic diversity and a wide geographic distribution. Furthermore, opisthodontians appear to be exclusively herbivorous, and their Triassic representatives indicate the earliest radiation of any herbivorous lepidosaur clade. The only other clade of lepidosaurs showing a similar evolutionary pattern are clevosaurs, which are represented by six distinct species and several indeterminate occurrences in the Triassic (Table 1). The earliest clevosaurid is *Clevosaurus hadroprodon* from the Carnian of Gondwana (Hsiou et al., 2019). Norian-aged clevosaurs include *Clevosaurus brasiliensis* Bonaparte and Sues, 2006 from Gondwana, and a possible occurrence in Equatorial Pangaea (Martz et al., 2013). Rhaetian-aged clevosaurs occur exclusively in high northern latitudes of Pangaea (Europe), and include *Clevosaurus hudsoni*, *Clevosaurus sectumsemper* Klein et al., 2015, *Clevosaurus minor* Fraser, 1988, and *Clevosaurus cambrica* Keeble, Whiteside, and Benton, 2018 (Fraser, 1988; Klein et al., 2015; Keeble et al., 2018). Broad evolutionary

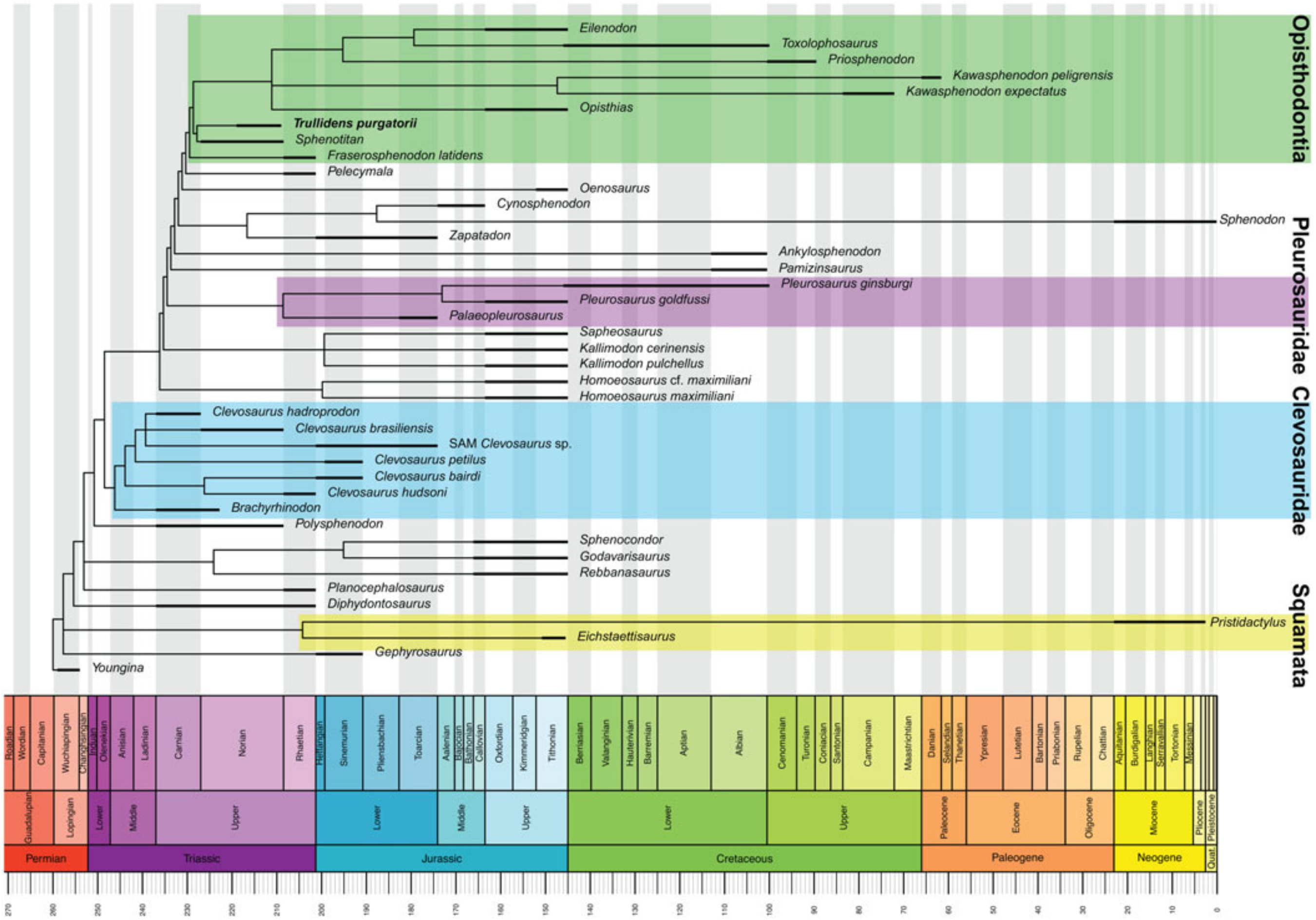

Figure 6. Time-scaled 50% majority rule consensus tree of Rhynchocephalia (tree from parsimony analysis); thickened lines represent temporal range of each taxon.

trends shared by Triassic opisthodontians and clevosaurids include: (1) Strong support for monophyly of each clade respectively, based on suites of derived craniodental features; (2) earliest records from the Carnian to middle Norian; and (3) wide distribution across Pangaea, north and south of the paleoequator by the Late Triassic. Clevosaurs and opisthodontians are characterized by relatively robust cranial elements and jaws compared to other Triassic rhynchocephalians with more delicate skeletons such as *Diphydontosaurus avonis* Whiteside, 1986 or *Lanceirosphenodon ferigoloi* Romo de Vivar et al., 2020, and taphonomic or collection biases may account for the more complete Triassic record of opisthodontians and clevosaurids.

Comparison of the dental tissues in *Trullidens purgatorii* n. gen. n. sp. to that of *Priosphenodon avelasi* shows that features including the sheet-like vascular beds and the overlapping attachment of adjacent additional tooth bases have a deep evolutionary history dating to at least the middle Norian within opisthodontians. All opisthodontians except *Fraserosphenodon latidens* share a well-developed, anterodorsally projected symphyseal spur. In *Trullidens purgatorii* n. gen. n. sp., the symphysis bears an 'incisor-like' tooth that resembles the morphology of the symphyseal spur in other opisthodontians, but in *Trullidens purgatorii* n. gen. n. sp. it is hyperextended and enamel-covered on its labial and mesial surfaces. A tooth-bearing symphyseal spur may represent the plesiomorphic condition, where the tooth was lost in later-diverging opisthodontians, or it could also represent a derived state autapomorphic to *Trullidens purgatorii* n. gen. n. sp.

Functional morphology and paleoecology.—Opisthodontians are the earliest lepidosaur clade to acquire specialized craniodental features for herbivory, a feeding ecology commonly seen in extant lizards. Therefore, the functional origins of herbivory in Lepidosauria dates back to the Late Triassic, when opisthodontians diversified and distributed. The broad distribution of opisthodontians by the Norian suggests that they may have played important roles in terrestrial ecosystems globally as small to medium body sized herbivores. Several features of the lower jaw and teeth shared in Triassic opisthodontians indicate herbivorous functions including: (1) additional teeth with rectangular tooth bases expanded along the labiolingual axis; (2) truncation of the tooth crowns on their labial margin by a wear facet (created by shearing occlusion with the lingual surface of the maxilla), exposing in cross section the enamel and dentin tissues; (3) continuation of the aforementioned dental wear facet onto the lateral side of the dentary, forming an extensive wear surface;

Table 1. Table of Triassic-aged rhynchocephalian occurrences organized by continent and from oldest to youngest, respectively, within continental groups. Occurrence nomens are displayed geographically in Figure 8.

Continent*	Locality	Geological Unit and Age	Taxa
North America			
NA1	Tomahawk Locality, Chesterfield County, Virginia, USA	Vinitia Formation, Richmond Basin, Late Triassic, Carnian (Kozur and Weems, 2007)	(1) Rhynchocephalia indet. (Sues and Olsen, 1990)
NA2	Moncure Locality (NCPALEO1904), Chatham County, North Carolina, USA	Cumnock Formation, Deep River Basin, Late Triassic, Norian, ca. 225 Ma (Whiteside et al., 2011)	(1) Rhynchocephalia indet. (Heckert et al., 2012)
NA3	Rotten Hill Bonebed (SMU Locality 121), Oldham and Potter counties, Texas, USA	Tecovas Formation, Late Triassic, Norian, Adamanian holochronozone (Martz et al., 2013; Lucas et al., 2016)	(1) Sphenodontia indet. (Lucas et al., 2016)
NA4	Post Quarry (MOTT 3624), Garza County, Texas, USA	Tecovas Formation, Late Triassic, Norian, Adamanian holochronozone (Martz et al., 2013)	(1) Sphenodontia indet., possibly Clevosauridae (Martz et al., 2013)
NA5	Lower Kalgary Locality (NMMNH 1312, Crosby County, Texas, USA	Tecovas Formation, Late Triassic, Norian, Adamanian holochronozone (Heckert, 2004; Martz et al., 2013)	(1) *Paleollanosaurus fraseri* (2) Sphenodontia indet. (Heckert, 2004)
NA6	Upper Kalgary Locality (NMMNH 1430, Crosby County, Texas, USA	Tecovas Formation, Late Triassic, Norian, Adamanian holochronozone (Heckert, 2004; Martz et al., 2013)	(1) *Planocephalosaurus lucasi* (2) Sphenodontia indet. (Heckert, 2004)
NA7	Stinking Springs, SMU Locality 252, Apache County, Arizona, USA	Blue Mesa Member, Chinle Formation, Late Triassic, middle Norian, 225.185 ± 0.079–219.317 ± 0.080 Ma (Ramezani et al., 2011).	(1) Sphenodontia indet. (Polcyn et al., 2002)
NA8	Placerias Quarry (MNA 207-2), Apache County, Arizona, USA	Sonsela Member, Chinle Formation, Late Triassic, Norian, Adamanian holochronozone, 219.39 ± 0.16 Ma (Ramezani et al., 2014)	(1) Sphenodontia indet. (Murry, 1987b; Kaye and Padian, 1994)
NA9	Lungfish Locality (SMU 227), Navajo County, Arizona, USA	Petrified Forest Member, Chinle Formation, Late Triassic, Norian, Revueltian holochronozone, 213.124 ± 0.069–209.926 ± 0.072 Ma (Ramezani et al., 2014)	(1) Sphenodontia indet. (Murry and Long, 1989)
NA10	SMU Locality 129, Quay County, New Mexico, USA	Redonda Formation, Late Triassic, Norian (Murry and Long, 1989)	(1) Sphenodontia indet. (Murry and Long, 1989)
NA11	Near the junction of Routes 6A, 91, and 15, between Meriden and Middletown, Connecticut, USA	New Haven Arkose, Hartford Basin, Newark Supergroup, Late Triassic, middle Norian, ca. 212 ± 2 Ma (Wang et al., 1998)	(1) *Colobops noviportensis* (Sues and Baird 1993; Pritchard et al., 2018; Scheyer et al., 2020)
NA12	DMNH loc. 18821, Las Animas County, Colorado, USA	Upper Triassic Rocks in Purgatoire River Canyonlands, Late Triassic, Norian, Revueltian holochronozone	(1) *Trullidens purgatorii* n. gen. n. sp.
NA13	Billingsley Bonebed (MNA 360), Coconino County, Arizona, USA	Owl Rock Member, Chinle Formation, Late Triassic, Rhaetian, 207.8 Ma (Ramezani et al., 2011)	(1) Sphenodontia indet. (Kirby, 1991)
NA14	MNA 791, Coconino County, Arizona, USA	Owl Rock Member, Chinle Formation, Late Triassic, Rhaetian, 207.8 Ma (Ramezani et al., 2011)	1) Sphenodontia indet. (Kirby, 1991)
NA15	*Coelophysis* Quarry (Block C-8-82), Rio Arriba County, New Mexico, USA	Rock Point Member, Chinle Formation, Late Triassic, Rhaetian (Ziegler et al., 2008)	1) *Whitakersaurus bermani* (Heckert et al., 2008)
NA16	Saints and Sinners Quarry (BYU loc. 1442), Wasatch County, Utah, USA	Nugget Sandstone, Late Triassic, Late Norian or Rhaetian (Britt et al., 2016, 2018)	(1) Sphenodontia indet.—elongate jaw morphotype (2) Sphenodontia indet.—shorter jaw morphotype (Britt et al., 2016)
NA17	Area VI, Jameson Land, Greenland	Carsberg Fjord Beds, Flemming Fjord Formation, Late Norian–early Rhaetian (Clemmensen et al., 2016)	(1) Sphenodontia indet. (Jenkins et al.,1994)
NA18	Area VI, Jameson Land, Greenland	Tait Bjerg beds, Flemming Fjord Formation, Late Norian–early Rhaetian (Clemmensen et al., 2016)	(1) Sphenodontia indet. (Jenkins et al., 1994)
South America			
SA1	Linha Bernardino locality, Candelária municipally, Rio Grande do Sul State, Brazil	Santa Maria Formation (Supersequence Santa Maria, Candelária Sequence, Hyperodapedon Zone), Late Triassic, late Carnian, ca. 233.23 ± 0.73 Ma (Langer et al., 2018)	(1) *Clevosaurus hadroprodon* (Hsiou et al., 2019)
SA2	Linha Sao Luiz outcrop, Faxinal do Soturno city, Rio Grande do Sul State, Brazil	Candelaria Sequence, Santa Maria Supersequence (Riograndia Vertebrate Assemblage Zone), Late Triassic, Norian, ca. 225.42 ± 0.37 Ma (Langer et al., 2018)	(1) *Clevosaurus brasiliensis* (Bonaparte and Sues, 2006) (2) *Lanceirosphenodon ferigoloi* (Romo de Vivar et al., 2020)
SA3	'Balde de Leyes' fossil locality, San Juan Province, Argentina	Upper layers of the Quebrada del Barro Formation of the Marayes-El Carrizal Basin, Late Triassic, Norian (Martinez et al., 2013; Martinez and Apaldetti, 2017)	(1) *Sphenotitan leyesi* (Martinez et al., 2013)
India			
IN1	Red mudstone bed above the *Unio* bed exposed near Jora village, Shahdol district of Madhya Pradesh, India	Tiki Formation, Late Triassic, Carnian or Norian (Datta and Das, 2001)	(1) Rhynchocephalia indet. (Ray et al., 2016; Kumar and Sharma, 2019)

Table 1. Continued.

Continent*	Locality	Geological Unit and Age	Taxa
Europe			
EU1	Schumann Quarry, Eschenau near Vellberg (bed E6), Baden-Württemberg, Germany	Erfurt Formation, Middle Triassic, Ladinian, 238–238.8 (Kozur and Bachmann, 2010)	(1) Rhynchocephalia indet. (cf. *Diphydontosaurus*)—Type R17, (Jones et al., 2013; Schoch et al., 2018) (2) Rhynchocephalia indet.—Type R18 (Schoch et al., 2018)
EU2	"Reptiliferous beds" of Lossiemouth, Scotland, United Kingdom (Huxley, 1867)	Lossiemouth Sandstone Formation, Late Triassic, Carnian (Benton and Walker, 1985)	(1) *Brachyrhinodon taylori* (Huene, 1910; Fraser and Benton, 1989)
EU3	Hoffmannsthal near Fallersleben, Lower Saxony, Germany	Middle Keuper, Late Triassic, Carnian or Norian (Fraser and Benton, 1989)	(1) *Polysphenodon muelleri* (Jaeckel, 1911; Fraser and Benton, 1989)
EU4	"Fossiliferous Locality of Cene", Lombardy, Italy (Renesto, 1995)	Riva di solto shales, Zorzino limestone, Late Triassic, Norian (Renesto, 1995; Tintori and Lombardo, 2018)	(1) *Diphydontosaurus* sp. (Renesto, 1995)
EU5	Clay pit at Krasiejow, Opole Province, Poland	Keuper unit, Late Triassic, Norian (Racki and Szulc, 2015; Szulc et al., 2015)	(1) *Diphydontosaurus* sp. (2) *Planocephalosaurus* sp. (3) Rhynchocephalia indet. (Kowalski et al., 2019)
EU6	Cromhall Quarry, South Gloucestershire, England, United Kingdom	Fissure-fill deposit, Late Triassic, Rhaetian (Whiteside et al., 2016; Morton et al., 2017)	(1) *Planocephalosaurus robinsonae* (Fraser and Walkden, 1984) (2) *Clevosaurus hudsoni* (Swinton, 1939) (3) *Clevosaurus minor* (Fraser, 1988) (4) *Fraserosphenodon latidens* (Fraser, 1993; Herrera-Flores et al., 2018) (5) *Sigmala sigmala* (Walkden and Fraser, 1983) (6) *Pelecymala robustus* (Walkden and Fraser, 1983)
EU7	Holwell Quarry, Somerset, England, United Kingdom	Fissure-fill deposit, Late Triassic, Rhaetian (Whiteside et al., 2016)	(1) *Gephyrosaurus evansae* (2) *Penegephyrosaurus curtiscoppi* (Whiteside and Duffin, 2017)
EU8	Emborough Quarry, Somerset, England, United Kingdom	Fissure-fill deposit, Late Triassic, Rhaetian (Whiteside et al., 2016)	(1) *Sphenodontia* sp. (Fraser, 1993)
EU9	Tytherington Quarry, South Gloucestershire, England, United Kingdom	Fissure-fill deposit, Late Triassic, Rhaetian (Whiteside et al., 2016)	(1) *Diphydontosaurus avonis* (Whiteside, 1986) (2) *Clevosaurus* sp. (Whiteside and Marshall, 2008) (3) *Planocephalosaurus* sp. (Whiteside and Marshall, 2008)
EU10	Woodleaze Quarry, Gloucestershire, England, United Kingdom	Fissure-fill deposit, Late Triassic, Rhaetian (Whiteside et al., 2016)	(1) *Clevosaurus sectumsemper* (2) *Diphydontosaurus avonis* (Klein et al., 2015)
EU11	Durdham Down, Bristol, England, United Kingdom	Fissure-fill deposit, Late Triassic, Rhaetian (Whiteside et al., 2016)	(1) *Diphydontosaurus avonis* (2) *Clevosaurus* sp. (3) *Planocephalosaurus* sp. (Foffa et al., 2014)
EU12	Pant-y-ffynnon Quarry, Glamorgan, Wales, United Kingdom	Fissure-fill deposit, Late Triassic, Rhaetian (Whiteside et al, 2016)	(1) *Clevosaurus cambrica* (2) *Diphydontosaurus* sp. (3) Rhynchocephalia sp. (Keeble et al., 2018)
EU13	Ruthin Quarry, Wales, United Kingdom	Fissure-fill deposit, Late Triassic, Rhaetian (Whiteside et al., 2016)	(1) *Planocephalosaurus* sp. (2) *Diphydontosaurus* sp. (Skinner et al., 2020)
EU14	Hallau-Bratelen, Canton Schaffhausen, Switzerland	Klettgau Formation, Late Triassic, Norian–Rhaetian (Whiteside et al., 2017)	(1) *Deltadectes eselvetica* (2) *Diphydontosaurus* sp. (3) *Paleollanosaurus* sp. (4) Sphenodontia sp. (Whiteside et al., 2017)

*occurrence nomens (e.g., NA1, NA2, etc…) correspond to map in Figure 8

(4) a robust dentary that is dorsoventrally deep and mediolaterally thickened; and (5) a thickened enamel layer on additional teeth (Throckmorton et al., 1981; Jones, 2008, 2009; Martinez et al., 2013). Teeth with expanded tooth bases, high surface area, and thickened enamel can withstand greater forces during mastication without breaking while concurrently providing a large surface area for food processing (Lucas and Luke, 1984; Jones, 2008, 2009). Extensive wear facet structures point to a shearing action during occlusion, and the robust jaw structure indicates increased muscle attachment for a strengthened bite force (Throckmorton et al., 1981; Jones, 2008, 2009).

The 'incisor-like' tooth in the dentary of *Trullidens purgatorii* n. gen. n. sp. is unique among lepidosaurs, and comparisons must be made to non-lepidosaur amniotes with similar morphologies to infer its ecological function. Among lepidosaurs, caniniform teeth are a common feature in some taxa including *Sphenodon punctatus* (Fig. 7.1). But only *Trullidens purgatorii* n. gen. n. sp. (Fig. 7.2) possesses a hyperextended, enamel-bearing, 'incisor-like' tooth in the anterior-most tooth position of the dentary. *Sphenotitan leyesi* (Fig. 7.3) and *Trullidens purgatorii* n. gen. n. sp. share deep, robust lower jaws, but *Sphenotitan leyesi* lacks an 'incisor-like' tooth. The only other diapsids with deep, robust lower jaws and an anterodorsal projection of the anterior-most dentary are rhynchosaurs (Archosauromorpha), where an 'incisor-like' structure is formed by dense dentary bone (Fig. 7.4). Rhynchosaurs are widely regarded as herbivorous, with a precision-shear bite, and grinding action between their teeth (e.g., Benton, 1983, 1984). This suite of features is also seen in some mammals (Apesteguía, 2008; Apesteguía and Carballido, 2014), including a robust and deep lower jaw with a tall coronoid process, expanded posterior teeth, and an anteriodorsally projected 'incisor-like' tooth in the lower jaw (Fig. 7.5, 7.6). In extant mammals, these features are often related to herbivory, as in rodents such as *Sciurus carolinensis* Gmelin, 1788 (Fig. 7.6), but are not exclusive to herbivores and are present in the insectivorous *Daubentonia madagascariensis* (Gmelin, 1788) (Fig. 7.5). Although *Daubentonia madagascariensis* is insectivorous, its incisors are used for biting into wood, exposing the insects inside, which are then extracted with their elongate third manual digit (Petter, 1977). The structure of the 'incisor-like' tooth strongly resembles the 'nipper-facet' mode of incisor wear seen in rodents, lagomorphs, and *Daubentonia madagascariensis* (Koenigswald, 2018). Nipper-facets are formed on the paired lower incisors in the aforementioned mammals, where enamel is worn off the apical surface of the teeth leaving a dentine field, and enamel is only present on the labial and mesial surfaces. The apical wear surface is formed via abrasion with the upper incisors. Nipper-faceted incisors in lagomorphs and rodents are used for gnawing on various botanical substrates (Koenigswald, 2018). The morphological convergence of the 'incisor-like' tooth in *Trullidens purgatorii* n. gen. n. sp. to the nipper-faceted incisors in these mammals indicates its function in *Trullidens purgatorii* n. gen. n. sp. was for gnawing, and its ecological role was likely as a small-bodied herbivore with a specializing craniodental apparatus for gnawing plant material.

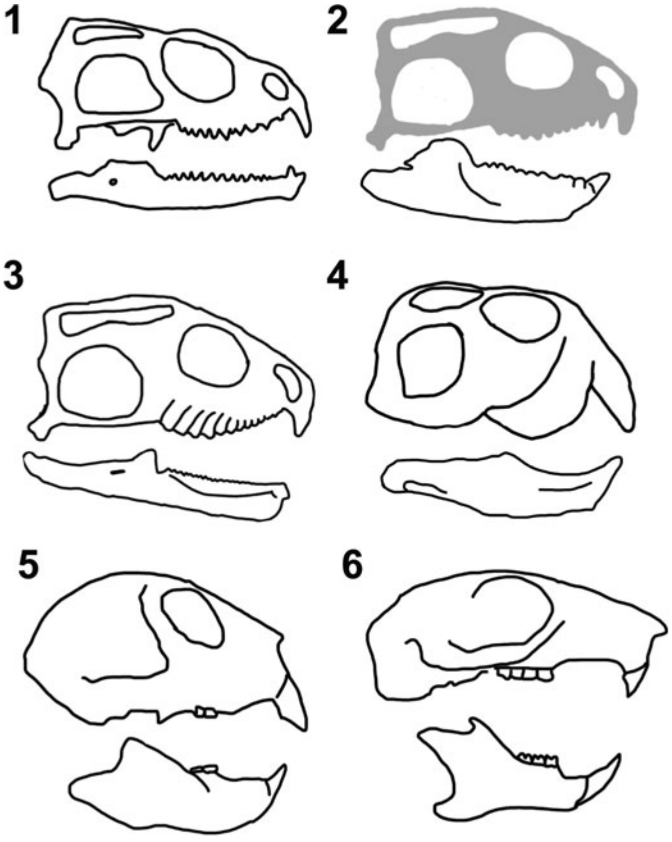

Figure 7. Comparative skull osteology of select amniotes. (**1**) *Sphenodon punctatus* (Gray, 1842); (**2**) *Trullidens purgatorii* n. gen. n. sp. (cranium based on *Sphenotitan leyesi* Martinez et al., 2013); (**3**) *Sphenotitan leyesi* (modified from Martinez et al., 2013); (**4**) *Teyumbaita sulcognathus* Montefeltro, Langer, and Schultz, 2010 (modified from Montefeltro et al., 2010); (**5**) *Daubentonia madagascariensis* (Gmelin, 1788; (**6**) *Sciurus carolinensis* Gmelin, 1788 (**5** and **6** modified from Morris et al., 2018).

Biogeography.—To analyze the biogeographic context of *Trullidens purgatorii* n. gen. n. sp., we assembled a novel dataset of all reported Triassic-aged rhynchocephalian occurrences (Table 1), visualized in Figure 8. The record of Triassic-aged rhynchocephalians from western North America is characterized by many occurrences of highly fragmentary specimens. Named taxa include *Paleollanosaurus fraseri* Heckert, 2004 and *Planocephalosaurus lucasi* Heckert, 2004 from the Tecovas Formation (Norian) in Kalgary County Texas (Heckert, 2004), and *Whitakersaurus bermani* Heckert et al., 2008 from the Chinle Formation (Rhaetian) in Rio Arriba County, New Mexico (Heckert et al., 2008). The evolutionary relationships of *Paleollanosaurus fraseri*, *Planocephalosaurus lucasi*, and *Whitakersaurus bermani* have yet to be analyzed in a phylogenetic analysis, but they resemble the early-diverging sphenodontian taxa *Diphydontosaurus avonis* and *Planocephalosaurus robinsonae* Fraser, 1982 from the Late Triassic of Europe due to the presence of dentary teeth with acrodont implantation posteriorly and pleurodont implantation anteriorly (e.g., Fraser, 1982; Whiteside, 1986). Other records of rhynchocephalians from the Triassic of western North America are reported from Arizona, New Mexico, and Texas, but are too fragmentary to establish relationships beyond Rhynchocephalia (Murry 1987a, b; Murry and Long, 1989; Kirby, 1991; Kaye and Padian, 1994; Polcyn et al., 2002;

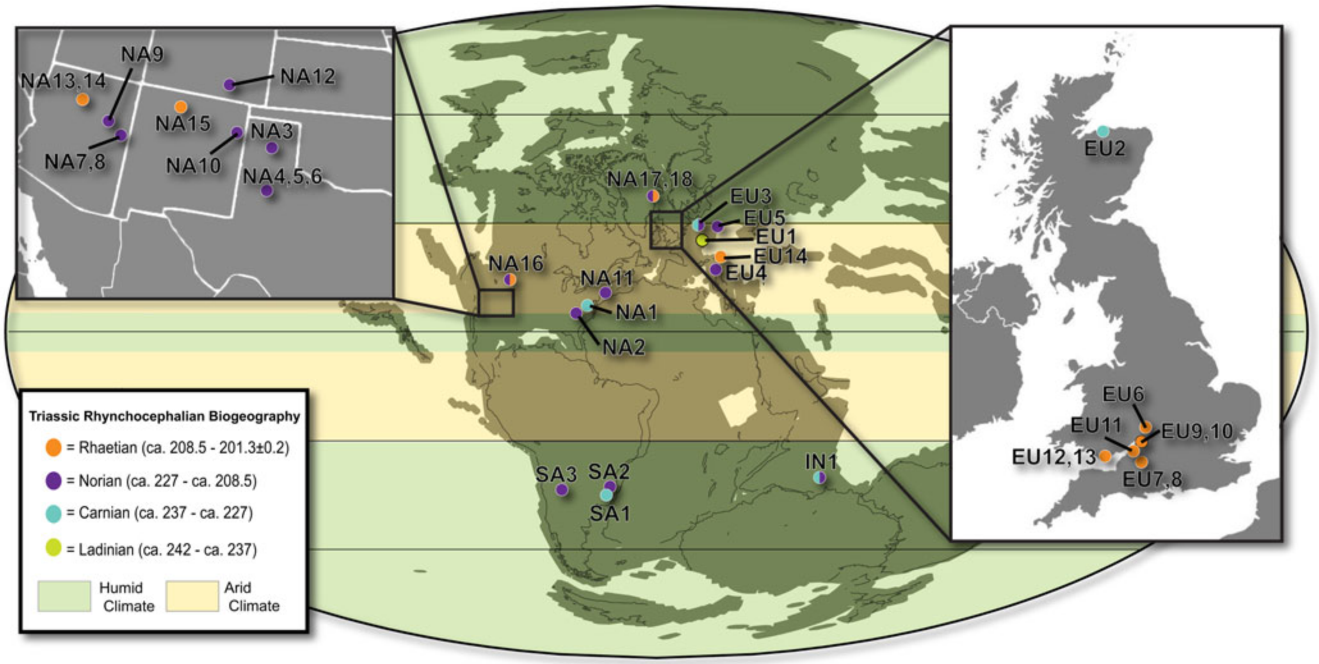

Figure 8. Paleogeographic map showing reported occurrences of rhynchocephalians during the Triassic. Locality, stratigraphic, and taxonomic information for each occurrence is included in Table 1. Paleoclimate data from Whiteside et al., 2011. Paleogeographic map modified from a map produced using the online paleogeographic map generator (Alroy, 2013).

Heckert, 2004; Martz et al., 2013; Britt et al., 2016; Lucas et al., 2016). An acrodont jaw fragment (MNA V3684; Kaye and Padian, 1994) from the *Placerias* Quarry (MNA 207-2) was referred to the opisthodontian *Clevosaurus latidens* (renamed *Fraserosphenodon latidens* sensu Herrera-Flores et al., 2018) by Fraser (1993), but a taxonomic reassessment of this and other similar fragmentary jaws from the lower Chinle Formation places them in the enigmatic diapsid genus *Palacrodon* (Kligman et al., 2017). The occurrence of *Trullidens purgatorii* n. gen. n. sp. indicates that rhynchocephalians were a common element of Late Triassic ecosystems in western North America, but prior to this study the fragmentary record obscured the importance of this region to the Triassic rhynchocephalian radiation. The discovery of *Trullidens purgatorii* n. gen. n. sp. is the first Triassic record of an opisthodontian rhynchocephalian from North America. Therefore, the Late Triassic rhynchocephalian biota of western North America includes both early diverging taxa, including *Paleollanosaurus fraseri*, *Planocephalosaurus fraseri*, and *Whitakersaurus bermani*, as well the well-nested taxon *Trullidens purgatorii* n. gen. n. sp. This assemblage is broadly similar to Late Triassic rhynchocephalian biotas from Europe and South America where assemblages include both early diverging and well-nested rhynchocephalian taxa, demonstrating the biogeographic and phylogenetic diversification of this clade by the Late Triassic in these continents (Table 1).

Trullidens purgatorii n. gen. n. sp. is one of three known Triassic-aged opisthodontian rhynchocephalians, revealing the wide geographic distribution of this clade by the Late Triassic. *Sphenotitan leyesi*, an opisthodontian notable for its large body size, is known from the Quebrada del Barro Formation (Norian) of Argentina (Martinez et al., 2013). *Fraserosphenodon latidens* is an opisthodontian known from fragmentary dentigerous material from the Rhaetian-aged Cromhall Quarry in England (Herrera-Flores et al., 2018). *Trullidens purgatorii* n. gen. n. sp. is the first opisthodontian reported from the Triassic of North America, demonstrating the widespread distribution of opisthodontians across Pangaea by the Late Triassic, with a range spanning the paleo-equator from high latitude southern Gondwana (*Sphenotitan leyesi*) to low latitude equatorial Pangaea (*Trullidens purgatorii* n. gen. n. sp.) to high latitude Laurasia (*Fraserosphenodon latidens*). This biogeographic pattern indicates that this clade either distributed across latitudinally arranged climate bands characteristic of the Late Triassic (Whiteside et al., 2011; Kent et al., 2014) or had established their range earlier in the Triassic, prior to the aforementioned Late Triassic climate regime.

The post-Triassic biogeographic distribution of opisthodontians in North America includes two Jurassic occurrences, *Opisthias rarus* (Kimmeridgian–Tithonian, Wyoming, USA; Gilmore, 1909), and *Eilenodon robustus* (Kimmeridgian–Tithonian, Colorado, USA; Rasmussen and Callison, 1981), as well as one from the Cretaceous, *Toxolophosaurus cloudi* (Aptian–Albian, Montana, USA; Throckmorton et al., 1981). In South America, there are four Cretaceous taxa, *Priosphenodon minimus* Apesteguía and Carballido, 2014 (Albian, Argentina; Apesteguía and Carballido, 2014), *Priosphenodon avelasi* (Cenomanian–Turonian, Argentina; Apesteguía and Novas, 2003), *Kaikaifilusarus calvoi* (Cenomanian, Argentina; Simón and Kellner, 2003), *Kawasphenodon expectatus* (Campanian, Argentina; Apesteguía, 2005), and *Kawasphenodon peligrensis* (Paleogene, Argentina; Apesteguía, et al., 2014). The distribution of this clade in the Triassic suggests that they became established in North and South America during the Late Triassic, where they persisted into the Cretaceous and Paleogene. Assuming that *Fraserosphenodon latidens* is an opisthodontian, this clade also occurred in Europe during the Late Triassic, but later went extinct in that area after the breakup of Pangaea (or are yet to be found in the Old-World record). If *Fraserosphenodon latidens* is not an opisthodontian, then this clade may be entirely endemic to the Americas.

Conclusions

Trullidens purgatorii n. gen. n. sp., a Norian-aged opisthodontian sphenodontian, reveals the presence of sphenodontians with derived mandibular morphology from Upper Triassic rocks in western North America. It is also the most complete and phylogenetically informative Triassic-aged lepidosaur known from western North America. The dental morphology of *Trullidens purgatorii* n. gen. n. sp. indicates an herbivorous diet, and the unique 'incisor-like' tooth suggests a novel ecological function within Lepidosauria. Extant herbivorous lepidosaurs are important elements of global ecosystems, particularly in the tropics, and the presence of *Trullidens purgatorii* n. gen. n. sp. in the Upper Triassic paleotropics demonstrates the antiquity of herbivorous lepidosaur ecologies. The addition of this taxon to the rhynchocephalian assemblage from upper Triassic strata of western North America shows similarity of this fauna to coeval rhynchocephalian assemblages of Europe and South America, where there is a mixture of early-diverging taxa and well-nested taxa with derived craniodental morphologies. The presence of a Norian-aged opisthodontian from North America shows that this clade achieved a near-global distribution by the Late Triassic, with a hidden biogeographic radiation earlier in the Triassic.

Our investigation of the geology and paleontology of Upper Triassic strata exposed by the Purgatoire River in southeastern Colorado reveals the diversity of this assemblage, with biostratigraphic links to the Chinle Formation, as well as unique elements endemic to this system. Further investigation of this geological system may reveal other unique aspects of the fauna, as well as more robust links to other Upper Triassic strata both regionally and globally.

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Data availability statement

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.2jm63xsnw.

Supplemental data include: Supplemental data 1 (S1), re-coding of characters; Supplemental data 2 (S2), Nexus file containing character scorings used in phylogenetic analyses; Supplemental data 3 (S3), character list used in phylogenetic analysis; Supplemental data 4 (S4), complete list of unambiguous synapomorphies common to the seven MPTs obtained in the parsimony analysis; Supplemental data 5 (S5), complete list of unambiguous synapomorphies found in the consensus tree obtained in the parsimony analysis; Supplemental data 6 (S6), rhynchocephalian temporal range data set used in time-scaled analysis.

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