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ARTICLE

A NEW SPECIES OF THE RAY-FINNED FISH *SAURICHTHYS* (ACTINOPTERYGII) FROM THE DOCKUM GROUP OF TEXAS (UPPER TRIASSIC, NORIAN) HIGHLIGHTS THE LATE APPEARANCE OF ELONGATE JAWS IN NEOPTERYGIANS

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ABSTRACT—The Triassic fossil record (252–201 Ma) preserves shifts in ray-finned fish (Actinopterygii) assemblages from stem-group "palaeoniscoids" to primarily neopterygians, which comprise half of extant vertebrate species. Upper Triassic deposits in the western U.S.A. show the history of the transition in ray-finned fish assemblages in fluvio-lacustrine ecosystems. We describe isolated teeth and rostra of a new species of "palaeoniscoid" ray-finned fish, †*Saurichthys justitias* sp. nov., from the Upper Triassic (early ?Norian) Boren Ranch beds of Texas, U.S.A. We demonstrate that †*S. justitias* sp. nov. possesses a fused, elongate rostropremaxillary element that is unique to †*Saurichthys* among ray-finned fishes. The Dockum species is distinct from †*Saurichthys* from the Upper Triassic (Norian) Chinle Formation of Arizona in lacking dorsal-ventral ridges along the oral margin of the rostropremaxilla. The replacement teeth in the rostropremaxilla of †*S. justitias* grow intraosseously and dorsomedial to the erupted teeth, as indicated by micro-computed tomographic data. The †*Saurichthys* in the Dockum and Chinle expand the taxon's range outside of the marine Tethys in the Norian. †*Saurichthys justitias* was likely a jaw closing velocity-specialized predator like other contemporary marine species of †*Saurichthys*. The persistence of †*Saurichthys* in Norian freshwater and marine assemblages indicates that stem-group actinopterygians occupied jaw closing velocity-specialized predatory roles even as neopterygians diversified into jaw closing force-specialized roles. Therefore, this new †*Saurichthys* highlights the disjunct timing of the appearance of force- and velocity-specialized jaws in neopterygians, suggesting that different types of mechanically specialized jaws in ray-finned fishes evolved at different rates across deep time.

http://zoobank.org/urn:lsid:zoobank.org:pub:E0D2327F-23E6-46A9-9B4F-96D9CB817BBB

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INTRODUCTION

The tendency of morphology to converge under shared selection pressures is a common pattern across animal groups (McGhee, 2011). The mechanical relationship between the morphology of lower oral jaws in ray-finned fishes (Actinopterygii) and the transmission of force and motion in biting provides an explanation for similar jaw forms in disparate lineages of actinopterygians (Westneat, 1994, 2003, 2004). Mechanical models of jaw closing as a lever system indicate that there is a tradeoff between closing force and tip velocity as influenced by opposite ratios of the length (= outlever) and ~depth (= closing inlever) of the lower jaw (Barel, 1982; Westneat, 1994, 2003, 2004). Therefore, jaw morphology can maximize jaw closing velocity or force, but not at the same time (Wainwright & Bellwood, 2002; Westneat, 1994). For instance, the elongate lower jaws of actinopterygians such as needlefishes (i.e., Belonidae), gar (i.e., Lepisosteidae), and moray eels (i.e., Muraenidae) maximize jaw closing velocity at the expense of bite force (Near & Thacker, 2024; Westneat, 2004). Conversely, antero-posteriorly short but dorsoventrally deep jaws in ray-finned fishes such as piranhas (Serrasalmidae) and sheepshead (*Archosargus probatocephalus*, Sparidae) maximize bite force at the expense of jaw tip closing velocity (Fernandez & Motta, 1997; Grubich et al., 2012; Wainwright & Bellwood, 2002; Westneat, 2004). The presence of similar jaw morphologies in extinct ray-finned fishes indicates convergence on shared function for jaw closing velocity or force and are an opportunity to study the evolution of specialized feeding morphotypes in deep time.

The †Saurichthyidae were a widespread and speciose clade of ray-finned fishes that arose in the upper Permian (Changhsingian) and persisted into the Middle Jurassic (Beltan & Tintori, 1980; Liu & Wei, 1988; Maxwell, 2016; Maxwell & Stumpf, 2017; Romano et al., 2012). Saurichthyids have elongate jaws, slender and fusiform bodies, posteriorly placed median fins, and a symmetrical caudal fin, similar to the body plan of extant needlefishes, which engage in fast acceleration ram predation relying on rapid jaw closure (Collette, 2016; Kogan et al., 2015; Kogan et al., 2020; Porter & Motta, 2004). Although saurichthyids historically have been classified as close relatives of

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Acipenseriformes, which include extant sturgeon and paddlefish (Berg, 1947; Stensiö, 1925, 1932), recent phylogenetic analyses coupled with detailed study of the endocranial anatomy of †*Saurichthys* strongly indicate their placement along the actinopterygian stem (Argyriou et al., 2018). Therefore, the similarities between saurichthyids and neopterygian ram-biting predators evolved independently.

†*Saurichthys* is one of the most speciose and widespread genera of ray-finned fishes in the Early and Middle Triassic, with over 40 species described from marine, freshwater, and brackish deposits in present-day North America, Europe, Africa (including Madagascar), Asia, and Australia (Beltan & Tintori, 1980; Griffith, 1978; Kogan & Romano, 2016; Kogan et al., 2009; Mutter et al., 2008; Rieppel, 1985; Romano et al., 2012; Schaeffer & Mangus, 1976). However, by the Late Triassic, †*Saurichthys* was largely absent from freshwater environments, instead occupying the role of a large piscivore in the marine northwestern Tethys (Lombardo & Tintori, 2005; Romano et al., 2012, 2016; Tintori, 1998). Exceptions to this trend were, until recently, fragmentary occurrences referable to †*Saurichthys* in Upper Triassic freshwater deposits in East Greenland and northern China (Chou & Liu, 1957; Fang & Wu, 2019; Jenkins, 1994). An additional possible exception is †*Saurichthys calcaratus* from the Late Triassic (Carnian) Polzberg biota of Austria, which is found within brackish/freshwater-influenced horizons of an otherwise marine assemblage (Griffith, 1977; Lukeneder & Lukeneder, 2021; Tintori & Lombardo, 2018). The recent discovery of †*Saurichthys sui* from the continental Baijiantan Formation (Upper Triassic, Carnian–Rhaetian) of Xinjiang, China clearly demonstrates that †*Saurichthys* persisted in Late Triassic freshwater environments (Fang & Wu, 2019). Further, the occurrence of †*Saurichthys* from a microvertebrate assemblage in the 'coprolite layer' of the upper Blue Mesa Member of the Chinle Formation of Arizona expanded the Norian range of the taxon into Upper Triassic fluvio-lacustrine deposits from the southwestern U.S.A. (Kligman et al., 2017). That finding indicated that the sparseness of †*Saurichthys* from Late Triassic fluviolacustrine assemblages may partially be the consequence of their occurrence as disarticulated microvertebrate remains, which are often challenging to recognize and make reliable, repeatable taxonomic assignments from.

We describe a series of rostral fragments and isolated teeth of †*Saurichthys* from the freshwater Upper Triassic Dockum Group (latest Carnian–earliest Norian) of Texas. These specimens of †*Saurichthys* are part of two novel microvertebrate assemblages collected from the Boren Ranch beds near Justiceburg in southern Garza County, western Texas (Martz, 2008). We document the morphology of the new †*Saurichthys* to place the finding into the biogeographic context of †*Saurichthys* in the Late Triassic and the temporal context of specialized jaw evolution in ray-finned fishes. We find that the internal anatomy of the rostral fragments is well preserved, allowing us to document the mechanism of tooth replacement in †*Saurichthys* for the first time. Our results also provide insight into actinopterygian evolution in the Triassic and the deep-time evolution of specialized jaw morphologies in ray-finned fishes.

MATERIALS AND METHODS

Collection and Preparation Methods

All referred specimens were found through screenwashing fossiliferous matrix collected from the MOTT VPL 3939-3 and MOTT VPL 3867-6 localities near Justiceburg, Garza County, Texas (Martz, 2008). Matrix was disaggregated in water and washed through TWP Inc. 35 Mesh T316 Stainless .011" Wire Dia wire mesh screens (minimum screen opening of ~0.5 mm, no. 35 mesh) to divide the fossiliferous matrix into size-sorted concentrate, which we picked under a dissecting microscope to isolate †*Saurichthys* specimens. One †*Saurichthys* rostrum (TTU P-24824) was broken into two pieces and re-associated by adhering the matching surfaces with Paraloid B-72.

Total Length Estimation

We estimated the total length (the straight-line distance between the anterior most part of the premaxilla and the most posterior parts of the caudal fin) of the novel †*Saurichthys* material with body size proportions from †*S. madagascariensis*, which has well-described body dimensions (Kogan & Romano, 2016). We assumed that the length of the skull (straight line between the anterior tip of the rostropremaxilla to the posterior most part of the cleithrum) is ~27% of the total length of the animal (Kogan & Romano 2016). Based on the estimate of the proportion of the preorbital length relative to the skull length in †*S. madagascariensis*, we estimate that the rostropremaxilla constitutes ~56% of skull length. Because †*S. madagascariensis* is an Early Triassic form and the postorbital size of the skull has been shown to decrease in Late Triassic saurichthyids, our calculations may slightly overestimate total length (Romano et al., 2012). Further, the rostropremaxillae from MOTT VPL 3939-3 (specimens TTU P-24824, TTU P-24825, TTU P-24826) show no separation at the midline or possess articulation surfaces with the frontals (see Kogan & Romano, 2016), indicating that they are the anterior part of the rostropremaxilla. The specimens of †*S. madagascariensis* figured by Kogan & Romano (2016) show that the anterior part of the rostropremaxilla without posterior and dorsal connection to the frontals is ~1/3 of the total length of the element. Further, TTU P-24824, TTU P-24825, and TTU P-24826 are broken both anteriorly and posteriorly, representing perhaps 90% of that 1/3. We base our calculation of the size of the rostropremaxilla, and subsequently total length, on the most complete specimen TTU P-24824.

We measured the length of TTU P-24824 as 20 mm. Assuming that this specimen is 90% complete, we estimate the length of the rostropremaxilla at ~22 mm. If we assume that the anterior part of the rostropremaxilla is ~22 mm long and ~1/3 the length of the whole rostropremaxilla, then the whole rostropremaxilla would be ~67 mm long. If the rostropremaxilla is ~67 mm long and is ~56% of the length of the skull, then the skull is ~120 mm long. Finally, if the skull is ~120 mm long and 27% of the total length, then the total length of the animal is ~444 mm or ~44 cm. Repeating the process for the other two rostropremaxillae (TTU P-24825 and TTU P-24826), which are approximately the same size but less complete (15 mm and 19 mm, respectively), we estimate those individuals at ~34 cm and ~42 cm in total length. We should note that, given a series of approximations, these measurements should be taken as rough estimates of total length. A series of assumptions had to be made to arrive at the total length, and a slight deviation (particularly at the beginning of the calculations) would change the estimation considerably. We should also note our assumption that these specimens are from adult individuals is critical, as there is evidence for negative allometry of the skull relative to the rest of the body in †*Saurichthys* (Maxwell et al., 2018). Therefore, our estimate would overestimate body size if the specimens were from juveniles.

Specimen Illustration

We photographed each specimen with an Olympus E-M5 Mark 2 digital camera and a M. Zuiko ED 60 mm F2.8 macro lens to compile image stacks to show all areas of the specimens in focus. Specimens were illustrated in Adobe Photoshop 24.7.0 by tracing features in the image stacks, with tracing decisions based on direct observation of the specimens under an Amscope brand dissecting stereomicroscope.

Computed Tomographic Methods

We μCT scanned three rostropremaxillae (TTU P-24824, TTU P-24825, TTU P-24826) with a Nikon XTH 225 ST high-resolution X-ray computed tomographic scanner in the Shared Materials Instrumentation Facility (SMiF) at Duke University. The scan parameters include source voltage = 220 kV, source current = 49 uA, and resolution (x, y, and z) = 11.16 μm. Scan data were processed using Materialise Mimics Research v. 20.0 to create cross-sectional images and 3D objects. We converted the tiff image stack from the μCT scan into LDA format and segmented/imaged the internal and external anatomy of specimens in Avizolite version 2020.3.1. The volumetric image series (.tiff stack) used to generate the images of the internal anatomy of the new *Saurichthys* rostra in this study is available on Morphosource.org (ID # 000671406). URL: https://www.morphosource.org/projects/000668516?locale=en.

Terminology

In our descriptions, length refers to the anterior-posterior dimension of the body, depth or height refers to the dorsal-ventral dimension of the body, and width refers to the mediolateral dimension of the body. We use Mickle (2015) as a source for definitions of cranial bones of the snout in early actinopterygians. We adopt the phylogenetic classification of Near & Thacker (2024) for the clade names of ray-finned fishes where possible, use an obelus symbol † to denote extinct taxa, and use the pan prefix to denote total groups. We use the term cap to refer to the acrodin cap of actinopterygian teeth and the term shaft to refer to the part of the tooth connecting the acrodin cap to the rostropremaxilla.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York, New York, U.S.A.; **BSPG**, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; **MCSNB**, Museo di Scienze Naturali de Bergamo, Bergamo, Italy; **MNHN**, Muséum National d'Histoire Naturelle, Paris, France; **MOTT VPL** Museum of Texas Tech University Vertebrate Paleontology Locality, Lubbock, Texas, U.S.A.; **NMMNH**, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, U.S.A.; **PEFO**, Petrified Forest National Park, Arizona, U.S.A.; **SMUSMP**, Southern Methodist University Shuler Museum of Paleontology, Dallas, Texas, U.S.A.; **TTU P**, Texas Tech University, Paleontology Collections, Lubbock, Texas, U.S.A.

GEOLOGICAL SETTING

The specimens examined for this project were collected by a joint Virginia Tech Paleobiology and Texas Tech team from two localities (MOTT VPL 3939-3 and MOTT 3867-6) near Justiceburg, southern Garza County, west Texas (Fig. 1). Both localities are within the Boren Ranch beds of the Dockum Group, which underly the Cooper Canyon Formation (Martz, 2008). We correlate the assemblage from MOTT VPL 3867-6 and MOTT VPL 3939-3 to the Otischalkian (Late Triassic, ?Norian) teilzone based on the occurrence of the archosauriform †*Doswellia* (TTU P-25076, TTU P-25075) and the phytosaur †*Angistorhinus* (TTU P-25077; Martz, 2008). Further evidence that the assemblage from MOTT VPL 3867 is Otischalkian in age is the occurrence of the non-phytosaurid phytosaur †*Parasuchus* (= †*Paleorhinus*, TTU P-11706; Martz, 2008; Kammerer et al., 2016). Finally, MOTT VPL 3867-6 stratigraphically underlies the Boren Quarry locality (MOTT VPL 3869, also called the Neyland site or Neyland Quarry), from near Justiceburg, Garza County, Texas, where †*Parasuchus* (= †*Paleorhinus*, TTU P-9423) has been recorded (Lehman & Chatterjee, 2005; Martz, 2008).

Our work expands on a diverse assemblage of non-tetrapod vertebrates from the Dockum Group, which includes lungfish, coelacanths, chondrichthyans, and actinopterygians (Brownstein, 2023; Gibson, 2018; Lucas et al., 1993; Martz, 2008; Murry, 1982, 1989a; Schaeffer, 1967; Warthin Jr., 1928). Although ray-finned fish remains are historically rarely found in southern Garza County, abundant actinopterygians have been collected from the Schaeffer Fish Quarry (NMMNH locality number L-3099), an ephemeral pond deposit in the Colorado City Formation of Howard County, Texas (Gibson, 2018; Lucas et al., 1993; Schaeffer, 1967). Additionally, a variety of isolated teeth and scales assignable to total-group Actinopterygii or Osteichthyes have been reported from the Dockum Group, including from the Lower Kalgary locality (NMMNH locality 1312) of the correlative Tecovas Formation of Crosby County, Texas (Heckert, 2004).

Bony fishes previously reported from southern Garza County, though rare, are primarily only assignable to total-group Actinopterygii or Osteichthyes currently (Martz, 2008). The exception is one specimen attributed to the "palaeoniscoid" actinopterygian †*Turseodus dolorensis* (TTU P-10361) from locality MOTT VPL 3792, which is most likely within the Boren Ranch beds or the lowermost Cooper Canyon Formation (Martz, 2008; Schaeffer, 1967). However, the scales of TTU P-10361 are smooth, lacking the low, sub-parallel ridges that are characteristic of †*Turseodus dolorensis* (Schaeffer, 1967). Although identifying an isolated patch of scales to genus is difficult at best, we think that TTU P-10361 is more likely from the smooth-scaled redfieldiid actinopterygian †*Lasalichthys* (Gibson, 2018).

SYSTEMATIC PALEONTOLOGY

PAN-ACTINOPTERYGII Moore & Near, 2020
†SAURICHTHYIDAE Owen, 1960 sensu Stensiö, 1925
†*SAURICHTHYS* Agassiz, 1834
†*SAURICHTHYS JUSTITIAS*, sp. nov.
(Figs. 2–5)

Holotype—TTU P-24824, partial tooth-bearing rostrum formed from the rostropremaxilla and vomer.

Etymology—Species epithet from the Latin term *iustitia* meaning justice, named for the town of Justiceburg, Texas, near the fossil locality.

Referred Specimens—MOTT VPL 3939-3: TTU P-24824, TTU P-24825, TTU P-24826 (rostropremaxilla). MOTT VPL 3867-6: TTU P-25072 (rostropremaxilla); TTU P-24827, TTU P-24828, TTU P-24829, TTU P-24830, TTU P-24831, TTU P-24832 (isolated teeth amongst hundreds from MOTT VPL 3867-6).

Diagnosis—Elongate, toothed rostropremaxilla (formed from the fusion of the rostral and premaxillae) bearing circular to elliptical pores along the lateral oral margin; lateral ornament of rostropremaxilla consisting of extremely fine (~0.1 mm) ridges oriented parallel along the long axis (anterior-posterior) of the element; rostropremaxillary teeth conical with striated shafts and smooth caps; replacement teeth grow intraosseously and dorsomedial to the functional teeth. Estimated total length of †*Saurichthys justitias* is between ~34 and 44 cm based on comparisons to the full body reconstruction of †*Saurichthys madagascariensis* (Kogan & Romano, 2016).

Comparison to Similar Species—†*Saurichthys justitias* is distinguished from †*Saurichthys* from the Blue Mesa Member of the Chinle Formation (Upper Triassic, Norian) of Petrified Forest National Park (Arizona, U.S.A.) by the ornament of the

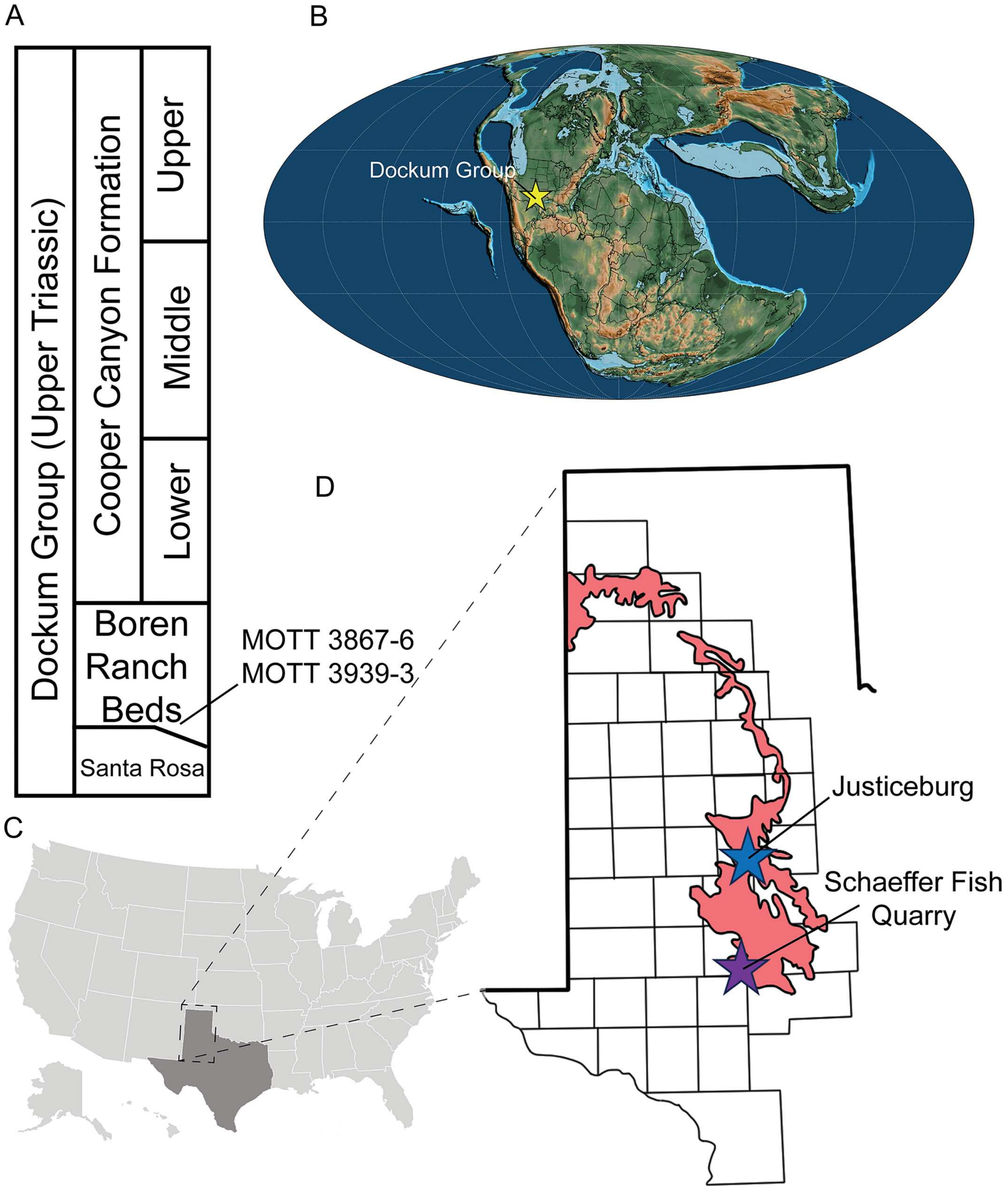

FIGURE 1. Geographic and paleogeographic context for the Dockum Group (in pink) of northwest Texas. **A**, stratigraphic context for MOTT VPL 3867-6 and 3939-3 within the Dockum Group, modified from Martz & Parker (2017). **B**, paleogeographic context of the Dockum Group in the ~early Norian stage, (210 Ma), map from Scotese (2021). **C**, location of Texas within the U.S.A. **D**, relative locations of the major localities with fish, modified from Martz et al. (2012:fig. 1) and Lehman (1994:fig. 1).

rostropremaxillae; †*S. justitias* lacks the anteriorly curved, perpendicular to the long axis of the jaw ganoine ridges that line the oral margin of the rostropremaxilla in the Chinle Formation occurrence of †*Saurichthys* (Kligman et al., 2017). †*Saurichthys justitias* can also be distinguished from †*S. taotie* from the Xiaowa Formation (Upper Triassic, Carnian) of Longbozi (Yunnan Province, China) by the ornament of the rostropremaxilla (Fang et al., 2019). Specifically, the dorsal part of the rostropremaxilla of †*S. taotie* is ornamented with thick, anterior-posterior ridges that are absent in †*Saurichthys justitias* (Fang et al., 2023). Further, †*S. taotie* is an estimated 60 cm in standard length, relatively larger than our estimated total length of †*S. justitias* (between 34 and 44 cm; Fang et al., 2023). Character not preserved in †*S. sui*, because the type (IVPP V 31230) does not preserve the rostropremaxillae (Fang & Wu, 2019). We can only compare our estimated total length of †*S. justitias* (between 34 and 44 cm) and that of †*S. sui* (40 cm), indicating that these species were similar in length (Fang & Wu, 2019). Similarly, the type of †*S. calcaratus* from the Late Triassic (Carnian) Polzberg biota of Austria is missing the anterior part of the rostropremaxilla (Griffith, 1977). Additionally, the standard length for †*S. calcaratus* is 40 cm, also within the size range we estimated for †*S. justitias*. Comparison of †*S. justitias* to species of †*Saurichthys* from the Zorzino Fauna of Italy and Austria is difficult because the morphology of the rostropremaxilla is rarely figured (Tintori, 1990). We can compare †*Saurichthys justitias* to the description of a well-preserved specimen (BSPG 1910/1/8) of †*Saurichthys deperditus* (= "†*S. krambergeri*") from Adnet, Austria, which possesses parallel ridges on the rostropremaxilla running perpendicular to the long axis of the jaw, which are absent in †*Saurichthys justitias* (Griffith, 1962). Further, the teeth of BSPG 1910/1/8 bear coarse ridges on their apical caps, which are absent in the teeth of †*S. justitias* (Griffith, 1962). We can also compare †*S. justitias* to a specimen (MCSNB 3319) of †*Saurichthys* "species A" figured by Gozzi (2004), which has a similar lateral ornament of the rostropremaxilla except for a lack of tubercles. Additionally, "species A" (Tintori, 1990) and the other Zorzino Fauna †*Saurichthys* examined by Gozzi (2004) have a median total length between 0.5 and 1 m, exceeding the estimated size range for †*S. justitias.* We can distinguish the teeth of †*S. justitias* from those of †*Birgeria* based on the smooth acrodin caps and the lack of a ridge between the acrodin cap and striated base of the teeth (Diependaal & Reumer, 2021; Fang et al., 2024).

It is difficult to make taxonomic assignments for novel disarticulated remains that correct for intraspecific variation in osteology. The literature for actinopterygians is filled with research on disarticulated, and often isolated, elements where cranial and scale ornament is a common criterion for distinguishing genera and species (Schultze et al., 2021). The present work is no exception, as we distinguish †*S. justitias* from the Chinle Formation occurrence of †*Saurichthys* based on cranial ornament. The ornamentation of the dermal bones in actinopterygians, including presence/absence, form (ridges, tubercles, denticles), and density (light versus heavy) can vary by cranial element and in skeletal ontogeny within a single species (Schultze et al., 2021). An excellent example of this phenomenon is in †*Saurichthys*, in which the form and presence/absence of dermal ornament varies across cranial elements (Kogan & Romano, 2016; Maxwell et al., 2018). Therefore, our taxonomic assignment of †*S. justitias* as a distinct species from the Chinle Formation †*Saurichthys* is only made possible by the inferred homology of the rostropremaxilla. By comparing homologous elements, we control for the potential confounding variable of intracranial ornament variation.

Locality and Age—Locality MOTT VPL 3867-6 and MOTT VPL 3939-3, Boren Ranch beds of the Dockum Group near Justiceburg, southern Garza County, Texas, U.S.A. We infer that the fossil assemblages from these localities belong to the Otischalkian (Late Triassic, ?Norian) teilzone based on the presence of the archosauriform †*Doswellia* (TTU P-25076, TTU P-25075), and the phytosaurs †*Angistorhinus* (TTU P-25077) and †*Parasuchus* (= †*Paleorhinus*, TTU P-11706; and Martz, 2008).

DESCRIPTION

Rostral Elements

We document four isolated rostra from MOTT VPL 3867-6 (TTU P-25072) and MOTT VPL 3939-3 (TTU P-24824, TTU P-24825, TTU P-24826; Fig. 2). We measured the length of TTU P-24824, TTU P-24825, and TTU P-24826 at 20 mm, 15 mm, and 19 mm, respectively. We also measured the width of TTU P-24824, TTU P-24825, and TTU P-24826 at 5 mm, 4 mm, and 6 mm, respectively. The ventral part of the rostropremaxillae bear a paired set of large teeth (= laniaries) interspersed with smaller teeth set directly posterior to each laniary. The larger teeth vary in labiolingual width from 1.7 mm to 1.2 mm, whereas the smaller teeth range from 1 mm to 0.7 mm. Although most of the rostropremaxillary teeth are broken off near their bases, the few that are complete bear acrodin caps, a synapomorphy of the actinopterygian total group (Friedman & Brazeau, 2010). The division of teeth in the Dockum rostra into two distinct size classes corresponds to other species of †*Saurichthys*, such as the †*Saurichthys* from the Chinle Formation of Arizona (Kligman et al., 2017) and †*Saurichthys madagascariensis* (Kogan & Romano, 2016; Stensiö, 1925). A ventrally flat, medial ossification bearing small, round teeth and empty sockets with irregular width (between 0.2 mm and 0.8 mm) is visible in ventral view in each isolated rostrum (Fig. 2). The medial position of a pavement-like, toothed ossification between the rostropremaxillae is a character state of the vomer of †*Saurichthys* (Argyriou et al., 2018; Stensiö, 1925).

In dorsal view, the rostra are dorsally convex and anteriorly narrow. The dorsal and lateral surfaces bear fine, regular, anterior-posteriorly aligned grooves and, in the most anterior portion, irregular, ovoid tubercles. The lateral ornament on the rostropremaxilla is less pronounced than in the Chinle occurrence of †*Saurichthys*, lacking the prominent, dorsoventral ganoine ridges along the lateral surface of the oral margin (Kligman et al., 2017). There are shallow pits tracing the oral margin in lateral view ranging from 0.2 mm to 0.6 mm in height and 0.3 mm to 0.9 mm in length. These openings vary in shape from circular to elliptical (with the long axis anterior-posterior) and do not form a straight line. Rather, where best preserved (TTU P-24824), an irregular path of lateral pits extends nearly to the anteriormost part of the rostropremaxilla. We interpret these as pores for the lateral line system because they are shallow depressions in the bone surface and not breakages, consistent with pores for canal neuromasts of the lateral line observed in extant ray-finned fishes (Webb, 2014). Specifically, we interpret the lateral line openings as the ethmoid commissure because of their position along the oral surface, whereas the mandibular canal in the dentary of †*Saurichthys* is more ventral (Kogan & Romano, 2016; Mickle, 2015). The combination of teeth and the ethmoid commissure, character states of both the premaxillae and rostral, respectively, indicates that the rostral elements are fusions of the rostral and premaxillae (Mickle, 2015). The plesiomorphic condition for ray-finned fishes is a median rostral bearing the ethmoid commissure canal and paired, toothed premaxillae (Cloutier & Arratia, 2004; Gardiner & Schaeffer, 1989; Mickle, 2015). A median rostral and paired premaxillae are retained in Polypteridae, whereas a median rostral is absent or reduced in neopterygians and premaxillae are absent in Acipenseriformes (Claeson et al., 2007; Gardiner & Schaeffer, 1989; Grande, 2010; Hilton et al., 2011).

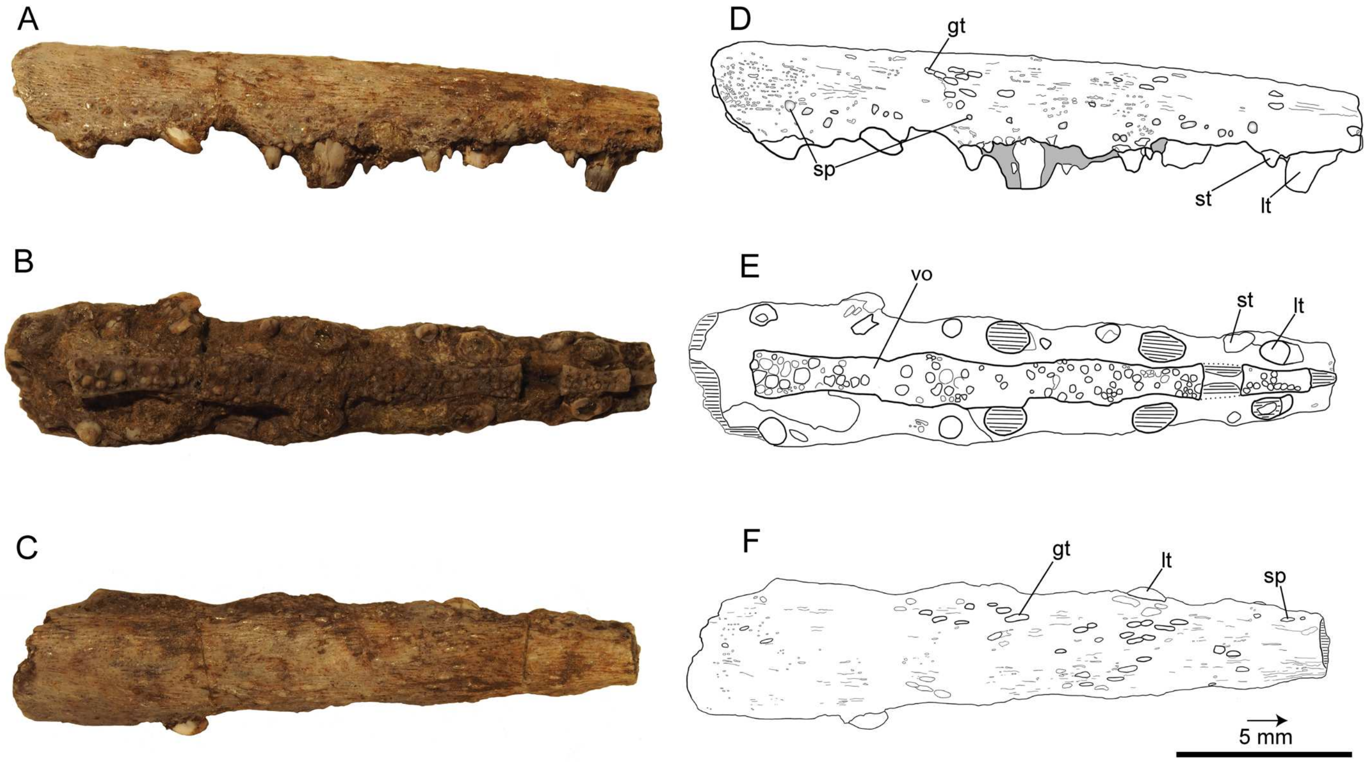

FIGURE 2. Rostropremaxilla of the holotype of †*Saurichthys justitias*, TTU P-24824, anterior on the right-hand side. **A–C**, photographs of TTU P-24824 in lateral, ventral, and dorsal view, respectively. **D–F**, line drawings of TTU P-24824 in lateral, ventral, and dorsal view, respectively. Slanted, parallel lines indicate broken surfaces and dotted lines show inferred boundaries between elements. Gray infill shows areas where bone is absent. Arrow indicates anterior direction. **Abbreviations**: **gt**, ganoine tubercle; **lt**, large teeth (= laniary); **sp**, lateral line sensory pore; **st**, small size class tooth; **vo**, vomer.

μCT scanning of the rostra yielded an unexpected wealth of data on the internal anatomy of these structures (Figs. 3, 4). †*Saurichthys justitias* provides the first look at the internal anatomy of the anterior part of the rostropremaxilla of †*Saurichthys* given that other †*Saurichthys* (from Europe, Greenland, and Spitsbergen; Argyriou et al., 2018, Stensiö, 1925) investigated with μCT lack the anterior part of the rostrum. The rostropremaxillae of †*S. justitias* are traversed by three anterior-posterior canals. The largest of the three follows the medial axis of the rostropremaxilla in TTU P-24824, TTU P-24825, and TTU P-24826. The median canal is oriented parallel to the anterior-posterior axis of the rostropremaxilla and narrows anteriorly. There are also paired canals lateral to the median canal in TTU P-24824, which also trace the entire preserved length of the rostropremaxilla. There are 15 lateral extensions on each lateral canal that are placed irregularly and asymmetrically along the anterior-posterior extension of the element. These lateral extensions vary in both length and width relative to each other. The lateral canals themselves show consistent width throughout the length of the rostropremaxilla. The lateral canals are ovoid in coronal view, whereas the median canal is rounded but broader dorsally and tapering ventrally.

Our identifications of the internal canals of the rostropremaxilla are preliminary, as the connections of these canals to the rest of the endocranial anatomy is not preserved. The internal anatomy of the rostropremaxilla is unfortunately not preserved in the specimen of †*Saurichthys* (NHM 157546 A) from the Early Triassic (Induan) of Greenland that Argyriou et al. (2018) use to describe the internal cranial anatomy of the genus. The most informative specimen for our identifications is MNHN F 1980-5 of †*S. nepalensis*, which preserves the internal cranial anatomy of the region immediately posterior to the anterior part of the rostropremaxilla (Argyriou et al., 2018). MNHN F 1980-5 shows paired nasobasal canals extending anteriorly into the rostropremaxilla which correspond in position to the paired canals in TTU P-24824. The nasobasal canals are thought to have carried the superficial ophthalmic nerve in †*Saurichthys*, a branch of the trigeminal nerve (Argyriou et al., 2018). Alternatively, the lateral canals may represent the internal part of the lateral line sensory system, with the lateral extensions connecting the internal canal to the external openings. The material figured by Argyriou et al. (2018) does not show a median canal, meaning that this structure is restricted to the anterior-most part of the rostropremaxilla in †*Saurichthys* or the median canal is not present or preserved in the species of †*Saurichthys* examined by Argyriou et al. (2018). In either case, we are not able to provide a firm identification of this structure with the information available in the Dockum material. Therefore, we leave the identification at median canal, and hope that future studies on †*Saurichthys* can clarify its identity.

Teeth

We describe isolated teeth (Fig. 5) from a sample of hundreds from MOTT VPL 3867-6, found in association with an isolated rostropremaxilla (TTU P-25072). Each tooth has a shaft ornamented with thin, closely packed, longitudinal striations and a smooth, white cap that can be translucent at the edges. This combination of traits are character states of †*Saurichthys*, which has teeth with a shaft formed from plicidentine

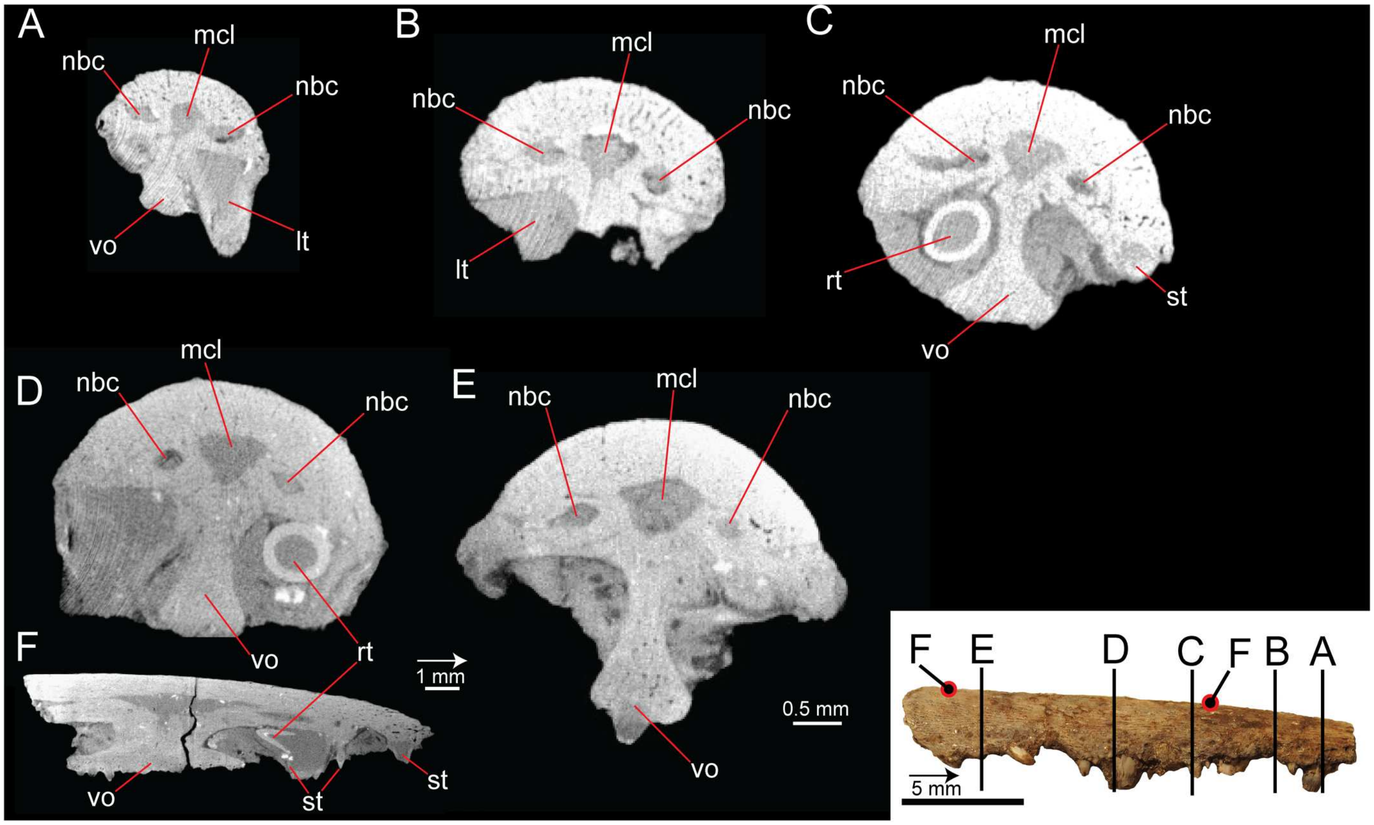

FIGURE 3. Internal anatomy of the rostropremaxilla of †*Saurichthys justitias* (TTU P-24824) from µCT data. **A–E**, coronal cross sections. **F**, sagittal cross section. Bottom right panel indicates location of cross sections on specimen photograph. **Abbreviations**: **lt**, large tooth; **mcl**, median canal; **nbc**, nasobasal canal; **rt**, replacement tooth; **st**, small tooth; **vo**, vomer.

and a smoother acrodin cap (Romano et al., 2012; Stensiö, 1925). Plicidentine is found in a variety of actinopterygians and is therefore not unique to †*Saurichthys* (Błażejowski et al., 2013; Germain & Meunier, 2019; Grande, 2010; Meunier et al., 2018; Viviani et al., 2022). However, the combination of striated shafts and translucent caps in the MOTT VPL 3867-6 isolated teeth and the close match to the teeth in the rostropremaxillae from MPL 3939-3 indicate that they likely belong to †*S. justitias*. The MOTT VPL 3867-6 teeth (TTU P-24827, TTU P-24828, TTU P-24829, TTU P-24830, TTU P-24831, TTU P-24832) vary considerably in height (between ~1 mm and ~5 mm) and therefore have a larger size range than the Chinle occurrence of †*Saurichthys*, where the tallest teeth are ~1 mm (Kligman et al., 2017). Additionally, the shape of the teeth varies between elongate, narrow teeth with sharp points, broad, triangular teeth, and conical teeth with blunt points (Fig. 4). Taller teeth show an increase in the height of the tooth shaft rather than the cap, which has a much more consistent size range throughout the teeth.

Teeth are present dorsal and medial to the external teeth in TTU P-24824, TTU P-24825, TTU P-24826 as shown in µCT cross sections (Fig. 3). These are replacement teeth, as is evident by their position within the bone, anterior-posterior orientation, and forming a 90° angle with the functional teeth that are visible in external view. Continuous tooth replacement is the standard in non-mammalian vertebrates, meaning that the presence of replacement teeth in †*S. justitias* is not indicative of the specimens being from an early stage in skeletal ontogeny (Huysseune & Witten, 2024). Tooth replacement patterns in actinopterygians are myriad and not necessarily regular even within the same species or different types of teeth within an individual (Bemis et al., 2019; Huysseune & Witten, 2024). However, the replacement teeth in †*S. justitias* are dorsal and medial relative to the externally visible teeth and were forming within the rostropremaxilla (Fig. 3D, F). Therefore, †*S. justitias* has intraosseous, dorsomedially placed tooth replacement of at least the larger size tooth class. Critically, intraosseous tooth replacement is not the norm in osteichthyans (extraosseous replacement is far more common) but is thought to have evolved independently in four extant clades of teleost actinopterygians (Acanthopterygii, Characiformes, Elopiformes, and Scombriformes) (Bemis et al., 2019; Berkovitz & Shellis, 2023; Trapani, 2001). Examples of similar tooth replacement in extant actinopterygians include the dentary teeth of the mottled conger moray (*Enchelycore nigricans*) and the premaxillary fangs of the Atlantic cutlassfish (*Trichiurus lepturus*), in which replacement teeth form within the bone at a 90° angle to the functional teeth and rotate into functional position (Bemis et al., 2019; Trapani, 2001). The replacement teeth in †*S. justitias* likely would have had a similar rotation in the process of becoming functional.

DISCUSSION

Tooth Replacement in †*Saurichthys* and Convergence with Predatory Teleosts

Extant teleosts that engage in fast-acceleration ram-predation show considerable convergence on the body shape, skull morphology, and hydrodynamic profile of †*Saurichthys* (Collette, 2016; Kogan et al., 2015, 2020; Porter & Motta, 2004). Our finding of horizontally oriented intraosseous replacement teeth

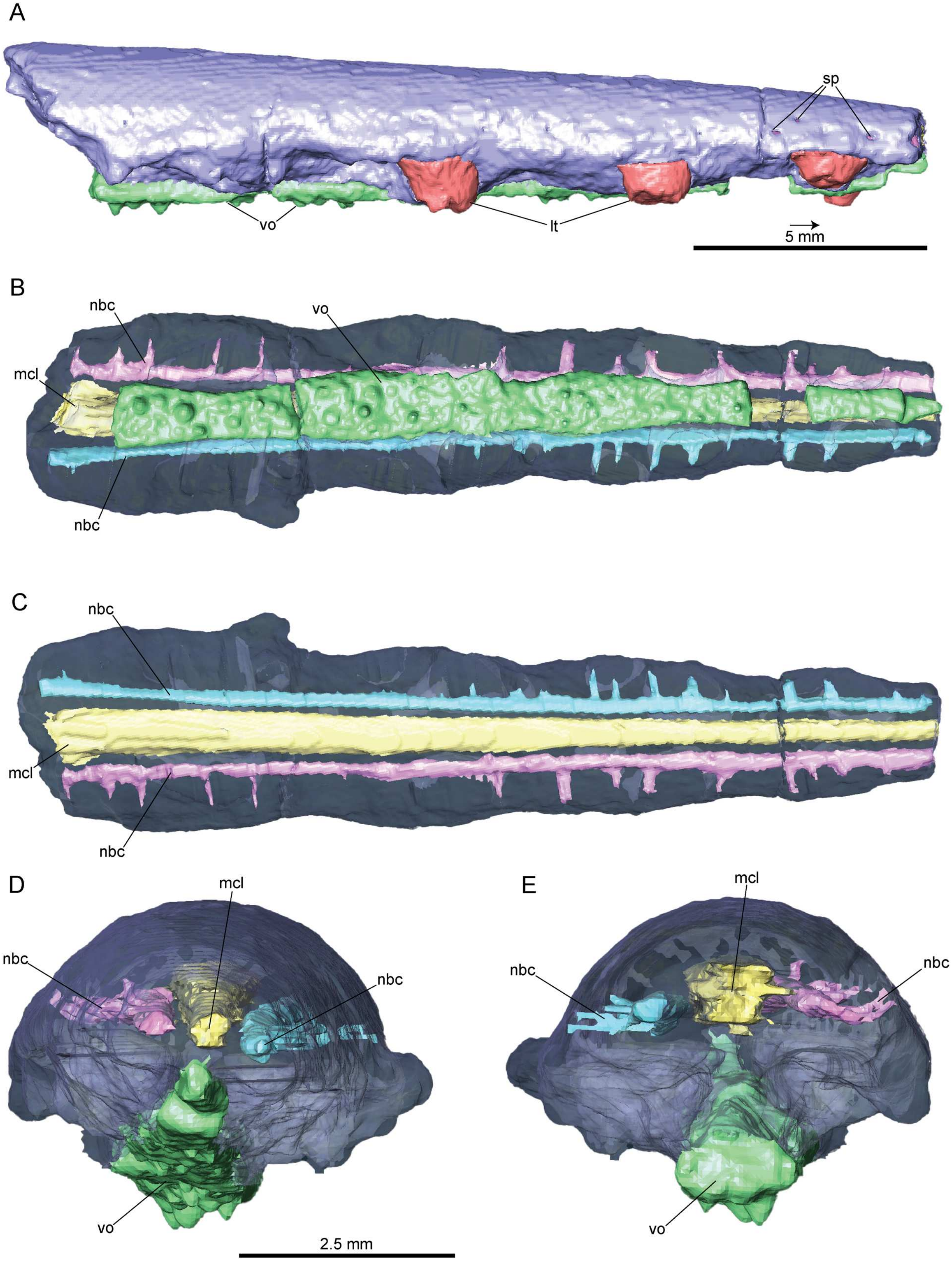

FIGURE 4. 3D reconstruction of the rostropremaxilla of †*Saurichthys justitias* (TTU P-24824) from µCT data. **A**, 3D model in lateral view, arrow indicates anterior direction. **B**, 3D model in ventral view (teeth removed). **C**, 3D model in dorsal view (teeth and vomer removed). **D**, 3D model in anterior view (teeth removed). **E**, 3D model in posterior view (teeth removed). **A–C** and **D–E** are scaled to each other, respectively. **Abbreviations**: **lt**, large tooth; **mcl**, median canal; **nbc**, nasobasal canal; **sp**, lateral line sensory pore; **vo**, vomer.

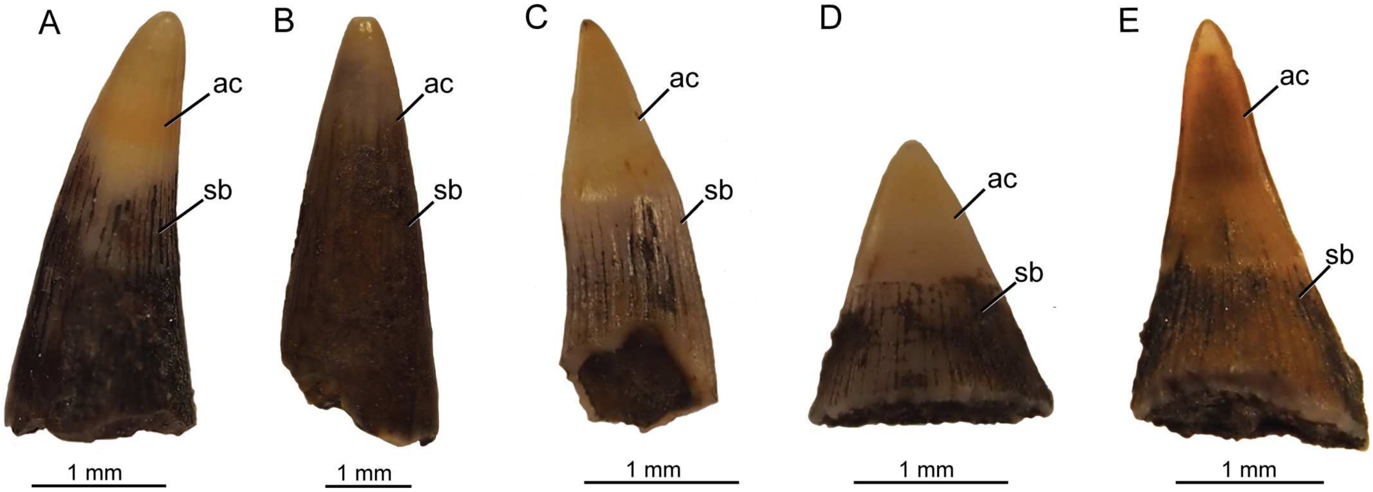

FIGURE 5. Isolated teeth referable to †*Saurichthys justitias* showing range of morphologies. **A**, TTU P-24832. **B**, TTU P-24831. **C**, TTU P-24829. **D**, TTU P-24830. **E**, TTU P-24828. **Abbreviations**: **ac**, acrodin cap; **sb**, striated base.

in †*Saurichthys justitias* suggests even deeper convergence between †*Saurichthys* and extant predatory teleosts. For example, intraosseous, horizontally oriented tooth replacement is present in the premaxillary fangs of cutlassfishes (Trichiuridae), a clade of pelagic ambush predators that use their teeth to capture other fishes and cephalopods (Bemis et al., 2019; Martins et al., 2005; Morgan, 1977). Similar tooth replacement mechanisms have evolved independently in other predatory biting teleosts, such as the mottled conger moray (*Enchelycore nigricans*) and dogtooth characins (Cynodontidae; Bemis et al., 2019; Trapani, 2001). A potential explanation for the convergent evolution of intraosseous tooth replacement is the observation that replacement teeth in fishes are fragile prior to mineralization and are therefore vulnerable in taxa that use their toothed jaws to capture prey (Shellis, 1978; Shellis & Berkovitz, 1976; Trapani, 2001). The intraosseous development with horizontal replacement in the larger size class of teeth in †*S. justitias*, most likely a biting, ram-feeding predator akin to other species of †*Saurichthys*, may have also protected teeth during development. There is also the possibility that intraosseous development is an adaptation to provide more room for functional teeth in the jaw (Trapani, 2001). These possibilities are not mutually exclusive, and we are not able to parse between them with the information available for this extinct species. However, the novel observation of intraosseous tooth replacement in †*S. justitias* indicates that morphological convergence between †*Saurichthys* and extant predatory biting teleosts includes the mechanism of tooth replacement.

†*Saurichthys* within the Actinopterygian Assemblage of the Dockum Group

Both occurrences of †*Saurichthys* from the early Norian of the western U.S.A. were collected from concentrated assemblages of microvertebrate fossils within the Chinle Formation and Dockum Group (Kligman et al., 2017). Paleoichthyological work on the Chinle Formation and Dockum Group shows a bountiful assemblage of both microfossils and macrofossils (Brownstein, 2023; Gibson, 2018; Heckert, 2004; Huber et al., 1993; Jacobs & Murry, 1980; Lucas et al., 1993; Martz, 2008; Murry, 1982, 1987, 1989a, 1989b; Schaeffer, 1967; Warthin Jr., 1928). Despite over 40 years of the application of modern microvertebrate collection techniques within the Chinle Formation and Dockum Group, and careful study of actinopterygian microfossils by several previous workers (Heckert, 2004; Huber et al., 1993; Murry, 1982), no remains of †*Saurichthys* were recognized until Kligman et al. (2017) and the present work. However, the tooth morphology we observe in †*Saurichthys justitias* corresponds to the ichthyolith “Morphotype A” described by Murry (1982) from a series of SMUSP specimens (67772, 6777, 67782, 67783, 67797-6780, 67892, 67894, 67895, 67897, 67899, 67903, 67906, 67907, 67912, 67914, 67930, 67937, 67944) from “the Otis Chalk Locality” of the lower portion of the Dockum Group in Howard County, Texas. The written description and accompanying figure depict a relatively large enameloid cap extending over half of the length of the tooth, and a “corrugate” texture of the shaft (Murry, 1982). Murry compared “Morphotype A” to that of semionotid neopterygians and the enigmatic “palaeoniscoid” †*Birgeria* (Stensiö, 1932). However, our finding of this tooth morphotype within fused rostropremaxillae strongly indicates that the ichthyolith ‘Morphotype A’ of Murry (1982) belongs to †*S. justitias*. We also found that two teeth (NMMNH P-41426 and P-34040) illustrated by Heckert (2004) from the Colorado City Formation of the †*Trilophosaurus* Quarry (NMMNH locality 860 = TMM 31025 = Otis Chalk Quarry 1) of the Dockum Group of west Texas share the large acrodin cap, conical shape, and corrugate shaft of the teeth. One other tooth (NMMNH P-31628) figured by Heckert (2004), and dozens of other specimens, from the Ojo Huelos Member of the San Pedro Arroyo Formation of central New Mexico (Chinle Group) also possess the traits associated with the teeth of †*S. justitias* (Nesbitt, pers. observ.). Like Murry (1982), Heckert (2004) identified those specimens as actinopterygian teeth but was unable to make a more specific identification because of their isolation. Therefore, the work of Kligman et al. (2017) and our study are not the first findings of †*Saurichthys* in the Dockum Group or Chinle Formation, but are the first time this taxon has been found from complete enough material to preserve multiple recognizable character states of †*Saurichthys*.

The actinopterygian assemblage from the Otischalkian part of the Dockum Group is composed primarily of the redfieldiids (pan-Neopterygii) †*Cionichthys* and †*Lasalichthys* (†*Lasalichthys* being synonymous with †*Synorichthys* Schaeffer 1967) and an isolated premaxilla assigned to the dapediid (pan-Holostei) †*Hemicalypterus* (Rotten Hill Locality, Potter County, Texas) (Gibson, 2018; Heckert, 2004; Murry, 1982; Near & Thacker, 2024; Schaeffer, 1967). Histological study of isolated elements referred to as tooth plates from †*Colobodus* and †*Perleidus* (Huber et al., 1993; Murry, 1982) are not identifiable to either of these taxa (Mutter & Heckert, 2006). Notably, †*Saurichthys* has not been recorded from the younger parts of the Dockum Group or Chinle Formation, or from the Newark Supergroup of the east coast of the U.S.A. (Heckert, 2004; Olsen et al., 1982). Therefore, the Dockum and Chinle occurrences may be the youngest representatives of the taxon from North America. The Chinle †*Saurichthys* and †*S. justitias* as the youngest occurrences of the taxon from continental deposits in North America lends partial support to the hypothesis of Romano et al. (2016) that Late Triassic freshwater faunas acted as refugia for taxa with 'archaic bauplans' (Romano et al., 2017). However, the presence of a dapediid and the earliest redfieldiids from North America clearly demonstrates that the Dockum assemblage contains groups that survived and were diverse well into the Jurassic in North America. Our finding of †*S. justitias* contributes to a reconstruction of the Dockum hosting a diverse assemblage of neopterygian and non-neopterygian actinopterygians, with a relatively low abundance of neopterygians compared with contemporaneous marine assemblages such as the Zorzino Limestone (Lombardo & Tintori, 2005; Tintori, 1998). Further, our work mirrors a slew of recent tetrapod microvertebrate discoveries from the Chinle Formation that highlight the enormous potential of concentrated work on Triassic microvertebrates (Kligman et al., 2020, 2023; Marsh & Parker, 2020; Marsh et al., 2020; Stocker et al., 2019). We predict that continued study of microvertebrate fish fossils from both the Chinle Formation and Dockum Group will show a more diverse actinopterygian fauna akin to discoveries in the tetrapod realm, where newly discovered specimens can be used to identify the numerous indeterminate actinopterygian remains collected in the past.

†*Saurichthys justitias* and the Triassic Biogeography of †*Saurichthys*

Prior to the last decade, Late Triassic occurrences of †*Saurichthys* outside of the marine Paleotethys were questionable in some aspects (Romano et al., 2012). For example, †*Saurichthys orientalis* from the Madygen Formation (Ladinian–Carnian, Kyrgyzstan) has a possible age range extending from the Middle Triassic into the Late Triassic (Jenkins, 1994; Kogan et al., 2009). Additionally, the occurrence of †*Saurichthys* from the Norian Fleming Fjord Formation of east Greenland is questionable in that the authors noted the presence of teeth and jaws that are likely referable to †*Saurichthys*, but no other details or figures were provided (Jenkins, 1994). †*Saurichthys huanshenensis* from the Ordos Basin of Shaanxi (China) was originally reported as Late Triassic but is now thought of as being uncertain in age and is therefore not considered further (Chou & Liu, 1957; Fang et al., 2023; Romano et al., 2012).

The Late Triassic distribution of †*Saurichthys* has broadened outside of the marine Paleotethys over the last decade, with new findings in the Chinle Formation and Dockum Group showing that †*Saurichthys* was present in the fluviolacustrine Upper Triassic systems of North America (Kligman et al., 2017; this study; Fig. 6). Further, the discovery of †*Saurichthys sui* from the continental Baijiantan Formation (Upper Triassic, Carnian–Rhaetian) of Xinjiang, China and †*S. taotei* from the marine Guanling Biota (Late Triassic, Carnian) of China show that †*Saurichthys* was also present in the marine eastern Paleo-Tethys and fluviolacustrine systems in present-day northwestern China in the Late Triassic. Taken together, we see that †*Saurichthys* had a considerably broader Late Triassic distribution

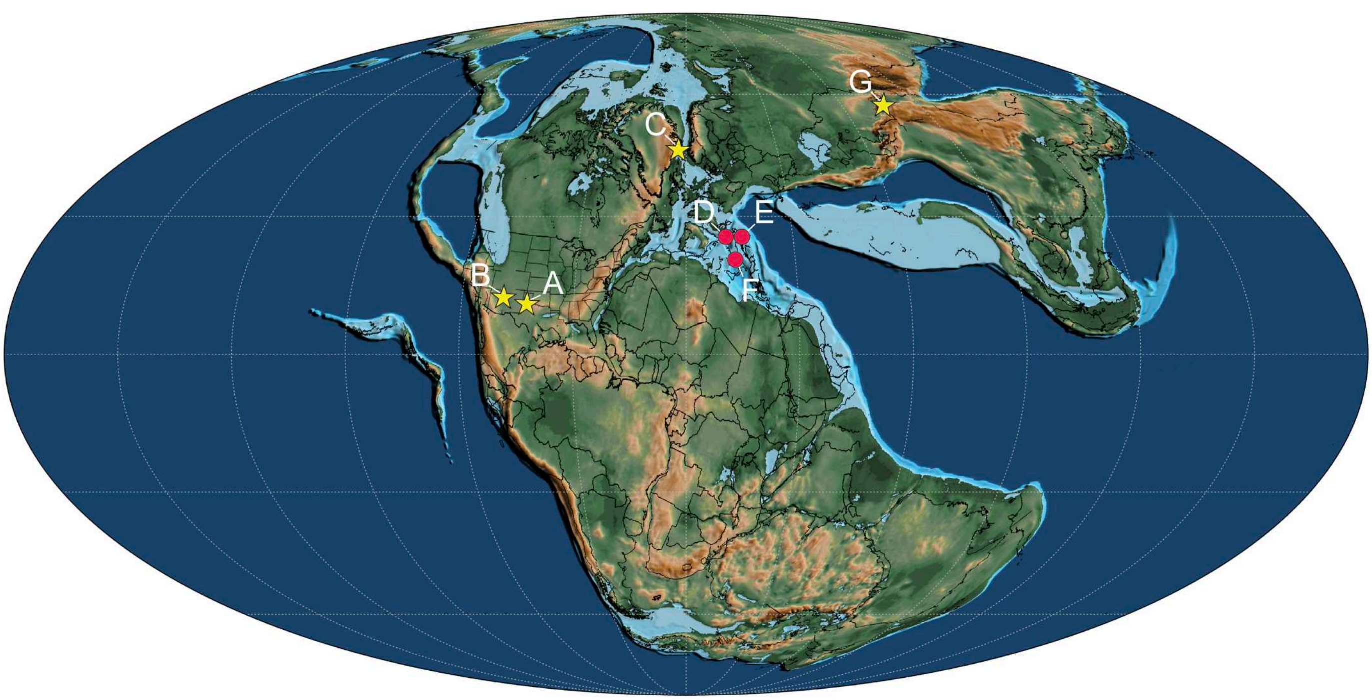

FIGURE 6. Paleobiogeography of †*Saurichthys* in the Late Triassic (late Norian, 210 Ma), map from Scotese (2021), where yellow stars are continental occurrences and red circles are marine occurrences. **A**, †*S. justitias*, Dockum Group, Texas, U.S.A. (this paper). **B**, †*Saurichthys* sp., Chinle Formation, Arizona, U.S.A. (Kligman et al., 2017). **C**, †*Saurichthys* sp., Fleming Fjord Formation, Greenland (Jenkins et al., 1994). **D**, †*S. deperditus*, †*S. seefeldensis*, and †*Saurichthys* sp., Lombardy, Italy (Norian: Tintori, 1990; Tintori & Lombardo, 2018). **E**, †*S. seefeldensis* and †*S. deperditus*, Friuli-Venezia Giulia, Italy/Salzburg, Austria (Griffith, 1962; Hornung et al., 2019; Zittel, 1887–1890). **F**, †*S. deperditus*, Campania, Italy (Tintori et al., 2020). **G**, †*Saurichthys sui*, Baijiantan Formation, China (Carnian–Rhaetian, Fang & Wu, 2019).

than was previously thought (Romano et al., 2012) and was not restricted to the northwestern Tethys.

We need to briefly review the biogeography of †*Saurichthys* in North America to put the Late Triassic occurrences of this genus in the U.S.A. into context. †*Saurichthys* has been recorded in North America since the Early Triassic, in marine deposits in the Early Triassic Boreal Sea and East Panthalassa (Romano et al., 2012). The oldest occurrence of †*Saurichthys* from North America, †*Saurichthys* aff. *dayi*, is from the Lower Triassic (Griesbachian) Wordie Creek Formation of Hold Within Hope, Greenland (Kogan, 2011; Nielsen, 1936; Romano et al., 2012). Other Early Triassic occurrences of †*Saurichthys* from North America that are not assignable to a more specific stage are from various sites in Canada, including †*S. dayi* from the Banff Massive of Alberta, †*S. toxolepis* and other material not assigned more specifically than †*Saurichthys* from the Sulphur Mountain Formation, Wapiti Lake, British Columbia, and finally material not assigned more specifically than †*Saurichthys* from the Blind Fiord Formation of Blind Fiord, Ellesmere Island, Nunavut (Embry, 1986; Mutter et al., 2008; Raymond, 1925; Schaeffer & Mangus, 1976). †*Saurichthys* also occurs in the East Panthalassa in the Early Triassic, based on the occurrence of †*Saurichthys* cf. *elongatus* from the Smithian Thaynes Formation of Bear Lake County, Idaho, U.S.A., and †*Saurichthys,* not assigned more specifically than the genus, from the Spathian Thaynes Group of Elko County, Nevada, U.S.A., (Romano et al., 2012, 2017). There is also a record of †*Saurichthys*, not assigned more specifically than the genus, from the marine Middle Triassic (Anisian) Favret Formation of the Augusta Mountains of Nevada, U.S.A. (Rieppel et al., 1996; Sander et al., 1994; Silberling & Nichols, 1982). Therefore, there is a considerable gap in time, ~20 million years, between the Anisian (~246.7–241.46 Ma) occurrence and the continental Norian occurrences from Petrified Forest National Park (Adamanian, ~225–219 Ma) and the older Dockum occurrences (Otischalkian) (Martz & Parker, 2017; Ramezani et al., 2014). Given the fragmentary preservation of the Chinle Formation and Dockum Group †*Saurichthys*, we cannot determine if these species are derived from Middle Triassic occurrences of the genus in East Panthalassa or Late Triassic occurrences from the Boreal Sea (Romano et al., 2012). However, given that the Dockum Group and Chinle Formation are parts of a massive fluviolacustrine system that connected with the Panthalassic Ocean in the west (Blakey et al., 1989; Riggs et al., 1996), we hypothesize that †*S. justitias* and the Chinle occurrence are derived from Panthalassa.

The Uneven Appearance of Jaw Closing Force and Velocity Specialized Morphologies in Neopterygians

Cranial elongation is widespread in extant ray-finned fishes and has a deep history in the group, with the oldest example being the Late Devonian (Famennian) †*Tegeolepis clarki*, preceding the oldest documented members of †Saurichthyidae in the latest Permian (Changhsingian) of China (Dunkle & Schaeffer, 1973; Liu & Wei, 1988). Late Paleozoic “palaeoniscoids” exhibiting cranial elongation were primarily brackish/freshwater taxa, including the Late Pennsylvanian (Missourian) †*Tanyrhinichthys mcallisteri*, an unnamed taxon from the Upper Pennsylvanian of Indiana (U.S.A.), and †*Phanerorhynchus armatus* from the Upper Pennsylvanian of the U.K. (Gill, 1923; Gottfried, 1987; Poplin, 1978; Stack et al., 2021). Stack et al. (2021) documented that cranial elongation in these taxa is associated with elements in the skull roof, rather than the jaws (as in †*Saurichthys*), suggesting a benthic-associated feeding mode analogous to extant sturgeons rather than jaw closing velocity-specialized feeding as had been previously hypothesized for †*Tanyrhinichthys* (Stack et al., 2021). Therefore, saurichthyids hold the distinction of the first documented ray-finned fishes with extreme elongation of the jaws, convergent with extant jaw closing velocity-specialized predatory actinopterygians (Kogan et al., 2015). There are a variety of neopterygian ray-finned fishes with pronounced, extremely elongate upper and lower jaws superficially like those of †*Saurichthys* that evolved independently, most notably needlefishes and gar (Grande, 2010; Gregory, 1933). However, the fusion of the rostral and premaxillae into a single, elongate element is almost unique to †*Saurichthys* amongst ray-finned fishes, with the lone exception being the neopterygian †*Luganoia* from the Middle Triassic of Italy, Switzerland, Spain, and China (Brough, 1939; Bürgin, 1992; Xu, 2020). However, the rostropremaxilla of †*Luganoia* has a narrow contribution to the oral surface and an elongate nasal process articulating with the frontals (Xu, 2020). The rostropremaxilla in †*Luganoia* is therefore distinct in form from that of †*Saurichthys*, in which the rostropremaxilla forms most of the oral surface of the upper jaw (Romano et al., 2012). Therefore, the elongate, tapering rostropremaxilla of †*Saurichthys* is apomorphic despite its superficial resemblance to longirostrine neopterygians.

Elongate and deepened jaws in ray-finned fishes are opposite ends of a biting mechanical spectrum, where morphology reflects tradeoffs for closing velocity or force, respectively (Westneat, 1994, 2004). The jaw closing velocity-specialized morphotype was occupied by †Saurichthyidae starting in the latest Permian and throughout the Triassic in both freshwater and marine environments, persisting in marine environments into the late Middle Jurassic (Aalenian) of Europe (Maxwell, 2016; Romano et al., 2012; Thies, 1985). Neopterygians convergently evolved similar jaw closing velocity-specialized morphotypes in the Middle Jurassic and beyond, the most †*Saurichthys*-like being some members of extinct pan-teleost †Aspidorhynchidae (†*Belonostomus*) and pan-aulopiformes (Teleostei) †Dercetidae (*Rhynchodercetis*) and the extant needlefish and gar (Brito, 1997; Gallo et al., 2005; Grande, 2010; Gregory, 1933). Jaw closing force-specialized morphologies have also evolved convergently in multiple lineages of neopterygians, with some examples being the extinct Pycnodontiformes and Dapediidae, extant members of Balistidae (*Balistes*), Diodontidae (porcupinefishes), Labridae (parrotfishes, hogfish), Serrasalmidae (pacus and piranhas), and Sparidae (*Archosargus probatocephalus*) (Fernandez & Motta, 1997; Gregory, 1933; Grubich et al., 2012; Huber et al., 2008; Poyato-Ariza, 2015; Thies & Waschkewitz, 2016; Westneat, 2004).

†*Saurichthys justitias* highlights a temporal gap in the appearances of specialized jaw morphologies in neopterygians. The marine assemblage of the Norian Zorzino Limestone includes a variety of neopterygians with anterior-posteriorly short, dorsoventrally deep lower jaws, including semionotids (†*Paralepidotus*), pycnodonts, †*Sargodon*, and macrosemiids (Lombardo & Tintori, 2005; Tintori, 1998). Those taxa are convergent on extant teleosts that bite prey items that are firmly attached to reef surfaces, with chisel-like teeth and powerful, force-specialized jaws (Bellwood, 2003; Corn et al., 2022). In contrast, the presumably piscivorous †*Saurichthys* alone occupied the jaw closing velocity-specialized morphotype in the Zorzino Limestone assemblage (Beltan & Tintori, 1980; Tintori, 1998). The Norian freshwater actinopterygian assemblages of the western U.S.A. do not show nearly as much neopterygian diversity as contemporary marine assemblages (Schaeffer, 1967). However, a similar pattern is present in the coprolite layer of the Blue Mesa Member of the Chinle Formation and in the Dockum Group, where the neopterygian †*Hemicalypterus* shows a jaw closing force-specialized jaw morphology (Fig. 7A) and †*Saurichthys* (Fig. 7B) alone had a velocity-specialized jaw morphology (Gibson, 2016; Kligman, 2023; Kligman et al., 2017). Neopterygians did not exhibit extreme jaw closing velocity-specialized morphologies until the appearance of the

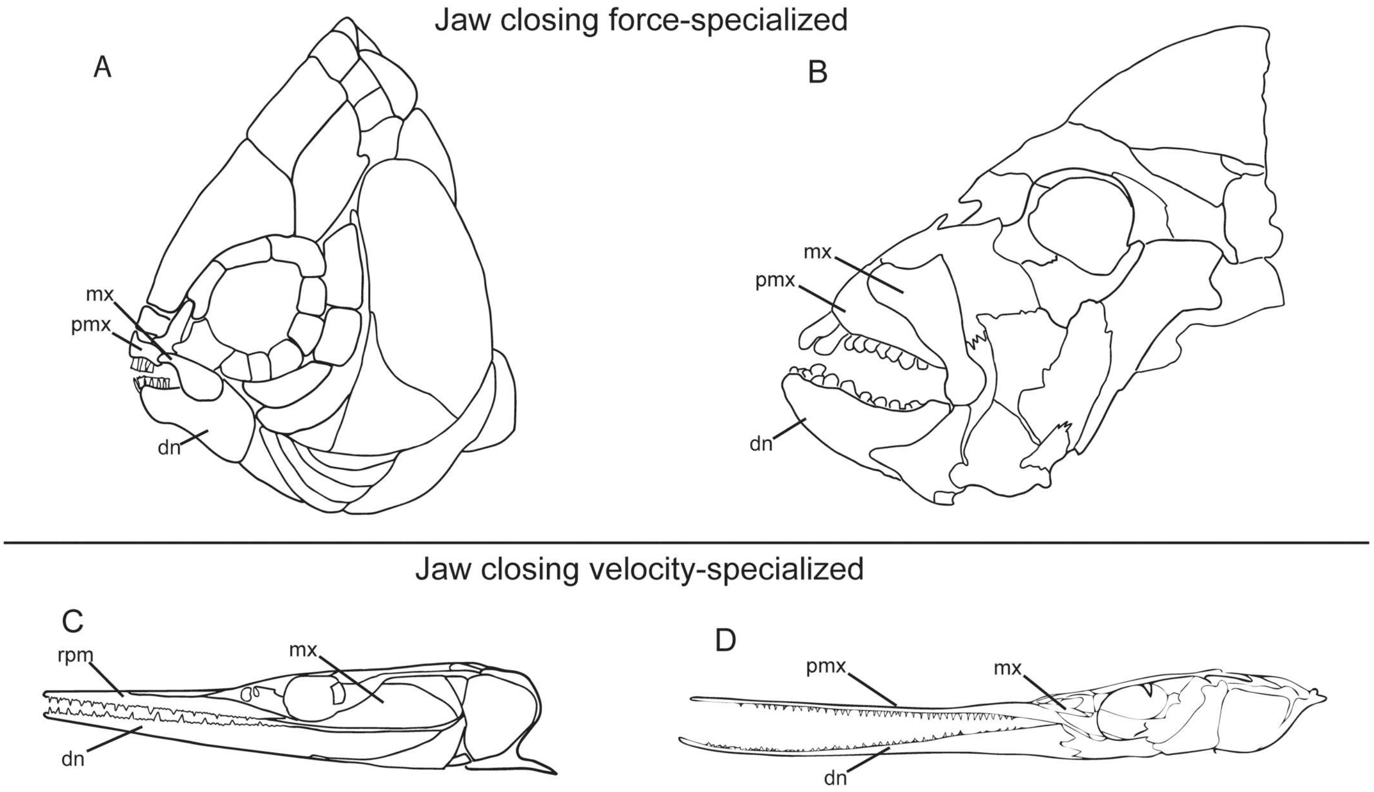

FIGURE 7. Convergence in force and velocity specialized cranial morphologies in ray-finned fishes. **A**, †*Hemicalypterus weiri*, modified from Gibson (2016:fig. 2). **B**, *Archosargus probatocephalus*, modified from Gregory (1933:fig. 123A). **C**, †*Saurichthys madagascariensis*, modified from Kogan & Romano (2016:fig. 11). **C**, **D**, *Tylosurus marinus*, modified from Gregory (1933:fig. 99A). **Abbreviations**: **dn**, dentary; **mx**, maxilla; **pmx**, premaxilla; **rpm**, rostropremaxilla. Not to scale.

aspidorhynchid pan-teleosts (such as †*Belonostomus kochii*) in the Middle Jurassic (Brito, 1997). Living actinopterygians with elongate jaws, such as the needlefish *Tylosurus marinus* (Fig. 7D) typically engage in ram-biting behavior, a relatively uncommon mode of feeding in which the animal propels its body and jaws at a prey item (Corn et al., 2022; Ferry et al., 2015; Porter & Motta, 2004). The fossil record therefore indicates that the Late Triassic ecological diversification of neopterygians included jaw closing force-specialized species, but not jaw closing velocity-specialized forms. The broader implication is that the transition in Triassic ray-finned fish assemblages from being primarily stem-group actinopterygians to neopterygians did not include ram-feeding, jaw closing velocity specialized species, roles which continued to be occupied by †*Saurichthys* in marine and continental environments in North America, Europe, and China into the Late Triassic.

CONCLUSIONS

We describe a new species of ray-finned fish, †*Saurichthys justitias*, from isolated teeth and rostra collected from novel microvertebrate assemblages in the Upper Triassic (Otischalkian, early ? Norian) Boren Ranch beds of the Dockum Group near Justiceburg, Texas. We found that †*S. justitias* has intraosseous replacement teeth oriented horizontal to the functional teeth, indicating that †*Saurichthys* had a tooth replacement mechanism like extant predatory biting teleosts. The stem-group actinopterygians †*S. justitias* and near contemporaneous †*Saurichthys* in the freshwater Chinle Formation (Arizona, U.S.A.) and the marine Zorzino Limestone (Italy and Austria) highlight the absence of neopterygians with elongate, closing velocity-specialized jaws in the Triassic. Therefore, the Triassic transition in ray-finned fish assemblages towards being composed of neopterygians did not include jaw closing velocity-specialized species, roles which were still occupied by †*Saurichthys* in marine and freshwater assemblages in China, Europe, and North America in the Late Triassic.

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AUTHOR CONTRIBUTIONS

JS wrote the manuscript and made the figures. MLS segmented the µCT data, assisted in describing/figuring specimen anatomy, and contributed to preparing the manuscript. SJN collected the

material and developed the project, screen-washed and identified the specimens, assisted with figure and specimen preparation, and contributed to preparing the manuscript. MRS collected the material and developed the project, assisted with figure and specimen preparation, and contributed to preparing the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on MorphoSource (ID # 000671406). URL: https://www.morphosource.org/projects/000668516?locale=en. The specimens this study is based upon are accessioned at Texas Tech University, Paleontology Collections, Lubbock, Texas, U.S.A.

DISCLOSURE STATEMENT

No potential conflict of interest was reported by the author(s).

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