

Fitting fangs in a finite face: A novel fang accommodation strategy in a 280-million-year-old ray-finned fish

Rodrigo T. Figueroa  | James V. Andrews 

Department of Earth and Environmental Sciences, University of Michigan, Ann Arbor, Michigan, USA

Correspondence

Rodrigo T. Figueroa, Department of Earth and Environmental Sciences, University of Michigan, Ann Arbor, MI, USA.
Email: rtfiguer@umich.edu

Funding information

University of Michigan Department of Earth and Environmental Sciences

Abstract

Though Paleozoic ray-finned fishes are considered to be morphologically conservative, we report a novel mode of fang accommodation (i.e., the fitting of fangs inside the jaw) in the Permian actinopterygian *†Brazilichthys macrognathus*, whereby the teeth of the lower jaw insert into fenestrae of the upper jaw. To better understand how fishes have accommodated lower jaw fangs through geologic time, we synthesize the multitude of ways living and extinct osteichthyans have housed large mandibular dentition. While the precise structure of fang accommodation seen in *†Brazilichthys* has not been reported in any other osteichthyans, alternate strategies of upper jaw fenestration to fit mandibular fangs are present in some extant ray-finned fishes—the needlejaws *Acestrorhynchus* and the gars of the genus *Lepisosteus*. Notably, out of our survey, only the two aforementioned neopterygians bear upper jaw fenestration for the accommodation of mandibular fangs. We implicate the kinetic jaws of neopterygians in this trend, whereby large mandibular fangs are more easily fit between the multitude of upper jaw and palatal bones. The restricted space available in early osteichthyan jaws may have led to a proliferation of novel ways to accommodate large dentition. We recommend a greater survey of Paleozoic actinopterygian jaw morphology, in light of these results and other recent reevaluations of jaw structure in early fossil ray-fins.

KEY WORDS

Actinopterygii, dentition, jaws, Osteichthyes, Paleozoic, Permian

1 | INTRODUCTION

The late Paleozoic (359.3–251.9 million years ago (mya) (Aretz et al., 2020; Henderson, Dunne, & Fasey, 2022)) represents an important interval for understanding the evolution and diversification of actinopterygians, the ray-finned fishes. During this time, ray-finned fishes first evolved a series of innovations that have arisen

many times since, including body elongation (Lund & Poplin, 2002), body deepening (Gill, 1925; Sallan & Coates, 2013), and various changes to feeding ranging from adaptations for durophagy (Friedman et al., 2018) to changes in jaw articulation (Argyriou et al., 2022). Despite the important morphological innovations taking place in the Carboniferous–Permian interval, few ray-finned fishes of this age have been studied in detail (Argyriou et al., 2022;

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial](#) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2022 The Authors. *Journal of Anatomy* published by John Wiley & Sons Ltd on behalf of Anatomical Society.

Figueroa et al., 2019), suggesting that many additional functional innovations remain unrecognized.

Classic studies established basic aspects of the jaw-closing mechanism of early ray-finned fishes (Lauder, 1982; Schaeffer & Rosen, 1961), and the relationship between the palate, suspensorium, and neurocranium is well understood for a handful of articulated and three-dimensionally preserved specimens (Argyriou et al., 2018; Figueroa et al., 2019; Friedman et al., 2018; Giles et al., 2015). However, little is known regarding jaw closing in Paleozoic ray-finned fishes that bear greatly enlarged, fang-like dentition on the upper and lower jaws.

With some notable exceptions, Paleozoic ray-finned fishes generally exhibit conservative body shapes (Friedman, 2015; Sallan & Coates, 2013). Similar structural homogeneity is generally assumed for the jaws and palate, with most taxa interpreted as bearing some variety of pointed teeth on both the upper and lower jaws, and finer denticulation on the palate and inner surface of the mandible. Nevertheless, several Paleozoic ray-finned fishes show morphology related to a highly predatory habitus, such as large conical teeth on upper or lower jaws, conical dentition present in multiple rows on labial and lingual sides of the jaws, a modified symphyseal series of teeth, and curvature of the lower jaw toward the symphysis (Choo, 2009; Dunkle & Schaeffer, 1973; Figueroa et al., 2021; Štamberg, 1991, 2006, 2018). Of these, the most common adaptation is the presence of large fangs (Choo, 2009; Dunkle & Schaeffer, 1973; Figueroa et al., 2019, 2021; Štamberg, 2006), with fangs here being defined as large canine-like teeth (Olson, 2017). However, little is known regarding the interactions between the mandibular fangs and the palate in most of these taxa. Taxa with these attributes appear to be dispersed through the stem of the ray-finned fish tree rather than united as a monophyletic lineage of large-fanged fossil taxa (Argyriou et al., 2022; Figueroa et al., 2019; Giles et al., 2017; Stack & Gottfried, 2021). Few of these fishes are sufficiently well preserved to determine how jaw closing accommodated enlarged dentition.

Extant actinopterygians have evolved a multitude of ways to house their lower jaw dentition. The large fangs and wide gape of some taxa, such as the deepwater-dwelling stomiids and the trachichthyiform *Anoplogaster*, have been interpreted as being utilized in prey retention after capture via suction feeding (Germain et al., 2019; Greven et al., 2009; Kierdorf et al., 2022). However, in the majority of marine and freshwater fishes with large fangs, it is more common for jaw closure to be complete and for the purpose of prey capture via ram feeding - with mandibular teeth accommodated between the bones of the upper jaw and suspensorium.

Here, we describe a novel strategy for interaction between jaw fangs, palate, and palatal dentition in the Lower Permian (298.9–274.4 mya (Henderson et al., 2020)) *†Brazilichthys macrognathus* (Cox & Hutchinson, 1991), one of the few Paleozoic large-toothed actinopterygians known from remains that permit investigation of the interaction between upper and lower jaws dentition. We compare the morphology of *†Brazilichthys* to other bony fishes—both fossil and living—in order to better understand the diversity of jaw-closing strategies in fang-bearing ray-finned fishes.

2 | MATERIALS AND METHODS

2.1 | Institutional codes

Institutional codes follow those of Sabaj (2020). **DGM**, Coleção de Paleontologia do Museu de Ciências da Terra, Serviço Geológico do Brasil, Ministério de Minas e Energia, Rio de Janeiro, Brazil; **JFBM**, James Ford Bell Museum of Natural History, University of Minnesota, Minneapolis, Minnesota, U.S.A.; **ROM**, Royal Ontario Museum, Toronto, Ontario, Canada; **UF**, University of Florida, Gainesville, Florida, U.S.A.; **UMMZ**, University of Michigan Museum of Zoology, Ann Arbor, Michigan, U.S.A.; **UW**, University of Washington, Seattle, Washington, U.S.A.; **YPM**, Yale University, Peabody Museum of Natural History, New Haven, Connecticut, U.S.A.

2.2 | Comparative materials

Acestrorhynchidae. *Acestrorhynchus falcatus* UF:Fish:189596. ark:/87602/m4/M159116.

Alepisauridae. *Alepisaurus ferox* YPM:Ich:025451. ark:/87602/m4/426485.

Amiidae. *Amia calva* UMMZ 235291.

Brazilichthyidae. *†Brazilichthys macrognathus*. DGM 1061-P. doi:10.6084/m9.figshare.7600103.

Channidae. *Channa marulius* UF:Fish:241571. ark:/87602/m4/M170165.

Cynodontidae. *Hydrolycus armatus* ROM:Fishes:88356. doi:10.17602/M2/M97833.

Gempylidae. *Promethichthys prometheus* UF:Fish:231977. ark:/87602/m4/M95620.

Lepisosteidae. *Lepisosteus oculatus* UMMZ 196974.

Muraenesocidae. *Muraenesox cinereus* UW:UWFC:021142. ark:/87602/m4/M114084.

Percidae. *Sander vitreus* JFBM:Fishes:35995. ark:/87602/m4/M57862.

Polypteridae. *Polypterus senegalus* UMMZ 195008.

Sciaenidae. *Cynoscion regalis* UW:UWFC:004152. ark:/87602/m4/M117179.

Sphyraenidae. *Sphyraena sphyraena* UF:Fish:137529. ark:/87602/m4/M81241.

Trichiuridae. *Trichiurus lepturus* UW:UWFC:014888. ark:/87602/m4/M91552.

One adult specimen per species was examined via microcomputed tomography (see Section 2.4 below). Standard lengths of digital specimens are infrequently uploaded along with other metadata - as such, these measurements are unknown.

2.3 | Analyzed specimen

The predatory Permian stem actinopterygian *†Brazilichthys macrognathus* was originally described based on a single specimen (DGM

1061-P) collected in the Pastos Bons locality of the Pedra de Fogo Formation (Cox & Hutchinson, 1991; Figueroa et al., 2019), which is considered to be Artinskian-Kungurian (290.1–273.01 mya (Henderson et al., 2020)) in age based on palynological and vertebrate fossil data (Iannuzzi et al., 2018).

2.4 | Microcomputed tomography (µCT)

µCT data for *†Brazilichthys macrognathus* was obtained from Figueroa et al. (2019) and processed using the software Mimics v 19.0 (Materialise, Belgium) to extract upper and lower jaw models. Comparative extant materials were acquired either from MorphoSource (for JFBM, ROM, UF, UW, or YPM specimens; see DOI and ARK identifiers for specific files), or via µCT scanning on a Nikon XT H 225 ST industrial CT scanner at the University of Michigan CT in Earth and Environmental Sciences (CTEES) facility. Scanned specimens are deposited in the collection of the University of Michigan Museum of Zoology (UMMZ). See Table S1 for more detailed information on comparative material used in this study.

2.5 | Modeling and visualization

Using Blender 3.2 (blender.org), .ply objects of the left jaws of *†Brazilichthys* were rendered using a simple shading and lighting scheme. For visualization of the jaw closing mechanism, the lower jaw was repositioned in relation to the upper jaw to better reflect the expected life orientation. Setting a single articulation point on the glenoid fossa of the lower jaw permitted simple animation of jaw movement (File S1) and observation of the interaction between fangs and palate.

2.6 | Abbreviation list

ac.v – accessory vomer; ad.f – adductor fossa; ang – angular; cor – coronoids; de – dentary; de.fa – dentary fangs; de.la.te – dentary labial dentition; gle – glenoid fossa; mx – maxilla; mx.fa – maxillary fangs; mx.fa.so – maxillary fang sockets; mx.la.te – maxillary labial dentition; part – prearticular; pmx – premaxilla; pq – palatoquadrate; pq.s – palatoquadrate suborbital lamina; pq.te – palatoquadrate teeth; psp – parasphenoid; te.fe – fenestra for teeth on the palate.

The obelus (†) indicates extinct taxa, following Patterson and Rosen (1977).

3 | RESULTS AND DISCUSSION

3.1 | Jaw closing in *†Brazilichthys macrognathus*

Although *†Brazilichthys* was originally compared to acrolepids and birgeriids, due to the large fangs on both upper and lower jaws (Cox & Hutchinson, 1991; Romano & Brinkmann, 2009), micro-computed

tomography (µCT) revealed anatomical structures that contradict these placements. Instead, a formal phylogenetic analysis places *†Brazilichthys* as part of an unresolved group that includes most late Paleozoic (Carboniferous and Permian) actinopterygians (Figueroa et al., 2019). Like many other Paleozoic ray-finned fishes, *†Brazilichthys* bears multiple rows of teeth on the upper and lower jaws, associated with the premaxilla, maxilla, palatoquadrate, dentary, and coronoids (Figueroa et al., 2019). Thus, three rows of teeth are present on each jaw—two on the labial surface (maxilla and dentary), and one mesially (palatoquadrate and coronoids). The teeth from both rows (labial and lingual) in the maxilla and dentary are conical, but the lingual row is formed by large curved fangs. The dentition on the coronoids and palatoquadrate is similar, formed by numerous closely-spaced conical teeth forming a continuous row.

With the jaw closed, the dentition of the upper jaw overlies the lateral surface of the dentary, while the dentition of the lower jaw lies mesial to the external surface of the maxilla (Figure 1). Anterior to the maxilla, the premaxilla bears a single row of three small conical teeth. Since the dentition of the lower jaw also includes large fangs, closure of the jaw is only possible due to the presence of fenestrae for the insertion of the lower jaw fangs into the mesial surface of the maxilla, lingual to the maxillary dentition and labial to the dentition of the palatoquadrate (Figure 1b,c). The most anterior portion of the maxilla lacks fenestration, as the mandibular fangs nearer to the symphysis are smaller than those more proximal. The way these fenestrae develop is not clear from the CT-data alone, but their positioning suggests they are formed by U-shaped serial fenestration of the maxilla in contact with the lateral margin of the palate. The presence of these fenestrae permits the complete closure of the jaws so that the dentition of the coronoids and the palatoquadrate can contact each other when the jaws are completely closed. We discard the hypothesis that these fenestrae could be associated with the replacement of maxillary fangs, as the fenestrae are not aligned with the maxillary teeth, which are positioned labially to the fenestrae. Additionally, in between the upper jaw fangs, there are depressions that correspond to sockets for fang replacement (Figures 1c and 2). Similar sockets are present in other Paleozoic taxa, including several sarcopterygians (Downs & Daeschler, 2020) and fang-bearing actinopterygians (Dunkle & Schaeffer, 1973; Štamberg, 1991). Similar sockets for tooth replacement are present in extant actinopterygians such as the dentary and maxilla of the bichir *Polypterus senegalus* (Clemen et al., 1998; Wacker et al., 2001) and the lateral dentition of the cutlassfish *Trichiurus lepturus* (Bemis et al., 2019).

The fenestrae of the maxilla are filled with fangs from the lower jaw in an alternate manner, meaning that one fenestra is filled with a fang while the subsequent one remains empty. These empty fenestrae seem to align with empty tooth sockets on the dentary (Figure 2). Some of these tooth sockets bear fangs in the early stages of development (Figure S1). Thus, it is likely that the fangs of *†Brazilichthys* were replaced in an alternate pattern. However, on the right jaws of *†Brazilichthys*, the tooth sockets that are empty in the left jaw are filled with fangs. These fangs are poorly attached to the dentary bone and only partially pierce the fenestration of the

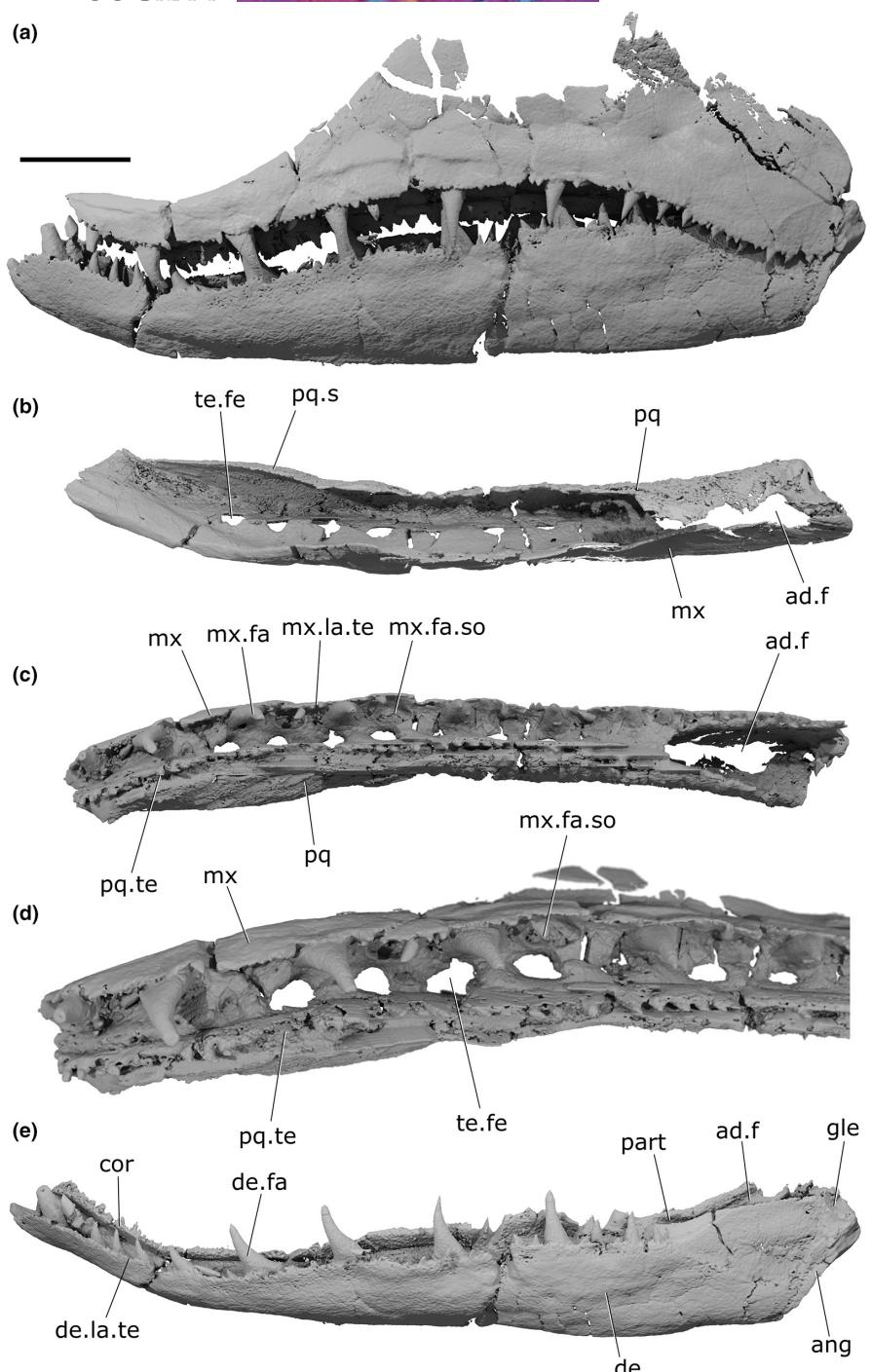


FIGURE 1 Left jaws of †*Brazilichthys macrognathus* (DGM 1061-P). (a) Upper and lower jaws in left lateral view; (b) upper jaw in dorsal view; (c) upper jaw in ventral view; (d) distal end of the upper jaw in ventral view; (e) left lower jaw in dorsolateral view. Scale bar = 10 mm.

maxilla (Figures 1 and 2). This indicates that tooth replacement in †*Brazilichthys* was done in an alternate manner on each dentary and that this process would occur separately on each jaw, meaning that replacement is bilaterally asymmetrical.

Similar alternate pattern of tooth replacement is known in extant actinopterygians. Many predatory actinopterygians show replacement of teeth by filling empty sockets between the older teeth set (Bemis et al., 2005, 2019). However, information on tooth

development and replacement is lacking for most teleosts (Bemis et al., 2005, 2019; Kolmann et al., 2019; Morgan & King, 1983; Stuart et al., 2021). In terms of asymmetrical replacement of teeth of the lower jaw, extant examples include macropredatory characiforms, such as serrasalmids (Kolmann et al., 2019; Stuart et al., 2021). The presence of both alternate and asymmetrical tooth replacement in †*Brazilichthys* further corroborate the macropredatory habitus of this species.

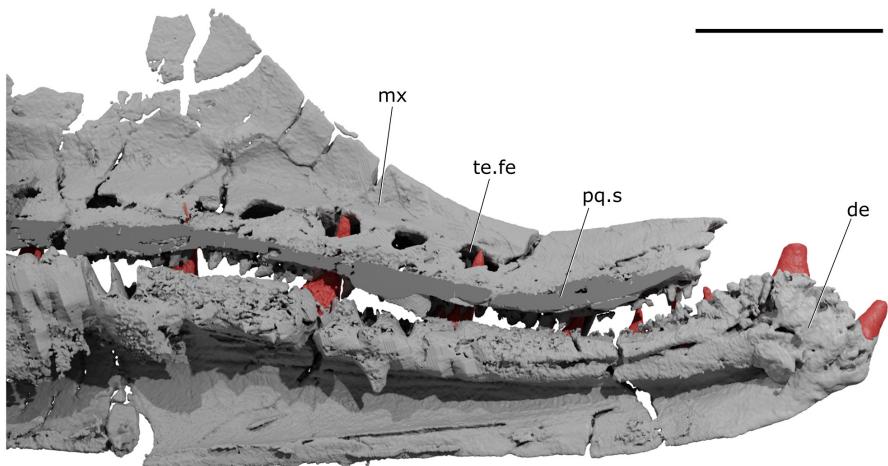


FIGURE 2 Left jaws of †*Brazilichthys macrognathus* (DGM 1061-P) in mesial view. Palatoquadrate sectioned to expose the fenestration of the maxilla and the fangs of the lower jaw (in red). Scale bar = 10mm.

The morphology of the adductor mandibulae muscle in Paleozoic ray-finned fishes is still poorly understood. In Paleozoic ray-finned fishes, this muscle bundle appears to have been constrained within the maxillary-palatoquadrate chamber of the lower jaw, attaching to the palatoquadrate and the hyomandibula, as in living non-teleost ray-finned fishes (Datovo & Rizzato, 2018; Lauder, 1980). Lauder (1980) proposes that the anterior adductor mandibulae muscle would attach to the anterior portion of the palatoquadrate, following the suborbital blade of the upper jaw. If this is true, then the presence of lower jaw fangs inserting into the maxilla-palatoquadrate chamber would at least partially constrain the placement and size of the anterior adductor mandibulae muscle. Further, a cartilaginous or membranous tissue layer would be needed to protect musculature from being punctured by the lower jaw fangs. Thus, there are two potential muscle morphologies to cope with the presence of the fangs accommodation: (1) the anterior adductor mandibulae muscle being shortened and terminating more proximal to the adductor fossa, leaving the suborbital blade of the upper jaw free for fang accommodation; (2) the anterior adductor mandibulae muscle would remain fixed to the anterior portion of the palatoquadrate, but strongly dorsoventrally constrained and protected from the fangs by a cartilaginous or membranous tissue. Unfortunately, due to the lack of more specimens of †*Brazilichthys* and the absence of soft-tissue preservation in the holotype it is not possible to favor either of these hypotheses.

3.2 | Other Paleozoic osteichthyans

The mode of fang accommodation presented above is unique among Paleozoic actinopterygians. Other predatory taxa with similar dentition—such as †*Tegeolepis*, †*Progyrolepis*, and †*Nematoptychius*—do not show evidence of fenestration on the palate for fang insertion (Dunkle & Schaeffer, 1973; Poplin, 1999, fig. 2; Štamberg, 2018, figs. 7, 9, 11b). In these, taxa there seems to be only partial closure of the jaws, limited by the size of the dentary fangs, while fangs from the maxilla

lay labially, along the outer surface of the lower jaw. In some Devonian sarcopterygians—such as †*Eusthenopteron* (Figure 3b), †*Heddeleichthys*, †*Tristichopterus*, †*Megalichthys* (Downs & Daeschler, 2020; Jarvik, 1980; Parfitt et al., 2014; Snitting, 2009)—there is evidence of fossae on the lower jaw to fit the large palatal fangs, while the dentary dentition lays more dorsal over an elevated lateral jaw margin. This is evident in rhipidistians, which bear intercoronoid and precoronoid fossae on the lower jaw (Ahlberg & Clack, 1998). The most similar morphology to that of †*Brazilichthys* (Figure 3c) is found in †*Onychodus* (Figure 3a), where there is a large groove between the maxillary and palatal dentition that fits the extent of the dentary fangs. However, there is no fenestration within this palatal groove for individual fangs (Andrews et al., 2005; Schaeffer & Rosen, 1961).

3.3 | Extant actinopterygians

The following descriptions focus on fangs and how they are accommodated within the closed jaws of the taxa mentioned. For brief descriptions of how the other teeth of the low jaw are accommodated within the mouth, refer to Table S1.

3.3.1 | Tooth arrangements at the anterior margin of the jaws

Along the anterior margin of the gape, several extant actinopterygians house their mandibular teeth posteromesial to the premaxillary bone or alongside the premaxillary teeth, including the lancetfish *Alepisaurus ferox*, the bowfin *Amia calva*, the snakehead *Channa marulius*, the bichir *Polypterus senegalus*, the snake mackerel *Promethichthys prometheus*, the walleye *Sander vitreus*, and the cutlassfish *Trichiurus lepturus*.

S. vitreus bears elongate anterior mandibular fangs that insert into a soft tissue cavity between the premaxilla and vomerine head.

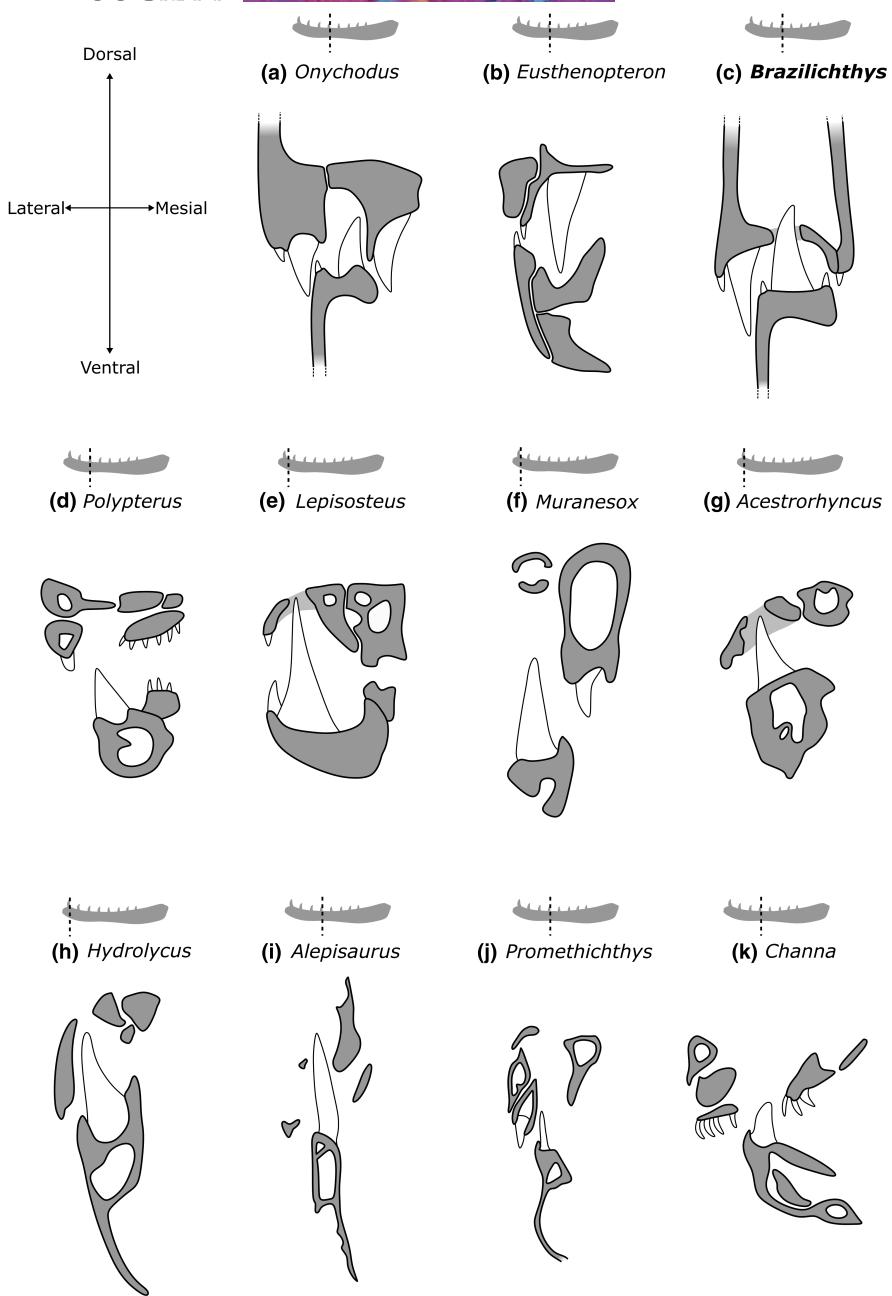


FIGURE 3 Transverse sections through the jaws of selected fanged osteichthyans showing various methods of fang accommodation, arranged phylogenetically (Dornburg & Near, 2021). (a) †*Onychodus* (based on Andrews, 2005); (b) †*Eusthenopteron* (based on Jarvik, 1980); (c) †*Brazilichthys* (DGM 1061-P); (d) *Polypterus* (UMMZ 195008); (e) *Lepisosteus* (UMMZ 196974); (f) *Muraenesox* (Morphosource UW:UWFC:021142); (g) *Acestorhynchus* (Morphosource UF:Fish:189596); (h) *Hydrolycus* (Morphosource ROM:Fishes:88356); (i) *Alepisaurus* (Morphosource YPM:Ich:025451); (j) *Promethichthys* (Morphosource UF:Fish:231977); (k) *Channa* (Morphosource UF:Fish:241571). Dark gray indicates bone, light gray areas indicate continuity of the bone behind a tooth in a fenestra.

Other fishes, such as *C. marulius*, bear anterior lower jaw dentition that interdigitate with the dentition of the upper jaw.

The vampire fish *Hydrolycus armatus* (Figure 3h) employs an alternative strategy, housing its massive anterior mandibular dentition within a void between the ethmoid, ectopterygoid, and maxilla posteromesially, and the premaxilla at the anterolateral margins.

The pike conger *Muraenesox cinereus* (Figure 3f), have large mandibular teeth anteriorly that are accommodated by a cavity along the posterior margin of the vomerine head.

3.3.2 | Tooth arrangements along the lateral gape

Most frequently, the mandibular teeth contributing to the lateral gape are accommodated between the premaxilla and the often tooth-bearing ectopterygoid, as in the sampled taxa *A. ferox* (Figure 3i), *A. calva*, the weakfish *Cynoscion regalis*, *P. prometheus* (Figure 3j), *S. vitreus*, and the barracuda *Sphyraena sphyraena*. Along the most posterior margin of the lateral gape, the mandibular dentition of these fishes slots between the maxilla and the ectopterygoid.

In *P. senegalus* (Figure 3d), the large mandibular teeth along the lateral gape are accommodated by a fossa on the ventral surface of the maxilla, lateral to the ectopterygoid and mesial to the upper jaw dentition.

Alternatively, the large teeth along the gape of the dentary of *C. marulius* (Figure 3k) are housed between the premaxilla, maxilla, and lachrymal on the lateral margin, and the ectopterygoid on the mesial margin, while becoming smaller and more conical posteriorly.

The more posterior lateral dentition of *H. armatus* is accommodated by a notch along the mesial margin of the maxilla and another notch along the lateral margin of the ectopterygoid.

In *M. cinereus*, the larger mandibular dentition along the anterior margin of the lateral gape is bounded by soft tissue. Along the posterior portion of the gape, the mandibular dentition slots into small depressions along the ventral margin of the maxilla, mesial to the maxillary tooth row.

None of the aforementioned extant taxa possess a jaw morphology or fang accommodation scheme comparable to that found in *†Brazilichthys*.

3.3.3 | Fangs penetrating bones of the upper jaw and palate

Extant actinopterygians possessing fenestrae in the upper jaw for the accommodation of dentary dentition are quite rare. Only two of the neopterygians sampled possessed a condition comparable in function to that found in *†Brazilichthys*, despite the clade accounting for nearly 99.9% of all extant actinopterygian species richness (Fricke et al., 2022) and possessing a wide breadth of phenotypic and ecological diversity (Nelson et al., 2016). This is most likely due to neopterygians having an upper jaw no longer firmly bound to the palate, as is found in other actinopterygians (Friedman, 2015).

The holostean *Lepisosteus* (Figure 3e) can possess fenestrae in the most anterior lacrimomaxillary bones and spaces between a lacrimomaxilla and the premaxilla, with variation ranging from complete absence to possessing one or two fenestrae depending on species (Grande, 2010). These fenestrae are restricted to the anterior of the snout and, like *†Brazilichthys*, accommodate teeth of the dentary. In *L. oculatus*, the posteriormost mandibular teeth along the lateral gape interdigitate with the teeth of the lacrimomaxillae (see Grande (2010) for illustration).

In the characiform *Acestrorhynchus falcatus* (Figure 3g), a singular mandibular fang at the anterior of the lateral gape is accommodated by the foramen for the dentary canine in the premaxilla (see Toledo-Piza (2007) for illustration). The remainder of the anterior dentition of the dentary fits along the posteromesial margin of the premaxilla, while the more posterior dentition fits into grooves along the ventrolateral margin of the maxilla. The dentition along the most posterior portion of the dentary is small and conical, fitting between the ectopterygoid and maxilla.

4 | CONCLUSIONS

The mode of jaw closing of *†Brazilichthys*—especially in terms of interaction between the lower jaw and palate—is unique among osteichthyans when considering osteological features. Several Paleozoic sarcopterygians adopt a similar strategy but with fenestration being present in the lower jaw rather than the palate. While a fenestrated upper jaw is present in *Acestrorhynchus* and *Lepisosteus*, it is never as sequential fenestrations of a single ossification, as the neopterygian palate is formed by multiple differentiated ossifications. Other predatory sarcopterygians, such as porolepiforms and onychodonts, bear paired internasal cavities on the anterior end of the mouth roof that accommodate teeth from the lower jaw tooth-whorls (Lu et al., 2016; Yu, 1998). Similarly, megalichthyids bear an apical fossa on the ethmosphenoid surface of the braincase (Downs & Daeschler, 2020) that might be associated with fitting anterior fangs of the lower jaw. Thus, the unique mode of jaw closure seen in *†Brazilichthys* further supports previous interpretations of a macro-predatory habitus for this taxon.

The presence of these maxillary fenestrae to accommodate the teeth of the lower jaw in *†Brazilichthys* adds to the list of characters of late Paleozoic actinopterygians. As noted by Figueroa et al. (2019), despite the abundance of ecomorphologically similar taxa and many families united by the presence of large fangs (e.g., acrolepids, rhabdolepids, cosmoptychids, etc.), there is little evidence to support these assignments, with most of the characteristics defining these groups being of weak systematic value. Further studies on the jaws of these predatory Paleozoic actinopterygians might shed light on their affinities and help us understand whether macropredatory ecomorphologies emerged multiple times along the actinopterygian stem.

Non-neopterygian actinopterygians account for only 43 extant species across 3 families (Polypteridae, Acipenseridae, and Polyodontidae) (Fricke et al., 2022), though their fossil richness is considerably higher in the Paleozoic (Henderson, Dunne, & Giles, 2022). While a more in-depth analysis is needed, the bound nature of the upper jaw and palate of non-neopterygians may have acted as a 'spandrel' of sorts (Gould & Lewontin, 1979), forcing novel ways of storing teeth in a physiologically-constrained space to emerge. Neopterygian fishes have more kinetic upper jaws—decoupling their maxilla and preoperculum (Friedman, 2015)—thereby allowing for the accommodation of mandibular teeth between the numerous bones of the jaw and palate that has led to a proliferation of novel ways to house dentition in the extraordinarily species rich and ecomorphologically diverse extant actinopterygian assemblage.

Although superficially similar in terms of skull dermal bone anatomy, early ray-finned fishes show considerable variation in body shape, fin morphology, and habitat (Friedman, 2015). Thus, we anticipate that strategies for coping with large fangs might be more diverse than previously thought, and a greater survey of Paleozoic actinopterygian jaws, coupled with anatomical revisions of poorly

known taxa, will increase our understanding of the feeding mechanisms employed by early ray-finned fishes.

AUTHOR CONTRIBUTIONS

Rodrigo T. Figueroa conceived the project, analyzed data, prepared figures, and wrote the manuscript; James V. Andrews analyzed data on extant species, prepared figures, and wrote the manuscript. Segmentation of *†Brazilichthys* was done by Rodrigo T. Figueroa while segmentation of extant species was conducted by James V. Andrews.

ACKNOWLEDGMENTS

This research was funded by the Department of Earth and Environmental Sciences of the University of Michigan. We thank Matt Friedman, Matt Kolmann, and Alessio Capobianco for valuable comments on an early version of this manuscript. Additionally, we thank Ramon Nagesan and Matt Kolmann for assistance with CT-scanning of extant specimens. This study includes data produced in the CTEES facility at the University of Michigan, supported by the Department of Earth and Environmental Sciences and College of Literature, Science, and the Arts. Funding sources for material accessed via MorphoSource include: NSF DBI-1701665; oVert TCN; NSF DBI-1701714; NSF DBI-1701769; NSF DBI-1702421.

DATA AVAILABILITY STATEMENT

Surface models (.ply) of the jaws of *†Brazilichthys macrognathus* are available through [10.5281/zenodo.7019347](https://doi.org/10.5281/zenodo.7019347). The μ -CT data on extant species (*Polypterus*, *Amia*, and *Lepisosteus*) that support the findings of this study are available through MorphoSource (*Polypterus senegalus*: [ark:/87602/m4/483259](https://doi.org/10.5281/zenodo.483259); *Amia calva*: [ark:/87602/m4/483252](https://doi.org/10.5281/zenodo.483252); *Lepisosteus oculatus*: [ark:/87602/m4/483297](https://doi.org/10.5281/zenodo.483297)).

ORCID

Rodrigo T. Figueroa  <https://orcid.org/0000-0001-9862-904X>

James V. Andrews  <https://orcid.org/0000-0001-7093-1335>

REFERENCES

Ahlberg, P.E. & Clack, J.A. (1998) Lower jaws, lower tetrapods—a review based on the Devonian genus *Acanthostega*. *Earth and Environmental Science Transactions of The Royal Society of Edinburgh*, 89, 11–46. Available from: <https://doi.org/10.1017/S026359330002340>

Andrews, M., Long, J., Ahlberg, P., Barwick, R., Campbell, K. (2005) The structure of the sarcopterygian *Onychodus jandemarrai* n. sp. from Gogo, Western Australia: with a functional interpretation of the skeleton. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, 96, 197–307. Available from: <https://doi.org/10.1017/S0263593300001309>

Aretz, M., Herbig, H.G., Wang, X.D. et al. (2020) The carboniferous period. In: Gradstein, F.M., Ogg, J.G., Schmitz, M.D. et al. (Eds.), *Geologic time scale 2020*. Oxford, United Kingdom: Elsevier, pp. 811–874. Available from: <https://doi.org/10.1016/B978-0-12-824360-2.00023-1>

Argyriou, T., Giles, S. & Friedman, M. (2022) A Permian fish reveals widespread distribution of neopterygian-like jaw suspension. *eLife*, 11, e58433. Available from: <https://doi.org/10.7554/eLife.58433>

Argyriou, T., Giles, S., Friedman, M., Romano, C., Kogan, I., Sánchez-Villagra, M.R. (2018) Internal cranial anatomy of early Triassic species of *†Saurichthys* (Actinopterygii: *†Saurichthyoformes*): implications for the phylogenetic placement of *†saurichthyoforms*. *BMC Evolutionary Biology*, 18, 161. Available from: <https://doi.org/10.1186/s12862-018-1264-4>

Bemis, K.E., Burke, S.M., St. John, C.A., Hilton, E.J., Bemis, W.E. (2019) Tooth development and replacement in the Atlantic Cutlassfish, *Trichiurus lepturus*, with comparisons to other Scombroidei. *Journal of Morphology*, 280, 78–94. Available from: <https://doi.org/10.1002/jmor.20919>

Bemis, W.E., Giuliano, A. & McGuire, B. (2005) Structure, attachment, replacement and growth of teeth in bluefish, *Pomatomus saltatrix* (Linnaeus, 1766), a teleost with deeply socketed teeth. *Zoology*, 108, 317–327. Available from: <https://doi.org/10.1016/j.zool.2005.09.004>

Choo, B. (2009) Basal Actinopterygian fish from the middle Devonian Bunga beds of New South Wales, Australia. *Proceedings of the Linnean Society of New South Wales*, 130, 37–46.

Clemen, G., Bartsch, P. & Wacker, K. (1998) Dentition and dentigerous bones in juveniles and adults of *Polypterus senegalus* (Cladistia, Actinopterygii). *Annals of Anatomy*, 180, 211–221. Available from: [https://doi.org/10.1016/S0940-9602\(98\)80076-9](https://doi.org/10.1016/S0940-9602(98)80076-9)

Cox, C.B. & Hutchinson, P. (1991) Fishes and Amphibians from the late Permian Pedra do Fogo formation of Northern of Brazil. *Palaeontology (oxford)*, 34, 13.

Datovo, A. & Rizzato, P.P. (2018) Evolution of the facial musculature in basal ray-finned fishes. *Frontiers in Zoology*, 15, 40. Available from: <https://doi.org/10.1186/s12983-018-0285-6>

Dornburg, A. & Near, T.J. (2021) The emerging phylogenetic perspective on the evolution of actinopterygian fishes. *Annual Review of Ecology, Evolution, and Systematics*, 52, 427–452. Available from: <https://doi.org/10.1146/annurev-ecolsys-122120-122554>

Downs, J.P. & Daeschler, E.B. (2020) A new species of *Megalichthys* (Sarcopterygii, Megalichthyidae) from the upper Devonian (Famennian) of Pennsylvania, U.S.A., and a report on the Cosmine-covered osteolepiform fossils of the Catskill formation. *Journal of Vertebrate Paleontology*, 40, e1774771. Available from: <https://doi.org/10.1080/02724634.2020.1774771>

Dunkle, D.H. & Schaeffer, B. (1973) *Tegeolepis clarki* (Newberry), a palaeonisciform from the upper Devonian Ohio shale. *Palaeontographica Abteilung A*, 143, 151–158.

Figueroa, R.T., Friedman, M. & Gallo, V. (2019) Cranial anatomy of the predatory actinopterygian *Brazilichthys macrognathus* from the Permian (Cisuralian) Pedra de Fogo formation, Parnaíba Basin, Brazil. *Journal of Vertebrate Paleontology*, 39, e1639722. Available from: <https://doi.org/10.1080/02724634.2019.1639722>

Figueroa, R.T., Weinschütz, L.C. & Friedman, M. (2021) The oldest Devonian circum polar ray-finned fish? *Biology Letters*, 17, 20200766. Available from: <https://doi.org/10.1098/rsbl.2020.0766>

Fricke R, Eschmeyer WN, Fong JD (2022) Eschmeyer's catalog of fishes - genera/species by family/subfamily. Available from: <https://researcharchive.calacademy.org/research/ichthyology/catalog/SpeciesByFamily.asp>. Accessed 16 August 2022.

Friedman, M. (2015) The early evolution of ray-finned fishes. *Palaeontology*, 58, 213–228. Available from: <https://doi.org/10.1111/pala.12150>

Friedman, M., Pierce, S.E., Coates, M., Giles, S. (2018) Feeding structures in the ray-finned fish *Eurynotus crenatus* (Actinopterygii: Eurynotiformes): implications for trophic diversification among carboniferous actinopterygians. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, 109, 33–47. Available from: <https://doi.org/10.1017/S1755691018000816>

Germain, D., Schnell, N.K. & Meunier, F.J. (2019) Histological data on bone and teeth in two dragonfishes (Stomiidae; Stomiiformes):

Borostomias panamensis Regan & Trewavas, 1929 and Stomias boa Reinhardt, 1842. *Cybium*, 43, 103–107. Available from: <https://doi.org/10.26028/CYBIUM/2019-431-010>

Giles, S., Darras, L., Clément, G., Blieck, A., Friedman, M. (2015) An exceptionally preserved late Devonian actinopterygian provides a new model for primitive cranial anatomy in ray-finned fishes. *Proceedings of the Royal Society B: Biological Sciences*, 282, 20151485. Available from: <https://doi.org/10.1098/rspb.2015.1485>

Giles, S., Xu, G.H., Near, T.J., Friedman, M. (2017) Early members of "living fossil" lineage imply later origin of modern ray-finned fishes. *Nature*, 549, 265–268. Available from: <https://doi.org/10.1038/nature23654>

Gill, E.L. (1925) The Permian Fish *Dorypterus*. *Transactions of the Royal Society of Edinburgh*, 53, 643–661.

Gould, S.J. & Lewontin, R.C. (1979) The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proceedings of the Royal Society of London Series B Biological Sciences*, 205, 581–598. Available from: <https://doi.org/10.1098/rspb.1979.0086>

Grande, L. (2010) An empirical synthetic pattern study of gars (lepisosteiformes) and closely related species, based mostly on skeletal anatomy. The resurrection of Holostei. *Copeia*, 10, 1–871.

Greven, H., Walker, Y. & Zanger, K. (2009) On the structure of teeth in the viperfish *Chauliodus sloani* Bloch & Schneider, 1801 (Stomiidae). *Bulletin of Fish Biology*, 11, 87–98.

Henderson, C.M., Shen, S.Z., Gradstein, F.M. et al. (2020) The Permian period. In: Gradstein, F.M., Ogg, J.G., Schmitz, M.D. et al. (Eds.) *Geologic Time Scale 2020*. Oxford, United Kingdom: Elsevier, pp. 875–902. Available from: <https://doi.org/10.1016/B978-0-12-824360-2.00024-3>

Henderson, S., Dunne, E.M., Fasey, S.A., Giles, S. (2022) The early diversification of ray-finned fishes (Actinopterygii): hypotheses, challenges and future prospects. *Biological Reviews*, 1–32. Available from: <https://doi.org/10.1111/brv.12907>

Henderson, S., Dunne, E.M., Giles, S. (2022) Sampling biases obscure the early diversification of the largest living vertebrate group. Available from: <https://doi.org/10.1101/2022.05.09.491144>

Iannuzzi, R., Neregato, R., Cisneros, J.C. et al. (2018) Re-evaluation of the Permian macrofossils from the Parnaíba Basin: biostratigraphic, palaeoenvironmental and palaeogeographical implications. *Geological Society, London, Special Publications*, 472, 223–249. Available from: <https://doi.org/10.1144/SP472.14>

Jarvik, E. (1980) *Basic structure and evolution of vertebrates*. New York, USA: Academic Press.

Kierdorf, H., Kierdorf, U., Greven, H., Clemen, G. (2022) Dental structure and tooth attachment modes in the common fangtooth *Anoplogaster cornuta* (Valenciennes, 1833) (Actinopterygii; Trachichthyiformes; Anoplogastridae). *PLoS One*, 17, e0272860. Available from: <https://doi.org/10.1371/journal.pone.0272860>

Kolmann, M.A., Cohen, K.E., Bemis, K.E., Summers, A.P., Irish, F.J., Hernandez, L.P. (2019) Tooth and consequences: Heterodonty and dental replacement in piranhas and pacus (Serrasalmidae). *Evolution and Development*, 21, 247–262. Available from: <https://doi.org/10.1111/ede.12306>

Lauder, G.V. (1980) Evolution of the feeding mechanism in primitive actinopterygian fishes: a functional anatomical analysis of *Polypterus*, *Lepisosteus*, and *Amia*. *Journal of Morphology*, 163, 283–317. Available from: <https://doi.org/10.1002/jmor.1051630305>

Lauder, G.V. (1982) Patterns of Evolution in the Feeding Mechanism of Actinopterygian Fishes 1 structurally and functionally complex systems come increasingly sophisticated and tech-line of information on the historical see- have largely obviated the need to base of the actinop. *American Society of Zoologists*, 285, 275–285. Available from: <https://doi.org/10.1093/icb/22.2.275>

Lu, J., Zhu, M., Ahlberg, P.E. et al. (2016) A Devonian predatory fish provides insights into the early evolution of modern sarcopterygians. *Science Advances*, 2, e1600154. Available from: <https://doi.org/10.1126/sciadv.1600154>

Lund, R. & Poplin, C. (2002) Cladistic analysis of the relationships of the Tarsiids (lower carboniferous Actinopterygians). *Journal of Vertebrate Paleontology*, 22, 480–486. Available from: [https://doi.org/10.1671/0272-4634\(2002\)022\[0480:CAOTRO\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2002)022[0480:CAOTRO]2.0.CO;2)

Morgan, E.C. & King, W.K. (1983) Tooth replacement in King mackerel, *Scomberomorus cavalla* (Pisces: Scombridae). *The Southwestern Naturalist*, 28, 261–269. Available from: <https://doi.org/10.2307/3670785>

Nelson, J.S., Grande, T.C. & MVH, W. (2016) *Fishes of the world*. New Jersey, USA: John Wiley & Sons.

Olson, E. (2017) The evolution of fangs across ray-finned fishes (Actinopterygii). *Culminating Projects in Biology*, 22, 1–96. Available from: https://repository.stcloudstate.edu/biol_etds/22

Parfitt, M., Johanson, Z., Giles, S., Friedman, M. (2014) A large, anatomically primitive tristichopterid (Sarcopterygii: Tetrapodomorpha) from the late Devonian (Frasnian) Alves beds, upper old red sandstone, Moray, Scotland. *Scottish Journal of Geology*, 50, 79–85. Available from: <https://doi.org/10.1144/sjg2013-013>

Patterson, C. & Rosen, D.E. (1977) Review of ichthyodectiform and other Mesozoic teleost fishes, and the theory and practice of classifying fossils. *Theory and practice of classifying fossils*, 158, 85–172.

Poplin, C. (1999) Un paléoniscoïde (Pisces, Actinopterygii) de Buxières-les-Mines, témoins des affinités fauniques entre Massif central et Bohème au passage Carbonifère-Permien. *Geodiversitas*, 21, 147–155.

Romano, C. & Brinkmann, W. (2009) Reappraisal of the lower actinopterygian *Birgeria stensioei* Aldinger, 1931 (Osteichthyes; Birgeriidae) from the middle Triassic of Monte san Giorgio (Switzerland) and Besano (Italy). *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen*, 252, 17–31. Available from: <https://doi.org/10.1127/0077-7749/2009/0252-0017>

Sabaj, M.H. (2020) Codes for natural history collections in ichthyology and herpetology. *Copeia*, 108, 593–669. Available from: <https://doi.org/10.1643/ASIHCODONS2020>

Sallan, L.C. & Coates, M.I. (2013) Styracopterid (Actinopterygii) ontogeny and the multiple origins of post-Hangenberg deep-bodied fishes. *Zoological Journal of the Linnean Society*, 169, 156–199. Available from: <https://doi.org/10.1111/zoj.12054>

Schaeffer, B. & Rosen, D.E. (1961) Major adaptive levels in the evolution of the Actinopterygian feeding mechanism. *American Zoologist*, 1, 187–204.

Snitting, D. (2009) *Hedleichthys*– a new tristichopterid genus from the dura Den formation, Midland Valley, Scotland (Famennian, late Devonian). *Acta Zoologica*, 90, 273–284. Available from: <https://doi.org/10.1111/j.1463-6395.2008.00376.x>

Stack, J. & Gottfried, M.D. (2021) A new, exceptionally well-preserved Permian actinopterygian fish from the Minnekahta limestone of South Dakota, USA. *Journal of Systematic Palaeontology*, 19, 1271–1302. Available from: <https://doi.org/10.1080/14772019.2022.2036837>

Štamberg, S. (1991) Actinopterygians of the central bohemian carboniferous basins. *Sborník Národního musea v Praze B, Přírodovědný = Acta Musei Nationalis Pragae B, Hist naturalis*, 47, 25–104.

Štamberg, S. (2006) Carboniferous-Permian actinopterygian fishes of the continental basins of the bohemian massif, Czech Republic: an overview. *Geological Society, London, Special Publications*, 265, 217–230. Available from: <https://doi.org/10.1144/GSL.SP.2006.265.01.10>

Štamberg, S. (2018) Actinopterygians of the Permian locality Buxières-les-mines (Bourbonl'archambault basin, France) and their relationship to other early Actinopterygians. *Fossil Imprint*, 74, 245–291. Available from: <https://doi.org/10.2478/if-2018-0017>

Stuart, C.E., Green, S.J., Vernygora, O., LeBlanc, A.R.H., Bertschi, M.H., Brown, M. (2021) New insights into patterns and rates of tooth replacement in serrasalmid and characid fishes, with implications

for the subsistence fishery of Peru's remote ribereños villages. *Journal of Fish Biology*, 98, 1196–1201. Available from: <https://doi.org/10.1111/jfb.14634>

Toledo-Piza, M. (2007) Phylogenetic relationships among *Acestrorhynchus* species (Ostariophysi: Characiformes: Acestrorhynchidae). *Zoological Journal of the Linnean Society*, 151, 691–757. Available from: <https://doi.org/10.1111/j.1096-3642.2007.00355.x>

Wacker, K., Bartsch, P. & Clemen, G. (2001) The development of the tooth pattern and dentigerous bones in *Polypterus senegalus* (Cladistia, Actinopterygii). *Annals of Anatomy - Anatomischer Anzeiger*, 183, 37–52. Available from: [https://doi.org/10.1016/S0940-9602\(01\)80011-X](https://doi.org/10.1016/S0940-9602(01)80011-X)

Yu, X. (1998) A new porolepiform-like fish, *Psarolepis romeri*, gen. Et sp. nov. (Sarcopterygii, Osteichthyes) from the lower Devonian of Yunnan, China. *Journal of Vertebrate Paleontology*, 18, 261–274. Available from: <https://doi.org/10.1080/02724634.1998.10011055>

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Figueroa, R.T. & Andrews, J.V. (2023)

Fitting fangs in a finite face: A novel fang accommodation strategy in a 280-million-year-old ray-finned fish. *Journal of Anatomy*, 242, 525–534. Available from: <https://doi.org/10.1111/joa.13798>