***Tanyrhinichthys mcallisteri*, a long-rostrumed Pennsylvanian ray-finned fish (Actinopterygii), and the simultaneous appearance of novel ecomorphologies in Late Paleozoic fishes**

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Running Header: Convergence in long-rostrumed Carboniferous fishes

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Abstract.— The Carboniferous radiation of fishes was marked by the convergent appearance of then-novel but now common ecomorphologies resulting from changes in the relative proportions of traits, including elongation of the front of the skull (rostrum). The earliest ray-finned fishes (Actinopterygii) with elongate rostra are poorly-known, obscuring the earliest appearances of a now widespread feature in actinopterygians. We redescribe *Tanyrhinichthys mcallisteri*, a long-rostrumed actinopterygian from the Upper Pennsylvanian (Missourian) of the Kinney Brick Quarry, New Mexico. *Tanyrhinichthys* has a lengthened rostrum bearing a sensory canal, ventrally inserted paired fins, posteriorly placed median fins unequal in size and shape, and a heterocercal caudal fin. *Tanyrhinichthys* shares these features with sturgeon, but lacks chondrostean synapomorphies, indicating convergence on a bottom-feeding lifestyle. Elongate rostra evolved independently in two lineages of bottom-dwelling, freshwater actinopterygians in the Late Pennsylvanian of Euramerica, as well as in at least one North American chondrichthyan (*Bandringa rayi*). The near-simultaneous appearance of novel ecomorphologies among multiple, distantly-related lineages of actinopterygians and chondrichthyans was common during the Carboniferous radiation of fishes. This may reflect global shifts in marine and freshwater ecosystems and environments during the Carboniferous favoring such ecomorphologies, or may have been contingent on the plasticity of early actinopterygians and chondrichthyans.

INTRODUCTION

The Carboniferous is defined by large diversification events among fishes and tetrapods following the end-Devonian mass extinction (359 Ma; Sallan & Coates, 2010; Sallan & Galimberti, 2015). This led to the establishment of the first ecosystems with faunas dominated by ray-finned fishes and chondrichthyans in both marine and freshwater settings, many exhibiting ecomorphologies shared with extant fishes (Sallan & Coates, 2010, 2013; Sallan & Friedman, 2012). Characterizing the historical patterns and evolutionary processes that drove these diversification events will require a thorough understanding of the ecomorphology of Carboniferous fishes worldwide. Unfortunately, while the ecological and taxonomic composition of Carboniferous fish and tetrapod faunas from the UK, Central Europe, Eastern North America, and elsewhere have received renewed attention of late, the southwestern US remains relatively neglected and poorly described despite abundant Paleozoic material (Kues & Lucas, 1992; Hodnett & Lucas, 2015).

This study is part of a larger effort to collect from and document bountiful Late Paleozoic faunas from the southwestern United States. These faunas include the Kinney Brick Quarry (KBQ), a source of abundant Carboniferous fossils that preserves an ancient estuary from the Late Pennsylvanian (Missourian, approximately 303.7–306 million years old) of New Mexico (Lucas *et al.,* 2011). KBQ contains an uncommon, mostly non-marine assemblage of diverse and well-preserved fishes from the Tinajas Member of the Atrasado Formation (Kues & Lucas, 1992; Lucas *et al.,* 2011; Williams & Lucas, 2013). While actinopterygian fossils are common, sharks and coelacanths are rare but diverse within the KBQ fish fauna (Zidek, 1992). The excellent degree of preservation of an entire assemblage of fishes, together with the rest of the KBQ

Lagerstätte, is a rare opportunity to study the morphology and paleoecology of Late Pennsylvanian fishes in-depth (Kues & Lucas, 1992; Williams and Lucas, 2013). The study of the KBQ fish fauna contributes to the body of knowledge that will be required to understand the Carboniferous diversification of fishes.

Tanyrhinichthys mcallisteri (Gottfried, 1987) is a small actinopterygian from KBQ previously known only from the holotype, KUVP 83503, collected as part of a larger group of fish fossils by a 1984 University of Kansas expedition to KBQ (Gottfried, 1987). KUVP 83503 has a badly-crushed skull, an incomplete tail, and nearly or completely lacks much of the median and paired fins (Gottfried, 1987; Fig. 1). *Tanyrhinichthys* was inferred to be morphologically convergent on the ram-feeding ambush predator morphotype of pike and gar described by Webb (1984a) (Gottfried, 1987). Since the initial description, five new specimens (NMMNH P-51192, NMMNH P-70413, NMMNH P-70411, NMMNH P-67687, and CM 30737) have been recovered, including the only complete specimen of *Tanyrhinichthys* (Hodnett and Lucas, 2015; CM 30737, Fig. 2). These specimens provide new information on structures that were poorly preserved in the holotype, most notably the skull (CM 30737, P-70413, and P-51192), the pectoral fins (CM 30737, P-70413, and P-51192), the overall shape of the body (CM 30737 and P-70413), the dorsal fin (CM 30737), the anal fin (CM 30737), and the caudal fin (CM 30737 and P-51192). Examination of these new specimens and reevaluation of KUVP 83503 forms the basis for a thorough revision of *Tanyrhinichthys*.

Tanyrhinichthys is one of several poorly-known long-rostrumed Paleozoic actinopterygians, including two other freshwater forms from a brief interval in the Late Carboniferous. The most complete of these fishes is *Phanerorhynchus armatus* (Gill, 1923), which is known from a single specimen (L. 8585) from the Pennsylvanian of the Middle Coal

Measures at Sparth, near Rochdale, UK (Gill, 1923). Poplin (1978) also documented a skull roof (PF 2289) of an undescribed long-rostrumed actinopterygian from the Pennsylvanian of Logan Quarry, Indiana. Additionally, two other long-rostrumed actinopterygians are known from other parts of the Paleozoic. *Tegeolepis clarki* (Newberry, 1888), from the Cleveland Shale Member of the Upper Devonian (Famennian) Ohio Shale (Ohio, USA) (Dunkle & Schaeffer, 1973) and *Eosaurichthys chaoi* (a possible junior synonym of *Saurichthys*, see Tintori, 2013; Liu & Wei, 1988), from the latest Permian (Changhsingian) of Zhejiang, China, bear elongate rostra. We compare our revised description of *Tanyrhinichthys* with previous descriptions of *Phanerorhynchus* (Gill 1923; Gardiner 1967), *Tegeolepis* (Gardiner, 1963; Dunkle & Schaeffer, 1973), *Eosaurichthys* (Liu & Wei, 1988), and the unnamed taxon from Indiana (Poplin, 1978) to determine the extent of the similarity between these taxa and make inferences regarding the early evolutionary history of elongate rostra in ray-finned fishes.

We redescribe the morphology of *Tanyrhinichthys* and create a more complete and accurate reconstruction of this fish as a living animal. We compare our reconstruction to modern analogues to re-evaluate the hypothesized paleoecology of *Tanyrhinichthys*. We also compare *Tanyrhinichthys* to other long-rostrumed Paleozoic actinopterygians to examine its potential evolutionary relationships and the evolution of elongate rostra amongst Paleozoic ray-finned fishes. Finally, we review other novel morphologies that arose in Carboniferous fishes to place *Tanyrhinichthys* into the broader context of ecomorphological evolution and diversification in the aftermath of the end-Devonian Hangenberg event.

MATERIAL AND METHODS

All catalogued specimens of *Tanyrhinichthys* from the New Mexico Museum of Natural History and Science (NMMNH), the University of Kansas Museum of Natural History (KUVP), and the Carnegie Museum of Natural History (CM) were examined, drawn, and photographed. In our interpretative drawings, dotted lines indicate inferred boundaries, dashed lines show physical breaks in the rock, light grey infill marks areas within the specimen where bone is absent, and dark grey infill marks area where the bone is degraded to the point where reliable identification of individual elements is not possible. The color of the photographs of CM-30737 was inverted in Adobe Photoshop CC to make details of the bones clearly visible. New specimens of *Tanyrhinichthys* were compared to KUVP 83503 and used to determine what previously undescribed features are preserved. The morphology of the new specimens of *Tanyrhinichthys* was then compared to modern analogs to make inferences regarding its ecology.

We compared our re-description of *Tanyrhinichthys* to published descriptions of other Paleozoic taxa with lengthened or enlarged snouts (Gill, 1923; Gardiner, 1967; Dunkle & Schaeffer, 1973; Poplin, 1978; Schultze & Bardack, 1987; Liu & Wei, 1988). J.S. also examined and photographed silicone-rubber peels of the holotype of *Phanerorhynchus* (P. 34421-2 and P. 50023-4) at the Natural History Museum, London, UK (NHM) and the holotype of *Illinichthys cozarti* (UC 21716) at the Field Museum of Natural History, Chicago, USA (FMNH). MicroCT scans of the holotype of *Phanerorhynchus* (L. 8585, deposited in the Manchester Museum, UK) provided by Matthew Friedman were also used for comparisons. These scans were conducted at the CTEES facility at the University of Michigan using a Nikon XT H 225 ST scanner. The parameters of the scan were as follows: resolution (26.6 microns), voltage (210 kV), current (235 uA), filter (2 mm Cu), projections (3141, 1 frame per second), and exposure time (1415 ms). The specimen (PF 2289) upon which Poplin's (1978) description of a long-rostrumed taxa from the

Logan Quarry of Indiana could not be located by J.S. at the FMNH. Figures were rendered using Adobe Photoshop CC from specimen photos scanned at 1200 dpi on an Epson Perfection V600 scanner. The photograph in Figure 7 was taken with a Leica DFC495 Microscope Camera mounted on a Leica DFC495 microscope, and the photograph in Figure 15 was taken with a Nikon D7000 camera with a 105.0 mm f/2.8 Macro lens.

Bone nomenclature follows the conventional terminology for actinopterygians (Gardiner, 1984) to facilitate comparisons to previous publications. In this terminology, the frontals and parietals of actinopterygians are homologous to the parietals and postparietals of sarcopterygians (Schultze, 2008).

Anatomical abrreviations

ab, anal basal fulcra; af, anal fin; afr, anal fin rays; an, angular; asq, axial squamation; br, branchiostegal rays; cf, caudal fin; cl, cleithrum; cr, coronoid; cv, clavicle; dcb, dorsal caudal lobe basal fulcra; dcf, dorsal caudal lobe fringing fulcra; dcr, dorsal caudal lobe fin rays; df, dorsal fin; dfb, dorsal fin basal fulcra; dfr, dorsal fin rays; dn, dentary; dr; dorsal ridge scales; ds, dermosphenotic; ex, extrascapular; ff, fringing fulcra; fr, frontal; ju, jugal; la, lacrimal; ll, lateral line; lsq, lateral squamation; mnc, mandibular canal; mx, maxilla; na, nasal; op, opercular; pa, parietal; pcr, pectoral fin rays; pe, pelvic fin; pf, pectoral fin; pm, premaxilla; po, preopercular; por, sensory pores; pt, post-temporal; pvb, pelvic basal fulcra; pvr, pelvic fin rays; quj, quadratojugal; ra, radial; ro, rostral; rs, rostrum; scl, supracleithrum; sk, skull; sr, sclerotic ring; sn, sensory canal; so, subopercular; sq, squamation; th, teeth; vcb, ventral caudal lobe basal fulcra; vcr, ventral caudal lobe fin rays; vr, ventral ridge scales; vsq, ventral squamation.

SYSTEMATIC PALEONTOLOGY

OSTEICHTHYES HUXLEY, 1880

ACTINOPTERYGII COPE, 1881

FAMILY INDET.

GENUS *TANYRHINICHTHYS* GOTTFRIED, 1987

Type and only species: Tanyrhinichthys mcallisteri Gottfried, 1987.

Holotype: KUVP 83503, part and counterpart. Nearly complete, articulated fish with a poorly preserved skull and caudal fin, lacking dorsal and pectoral fins.

Type locality and horizon: KUVP 83503 is from the Upper Pennsylvanian of north-central New Mexico, KBQ clay pit quarry locality, Bernalillo County, New Mexico (Gottfried, 1987). Originally attributed to the Wild Cow Formation, the source formation for KUVP 83503 is now regarded as the Missourian Tinajas Member of the Atrasado Formation (Gottfried, 1987; Lucas *et al.,* 2011; Williams & Lucas, 2013).

Additional Material: NMMNH P-51192 (part) and NMMNH P-51152 (counterpart), incomplete articulated fish including the skull but missing the anterior portion of the trunk; NMMNH P-70413 (part and counterpart), nearly complete articulated fish including the skull, but missing the caudal, median, and pelvic fins; NMMNH P-70411, incomplete section of scales; NMMNH P-67687, impression of the body scales of the trunk; CM 30737, complete, articulated fish with a well-preserved skull, median fins, paired fins, and caudal fin. All additional material is from the Missourian Tinajas Member of the Atrasado Formation at the KBQ.

Diagnosis (emended from Gottfried, 1987)

Elongate actinopterygian bearing a pronounced rostrum; rostrum composed of a prominent, pointed rostral, rostral contacted posteriorly by lengthened, paired frontals, pair of nasal bones surrounding the mid-posterior portion of the rostrum; rostrum base supported ventrally by a curved, strut-like premaxilla; frontals and parietals joined dorsal to the anteriormost edge of the orbit; rostral, frontal, and parietals ornamented with crosswise ridges; single pair of extrascapulars with some crosswise ridges and concave posterior margins; post-temporals lacking ornamentation; mouth subterminal with small, curved, peg-like, and sharpy pointed teeth; dentary posteriorly deepened, with curved dorsal and ventral margins and a pointed anterior margin; dentary ornamented with long, forward-curving ridges; maxilla ornamented with thin, sparse crosswise ridges; angular present; long, thin, anteriorly curved preopercular; tall cleithrum ornamented with thin, lengthwise ridges, with a rounded base and a pointed dorsal margin; rhombic scales bearing prominent dorsal pegs and ornamented with long, lengthwise ridges; dorsal ridge scales extending from the skull to the dorsal basal fulcra, grading from short, thick, rounded scales anteriorly into longer and more pointed scales posteriorly; ventral ridge scales extending from the base of the pectoral fin to the ventral caudal basal fulcra, grading from wide, rectangular, thick scales anteriorly into thinner, shorter, and longer scales posteriorly; deepened scales in the lateral flank region; small, ventrally inserted paired fins; fringing fulcra absent on paired fins; offset median fins positioned far posteriorly with a larger, more anteriorly placed anal fin; fringing fulcra present on the anterior margin of the dorsal and caudal fin; basal fulcra present on the insertions of the pelvic fin, median fins, and caudal fin; relatively small and shallowly cleft heterocercal caudal fin; dorsal and ventral lobe of caudal fin bearing large basal fulcra and smaller fringing fulcra; lepidotrichia of caudal fin closely packed, segmented, and branching distally.

DESCRIPTION

Skull: While the overall construction of the skull is as described by Gottfried (1987), the skull of the specimen used for this description (KUVP 83503) was severely crushed, rendering it difficult to adequately distinguish between individual bones and fractures (Gottfried, 1987). New specimens (NMMNH P-70413, CM 30737, and NMMNH P-51192) allow for a much more thorough description of the skull because they preserve many of the bones that could not be identified by Gottfried (1987). These include the dermosphenotic, frontals, nasals, extrascapulars, lacrimal, jugal, clavicle, premaxilla, branchiostegal rays, coronoids, and angular. In addition, we re-examined the skull of KUVP 83503 (Fig. 3), and can provide identifications for several fragmentary bones based on information from the new material, including the nasals, parietals, dermosphenotic, premaxilla, and frontals. Our identification of the elements in the skull of KUVP 83503 mostly align with those of Gottfried (1987, Fig. 4), except that we identify a rectangular element in-between the dentaries as a possible quadratojugal, not a quadrate, and we did not observe a separate preopercular or supraorbital sensory canal.

The anterior portion of the skull of *Tanyrhinichthys* is extended into an elongate rostrum composed of multiple elements. CM 30737 (Fig. 4 and 7) bears the best preserved and only complete rostrum, although incomplete rostra are present in KUVP 83503 (Fig. 3), NMMNH P-70413 (Fig. 5), and NMMNH P-51192 (Fig. 6). The rostra of NMMNH P-70413, CM 30737, and KUVP 83503 are short, thick, and pointed. These rostra are laterally flattened, giving them a thicker appearance than they would have had in life. The rostrum of NMMNH P-51192, preserved as an impression ("rs" in Fig. 6B), appears much longer and thinner than the rostra in CM 30737, KUVP 83503, and NMMNH P-70413 because it has been crushed dorso-ventrally, not laterally. These specimens indicate that the rostrum of *Tanyrhinichthys* would have been relatively long and thin, most likely with a laterally broad dorsal surface.

The most prominent element comprising the rostrum is a large unpaired median rostral ("ro" in Fig. 3B, 4B, 5B, and 7B), which is bound laterally by an elongate pair of nasals and followed by a pair of elongate frontals (Fig. 7). The rostral is an elongated, roughly triangular bone that has a pointed anterior margin and a curved posterior margin. It extends past the nasals to form a roughly triangular point at the tip of the rostrum and is ornamented with parallel, crosswise ridges and small, tubercle-like protuberances. The rostral bears pores and a sensory canal anteriorly. While we only observe the canal in CM-30737 ("sn" in Fig. 4B and 7B), rostral pores are visible in CM 30737 and NMMNH P-70413 ("por" in Fig. 4B and 5B). These pores are equal in size, circular in shape, and are shallowly placed at the margins of the bone. This canal and its associated pores are most likely a segment of the ethmoid commissure, a sensory canal that extends into the rostral bone of early actinopterygians (Gardiner, 1984). Fragmentary bone alongside the anterior portion of the rostral in CM 30737 and NMMNH P-70413 ("pm?", Fig. 4B, 5B, and 7B, suggests that the premaxillae may also contact the rostral ventrally, but the available specimens are not well-enough preserved to be certain.

The nasals are present in KUVP 83503 and NMMNH P-70413, but are best preserved in CM-30737 ("na?" and "na" in Fig. 3B, 4B, 5B, and 7B). The nasals are a pair of elongate bones that can be divided into a long and thin anterior portion that contacts the premaxilla anteriorly and the frontals dorsally, and a broad, ventrally expanded posterior portion that contacts the frontals anterdorsally, the parietals posterodorsally, and the dermosphenotic posteriorly. While the anterior portion lacks strong ornament, the posterior portion bears some cross-wise ganoine ridges. There is a slight separation between the anterior and posterior portions of the right nasal in CM 30737 (most easily observed in Figure 7A) that may represent a suture between a separate anterior and posterior nasal. While we cannot be certain without better preserved material, we interpret this separation as an area where bone is partially missing due to a break, not a suture.

The frontals are present but partially obscured in NMMNH P-70413, are potentially partially preserved in KUVP 83503, and are best preserved in CM 30737 ("fr?" and "fr" in Fig. 3B, 4B, 5B, and 7B). They are elongated, roughly rectangular bones that form the posterior half of the lengthened rostrum and are ornamented with cross-wise ganoine ridges. The frontals have rounded posterior margins where they contact the parietals and straight anterior margins where they contact the rostral. The frontals are bordered anteriorly by the rostral, laterally by the nasals, and posteriorly by the parietals. There is a piece of bone in the center of the rostrum of CM 30737 directly posterior to the rostral that we interpret as a partially broken anterior half of the right frontal. It is possible that this is a separate postrostral, but because there is no clear posterior margin that can be reliably distinguished from the thin cracks that run diagonally through the skull roof, we do not interpret this as a separate element. Additionally, there is no evidence for a separate postrostral in other specimens (KUVP 83503 and NMMNH P-70413) that preserve this section of the skull roof. However, we cannot be certain because of the crushed preservation of this region of the skull roof in CM 30737, KUVP 83503, and NMMNH P-70413. Better preserved skull roof material will be required to re-evaluate if a separate postrostral is present in *Tanyrhinichthys*.

The parietals ("pa" in Fig. 3B, 4B, 5B, and 7B) are preserved in KUVP 83503, NMMNH P-70413, and CM 30737. The parietals are elongate, rectangular bones that are ornamented with crosswise, parallel ridges. They are contacted anteriorly by the frontals, posteriorly by the extrascapulars, anterolaterally by the nasals, laterally by the dermosphenotics, and posterolaterally by an unidentified element behind the orbit. The extrascapulars are not present in KUVP 83503, but are preserved in both NMMNH P-70413 and CM 30737 ("ex" in Fig. 4B and 5B). They are short, roughly rectangular bones largely lacking ornament (besides a few thin ridges in CM 30737) that contact the parietals anteriorly, the post-temporals posteriorly, and the opercular posteroventrally. The posterior margin of each extrascapular is concave where they contact the post-temporal. The post-temporals are potentially partially preserved in KUVP 83503 ("pt?" in Fig. 3B), but are more complete in NMMNH P-70413 and CM 30737 ("pt" in Fig. 4B and 5B). They are long, unornamented, and roughly oval-shaped bones that contact the extrascapulars anteriorly and the opercular ventrally.

The orbit is formed (moving clockwise from the top of the orbit) by the nasals, lacrimal, jugal, and dermosphenotic. The dermosphenotic ("ds" in Fig. 3B and 4B and "ds?" in Fig. 5B) is present in KUVP 83503, CM 30737, and possibly NMMNH P-70413. It is best preserved in CM 30737, where it is a curved, roughly crescent-shaped bone forming the posterodorsal part of the orbit. The dermosphenotic has a broad ventral margin, a wide dorsal margin contacting the parietal, and a pointed anterior margin contacting the nasal. A piece of bone that may represent the jugal ("ju?" in Fig. 6B) is preserved in NMMNH P-51192. The potential piece of the jugal in NMMNH 51192 is concave and curved, and is contacted posteriorly by the postorbital expansion of the maxilla. However, this piece and the surrounding elements in NMMNH 51192 are not well-enough preserved to be certain of this identification. The lacrimal is a small, thin, and concave bone, preserved in CM 30737 and possibly in NMMNH P-70413 and NMMNH P-51192 ("la" in Fig. 4B and "la?" in Fig. 5B and 6B). The lacrimal sits dorsal to the infraorbital expansion of the maxilla and anterior to the jugal, forming the ventral and anteroventral portion of the orbit. The premaxilla reaches the anteriormost part of the orbit in CM 30737, suggesting that it also contributed to the anterior margin orbit. The sclerotic ring may be preserved in NMMNH P-70413 ("sr?" in Fig. 5)

The region of the skull posterior to the eye and anterior to the opercular is not well preserved in any of the examined specimens. In CM 30737 there is a large piece of bone ("?" in Fig. 4B) in the area of the skull posterior to the dermosphenotic and anterior to the opercular that appears to be a single element. This element is anteriorly broad and curved and has a very long, thin projection extending posteriorly. There is a similar piece of bone located directly posterior to the dermosphenotic in KUVP 83503 ("?" in Fig. 3B), which is also poorly preserved. These pieces are not well-enough preserved to determine if there is a single element (a fused dermopterotic) or two elements (a separate intertemporal and supratemporal) in this region of the skull. Therefore, we do not attempt an identification. We also cannot determine if there are separate suborbital bones.

The premaxilla is preserved in CM 30737, KUVP 83503, and NMMNH P-70413 ("pm" in Fig. 3B, 4B, 5B, and 7B). It is best preserved in CM 30737, where it seems to have a broad posterior margin that extends dorsally from the anteriormost tip of the maxilla to the most ventral point of the nasals. It also has a curved, strut-like section that extends anterodorsally, contacting the anterior section of the frontals and the posterior part of the rostral at the midpoint of the rostrum. In CM 30737 there are long pieces of bone lateral to the rostral ("pm?" in Fig. 4B and 7B) that may also represent the premaxilla. Because these are disarticulated and not well-preserved, we cannot determine if these represent the anterior extent of the premaxilla or if this is disarticulated bone that was fossilized next to the rostral. There is also a large gap in the region ventral to the rostrum in both NMMNH P-70413 and CM 30737 that may represent the actual interior border of the premaxilla or the product of decomposition before death. Because the premaxilla is not completely preserved in KUVP 83503, NMMNH P-70413, or CM 30737, its exact shape cannot be determined.

Opercular series: The opercular series of *Tanyrhinichthys* is largely as reconstructed by Gottfried (1987). The preopercular is only preserved in CM 30737 ("po" in Fig. 4B). Although Gottfried (1987, Figure 4) originally identified a possible preopercular in KUVP 83503, this specimen is not well-enough preserved to identify a separate preopercular. The preopercular is a long, thin, crescent-shaped bone that broadens into a circular expansion at its anterior-most point as it curves over the maxilla at a relatively shallow angle. The posterior margin of the preopercular is straight, while the anterior margin of the preopercular is broader and rounded. The preopercular contacts the unidentified element posterior to the dermosphenotic anterodorsally, the maxilla anteriorly, and the possible quadratojugal ventrally. The subopercular is most complete in KUVP 83503, is present but is not well preserved in NMMNH P-70413, and is possibly present as a fragment in CM 30737 ("so" in Fig. 3B, 4B, and 5B). The subopercular is a tall, anteriorly concave bone with a broad dorsal margin and a narrower ventral margin that lacks ornament. The subopercular is contacted posteriorly by the cleithrum, dorsally by the opercular, and ventrally by the branchiostegal rays. The opercular is broken in KUVP 83503, and is present but not better preserved in CM 30737 or NMMNH P-70413 ("op?" and "op" in Fig. 3B, 4B, and 5B). The opercular is a broad, roughly circular bone that is lightly ornamented with crosswise ridges. It is contacted ventrally by the suboperculum, posterodorsally by the post-temporal, anterodorsally by the extrascapular, and posteroventrally by the supracleithrum.

Gulars and branchiostegals: The gulars are not preserved in any of the examined material. Pieces of the branchiostegal rays are preserved in KUVP 83503, CM 30737, and NMMNH P-70413 ("br" and "br?" in Fig. 3B, 4B, and 5B). The branchiostegal rays are represented by disarticulated fragments in KUVP 83503 and CM 30737, which provide little information on their number and shape. However, the two articulated branchiostegal rays (and a third disarticulated element that is likely a branchiostegal ray) in NMMNH P-70413 show that these elements extended dorsally around the posterior margin of the dentary to the ventral margin of the subopercular, contacting the cleithrum posteriorly. Additional material that better preserves the ventral aspect of the skull will be required for a detailed description of the gulars and the shape and number of branchiostegal rays.

Shoulder Girdle: The shoulder girdle is largely as described by Gottfried (1987). The cleithrum is preserved in KUVP 83503, CM 30737, NMMNH P-70413, and NMMNH P-51192 ("cl" in Fig. 3B, 4B, 5B, and 6B). The cleithrum is a tall, cresent-shaped bone that is broad and slightly rounded at its base with a round, pointed dorsal margin. Along its anterior margin (from dorsal to ventral) the cleithrum is contacted by the opercular, subopercular, branchiostegal rays, and clavicles. The cleithrum is ornamented by thin, curved, lengthwise ganoine ridges. A crescent-shaped piece of bone above the cleithrum in KUVP 83503 ("scl?" in Fig. 3B) may represent part of a supracleithrum. However, this element and the region of the skull around it are broken and incomplete. Therefore, we cannot be certain of this identification, or describe the shape or size of the supracleithrum in detail. The clavicles ("cv" in Fig. 4B and 6B) are preserved in CM 30737 and NMMNM P-51192. In CM 30737 they are attached to the anterior part of the ventral margin of the cleithrum. While their anterior margins are not well-preserved, the clavicles have rounded, convex posterior margins and narrow anteriorly. The clavicles in NMMNH P-51192 are ornamented with thin, curved, and lengthwise ganoine ridges, while the clavicles in CM 30737 do not have ornament. This may be the result of differences in preservation, or even intraspecific variation in bone ornamentation. More specimens preserving the clavicles will be required to evaluate this variation fully.

Jaws and dentition: The jaws and dentition of *Tanyrhinichthys* are largely as described by Gottfried (1987). The maxilla is preserved in KUVP 83503, CM 30737, NMMNH P-70413, and NMMNH P-51192 ("mx" in Fig. 3B, 4B, 5B, and 6B). It has a broad, rounded postorbital expansion and a long, thin suborbital process. The dorsal margin of the postorbital expansion of the maxilla is curved, and the dorsal margin of its suborbital process is concave. The ventral margin of the maxilla is also deeply concave. The maxilla contacts the preopercular posteriorly and dorsally, the potential quadratojugal posteriorly, the dentary ventrally, and the lacrimal dorsally. It is ornamented with thin, parallel ridges. The dentary is preserved in CM 30737, NMMNM P-70413, NMMNH P-51192, and KUVP 83503 ("dn" in Fig. 3B, 4B, 5B, and 6B). It is a stout, posteriorly deepened bone with curved dorsal and ventral margins and is ornamented with long, forward-curving ganoine ridges. A prominent mandibular canal is preserved in the dentaries of KUVP 83503, NMMNH P-70413, and CM 30737 ("mnc" in Fig. 3B, 4B, and 5B). The mandibular canal originates in the ventral part of the angular. It is initially straight as it extends into the dentary, but approximately midway through the dentary it curves dorsally, continuing anteriorly to the anterior margin of the dentary. A disarticulated, ovoid element that is likely a coronoid is preserved in NMMNH P-51192 ("cr?" in Fig. 6B). This may also be a piece of the prearticular, the lower jaw is not well-enough preserved in this specimen to make a certain identification. There is a small, concave, curved angular contacting the posterior margin of the dentary ("an" in Fig. 4 and 5). The angular is preserved in CM 30737 and NMMNH P-70413, and can be distinguished from the dentary by its lack of ornamentation. We did not observe any evidence for the presence of a separate surangular, but the posterior dorsal region of the lower jaw is not well-preserved in any of the examined material. Therefore, we cannot definitively determine if *Tanyrhinichthys* possessed two infradentaries. KUVP 83503 and CM 30737 both preserve small, roughly rectangular elements contacting the posterodorsal margin of the dentary, which may represent quadratojugals ("quj?" in Fig. 3B and 4B). We do not attempt a certain identification because this region of the skull is not well preserved in either specimen.

Tanyrhinichthys has a strongly subterminal mouth with small, peg-like, curved, and sharply pointed teeth with acrodin caps that are preserved in KUVP 83503, CM 30737, and NMMNH P-51192 ("th" in Fig. 3B, 4B, and 6B). These teeth are in one row with little variation in shape or size between them.

Paired fins: The pelvic fin is poorly preserved in KUVP 83503 ("pe" in Fig. 1), and the pectoral fin is completely absent. Therefore, the pectoral and pelvic fins in the new material provide a wealth of novel morphological information, particularly on their size and shape (Fig. 8 and 9). Partial pectoral fins are present in NMMNH P-70413 (Fig. 8A), CM 30737 ("pf" in Fig. 2B; Fig. 8B), and NMMNH P-51192 ("pcr" in Fig. 6B). The most complete pectoral fin is present in NMMNH P-70413, showing that it is small, with a 45-degree insertion into the shoulder girdle.

The lepidotrichia in the pectoral fins ("pcr" in Fig. 8) are large, thick, cylindrical, unjointed, unbranching, and densely packed. NMMNH P-70413 preserves fragmentary elements proximal to the lepidotrichia that may be pieces of the radials ("ra?" in Fig. 8A). These elements are not well-enough preserved for a certain identification. There is no evidence of fringing fulcra preceding the pectoral fin. Because none of the specimens bear a complete pectoral fin, its exact shape is not known. The available material suggests that it is a short fin, narrow at its base, that broadens into a rounded distal margin.

The pelvic fin is represented in KUVP 83503 by a rounded patch of fin rays located approximately halfway along the ventral margin of the body ("pe" in Fig. 1). The pelvic fin is well preserved in CM 30737 ("pe" in Fig. 2; Fig. 9), showing that it is a small, rounded fin with a broad base. The lepidotrichia are of medium thickness, unbranched, lightly segmented, and closely packed ("pvr" in Fig. 9B). Small, round elements dorsal to the lepidotrichia may represent radials ("ra?" in Fig. 9B). However, this identification is not certain because the insertion of the fin is not well-preserved. Small, thin, and pointed pelvic basal fulcra are located directly anterior to the pelvic fin, with a longer, thinner basal pelvic basal fulcrum located anterior to these ("pvb" in Fig. 9B). Anterior to these fulcra are ventral ridge scales ("vr" in Fig. 9B). We were unable to identify several small, teardrop-shaped elements located posterior to the pelvic fin, because it is not clear if these are separate from the ventral ridge scales posterior to the pelvic fin or pieces of bone from the fin that were moved to their current position post-fossilization ("?" in Fig. 9B).

Median fins: The dorsal fin is absent in the holotype, and is known only from a partially complete fin in CM 30737 ("df", Fig. 2; Fig. 10). This fin is small and rounded, has its peak in its posterior half, and is placed in the posterior part of the dorsal margin of the body. The lepidotrichia are lightly segmented, unbranching, small, thin, and closely packed ("dfr" in Fig. 10B). Although much of the attachment of the dorsal fin to the body is not preserved, several small radials are present ventral to the anterior insertion ("ra" in Fig. 10B). Several small, thin, pointed elements at the anterior insertion of the fin, formed from expanded terminal segments of the leading lepidotrichia, are likely fringing fulcra ("ff" in Fig. 10B). Directly anterior to the fringing fulcra are three short, small, and thick dorsal basal fulcra, which are follow by a single, much larger dorsal basal fulcrum ("dfb" in Fig. 10B). Dorsal ridge scales sit directly anterior to the large dorsal basal fulcrum ("dr" in Fig. 10B).

The anterior third of the anal fin is present in KUVP 83503, showing that it was positioned farther posteriorly along the body than in most other early actinopterygians ("af", Fig. 1B). CM 30737 exhibits a partial but more complete anal fin that provides more information on its size and shape ("af", Fig. 2B; Fig.11). The anal fin of CM 30737 consists of three patches of fin rays. These patches represent the anterior insertion and a portion of the anterior margin, a disarticulated patch that may be from the distal peak of the fin, and the posterior insertion of the fin and the area surrounding it. The anal fin is placed anterior to the dorsal fin and has a considerably broader base. The posterior portion of the anal fin is short and rounded, while the anterior portion of the fin is longer and more triangular. While the anterior margin of the anal fin is not complete, the articulated patch of lepidotrichia from the anterior insertion is taller than the posterior margin, indicating that the peak was in the anterior half. The lepidotrichia in the anterior portion of the anal fin are densely packed, regularly segmented, and do not branch. The lepidotrichia in the posterior part portion of the anal fin are smaller, thinner, lightly segmented, and shallowly branched distally. The anal fin is preceded by at least two pairs of short, thick basal fulcra ("ab", Fig. 11B) and paired ventral ridge scales ("vr" in Fig. 11B). We do not observe fringing fulcra, but the anterior margins of this fin in CM 30737 and KUVP 83503 are not well-enough preserved to determine if these elements were present with certainty.

Tail and caudal fin: While the caudal fin is present in KUVP 83503 ("cf" in Fig. 1), the distal regions of the dorsal and ventral lobes and the median cleft of the fin are poorly preserved. Better preserved caudal fins are present in CM 30737 ("cf" in Fig. 1, Fig. 12A) and NMMNH P-51192 (Fig. 12B). The caudal fin of *Tanyrhinichthys* is relatively small and heterocercal, with a long and roughly triangular dorsal lobe with a rounded margin. The ventral lobe is shorter and thicker than the dorsal lobe, and also has a rounded margin. The area between the dorsal and ventral lobes is not well preserved in any of the specimens, but the available material indicates that the caudal fin had a relatively shallow median cleft. The lepidotrichia in the ventral lobe of the caudal fin of ("vcr", Fig. 12A/B) are thin, segmented, closely packed, and branch distally. The lepidotrichia of the dorsal lobe ("dcr" in Fig. 12A/B) are also segmented, closely packed, and branching distally, but are are thicker. The lepidotrichia in the ventral lobe of NMMNH P-51192 ("vcr" in Fig. 12B) are much thicker than those in the ventral lobe of CM 30737 ("vcr" in Fig. 12A).

The posterior portion of the dorsal surface of the caudal peduncle is covered by a series of large triangular basal fulcra ("dcb" in Fig. 12). The caudal basal fulcra each have a deeply concave dorsal margin that fits around the long, pointed posterior margin of the preceding fulcrum. A series of fringing fulcra that cover the dorsal margin of the caudal fin ("dcf" in Fig. 12) sit directly posterior to the caudal basal fulcra. These fringing fulcra become progressively longer and thinner posteriorly and have pointed apices. The axial squamation is preserved in both

CM 30737 and NMMNH P-51192 ("asq" in Fig. 12). In these specimens, the scales on the caudal peduncle grade into smaller, more elongate, thinner, and more pointed scales on the dorsal lobe. A shorter, less prominent series of 2-3 pairs of basal fulcra are present on the ventral lobe of the caudal fin of CM 30737 and NMMNH P-51192 ("vcb" in Fig. 12). We also observe some fringing fulcra posterior to the basal fulcra on the ventral lobe of the caudal fins of CM 30737 and NMMNH P-51192 ("ff" in Fig. 12).

Squamation: The squamation is well preserved in KUVP 83503 (Fig. 1), CM 30737 (Fig. 2), and NMMNH P-70413 and is present to some degree in every known specimen of *Tanyrhinichthys*. The squamation is largely as described by Gottfried (1987): the scales of *Tanyrhinichthys* are rhombic, ganoine-covered, and possess peg-and-socket articulations. The pegs are thick, triangular, short, and pointed, located on the posterodorsal margin of the scale. These features are typical of the scales of early actinopterygians (Moy-Thomas, 1971). The scales are ornamented with vertical, roughly parallel ridges, which often extend from the dorsal to the ventral external margin (Fig. 2). The scales in the lateral flank region are deeper than they are wide, and the scales in the anterior portion of the body are larger and deeper than those located more posteriorly. The scales become smaller and more rhomboidal on the caudal peduncle, very different in shape and size from the scales of the rest of the body. The region where the transition from body to caudal peduncle scale rows was not preserved in KUVP 83503, but CM 30737 and NMMNH P-51192 have well-preserved caudal peduncles that provide this information. The scales smoothly transition into smaller versions of the large and deepened body scales, and become smaller and more rhomboidal towards the caudal fin.

Dorsal ridge scales ("dr", Fig. 1 and 2), present in KUVP 83503 and CM 30737, run from the base of the skull to the scute and basal fulcra on the dorsal fin. They are short, thick, and rounded anteriorly, becoming longer, thinner, and more pointed posteriorly. The ventral squamation is best preserved in NMMNH P-70413 (Fig. 13), and is fragmentarily preserved in CM 30737 and KUVP 83503. Only NMMNH P-70413 preserves a series of 3-6 rows of squat, trapezoidal scales ("vsq" in Fig. 13B) running along the ventral surface of the body extending from the base of the pectoral fin to the caudal peduncle. These scales are shorter than the scales covering the trunk, and have smaller, less prominent dorsal pegs. Ventral to these in NMMNH P-70413 is a row of ventral ridge scales ("vr" in Fig. 9, 11, 12 and 13) that are distinguishable from the ventral squamation in being larger and thicker than the scale rows above them. The ventral ridge scales extend from directly posterior to the pectoral fin to the ventral caudal basal fulcra, but are interrupted by the pelvic and anal fins, with their respective scutes and basal fulcra. Anteriorly, these scales are squat, wide, thick, and roughly rectangular in shape. Although a section of them appears to be missing from the mid-posterior region of the body of NMMNH P-70413, they become thinner, shorter, and longer as they approach the caudal peduncle.

DISCUSSION

THE PALEOECOLOGY OF *TANYRHINICHTHYS*

Previous workers argued that *Tanyrhinichthys* was ecomorphologically similar to ram-feeding, esocid-like predators, based on the original reconstruction (Gottfried, 1987, Fig. 6A; Moyle & Cech, 2003; Williams & Lucas, 2013). Ram-feeding fishes, including pikes (Esocidae), are often lie-in-wait predators with fusiform bodies, broad, homocercal caudal fins, posteriorly placed dorsal and anal fins with similar forms and positions, and lengthened, terminal mouths with large, conical teeth (Webb 1984b; Moyle & Cech, 2003; Porter & Motta, 2004). These specialized features allow esociforms to perform sudden, high-velocity lunges at prey; the mirrored median fins, deeply-forked homocercal tail, and elongated, streamlined body form serving to maximize thrust while minimizing drag (Webb & Skadsen, 1980; Webb 1984a; Moyle & Cech, 2003; Porter & Motta, 2004). Our reconstruction of *Tanyrhinichthys* (Fig. 14) shows a body form distinct from esociforms, including displaced median fins unequal in form and a highly heterocercal caudal fin, ruling out an ability to generate equivalent bursts of forward motion. Furthermore, the esociform style of ram feeding requires a terminal mouth to capture prey head-on (Webb 1984b; Moyle & Cech, 2003; Porter & Motta, 2004). The mouth of *Tanyrhinichthys* is subterminal. Thus, an "ambush predator" ecology can now be ruled out for *Tanyrhinichthys.*

We reinterpret *Tanyrhinichthys* as a benthic-cruising predator, likely similar in general feeding ecology to sturgeon (Acipenseridae) (Billard & Lecointre, 2001). This interpretation is supported by features shared between *Tanyrhinichthys* and sturgeon, including a heterocercal tail with a long dorsal lobe, an elongate snout bearing a sensory canal, and ventrally-inserted paired fins (Bemis *et al.,* 1997; Miller, 2004; Vecsei & Peterson, 2004; Peterson *et al.,* 2007; Hilton *et al.,* 2011). Additionally, a large fossa in the skull of *Tanyrhinichthy*s, formed by the premaxilla and rostrum, may have contained soft tissue with additional sensory organs, such as electroreceptors. However, better preserved material is required to evaluate this possibility. These shared features have been documented as facilitating a bottom-cruising predatory lifestyle in sturgeon, and therefore most likely served a similar purpose in *Tanyrhinichthys*. For instance, the inequilobate tail and elongate anal fin in *Tanyrhinichthys* likely would have assisted with both descent to the bottom and rapid movement off the substrate. The ventrally-placed paired fins likely would have helped with station holding, as in modern sturgeon (Adams *et al.,* 1999; Liao & Lauder, 2000). The sensory apparatus on the rostrum of *Tanyrhinichthys*, together with its subterminal mouth, suggest that it searched for food in a manner similar modern sturgeon; swimming along the bottom and using the sensory organs associated with its rostrum to detect prey hidden in the substrate (Harkness & Dymond, 1961). This comparison is limited by the fact that sturgeon bear soft-tissue rostral sensory organs (including chemosensory barbels and epithelial electrosensory ampullary organs) (Jørgensen, 1980; Hilton *et al.,* 2011). While it is possible that *Tanyrhinichthys* possessed similar electrosensory or chemosensory organs, it is unlikely that the restrictions of the fossil record will allow for this to be determined.

Differences in jaw morphology also limit the inferred convergence between *Tanyrhinichthys* and sturgeon. While sturgeon have a highly specialized, protractible mouth that sucks in prey by rapid extension, *Tanyrhinichthys* has an upper jaw (maxilla) that is tightly fused to the rest of its skull, as in most other Paleozoic actinopterygians (Schaeffer & Rosen, 1961; Vecsei & Peterson, 2004; Peterson *et al.,* 2007). The fusion of the maxilla to the preopercular and infraorbital bones restricted *Tanyrhinichthys* and other Paleozoic actinopterygians to biting and seizing prey (Schaeffer & Rosen, 1961). Therefore, despite the apparent convergence between them, *Tanyrhinichthys* and sturgeon are distinct in mode of prey capture. Stomach contents have not been recovered, but the small, sharp, curved, and peg-like teeth, and relatively small gape of *Tanyrhinichthys* indicate that it fed upon small crustaceans, insects, and soft-bodied organisms (Williams & Lucas, 2013).

COMPARISONS TO OTHER PALEOZOIC TAXA

As noted by Gottfried (1987), *Tanyrhinichthys* possesses general characteristics of early actinopterygians traditionally assigned to the likely para- or polyphyletic taxonomic group for Paleozoic species, "paleonisciformes" (Sallan, 2014). This includes rhombic, ganoine-covered scales with peg-and-socket articulations, a strongly heterocercal caudal fin, and a maxilla with a pronounced, rounded postorbital expansion and narrow suborbital expansion (Moy-Thomas, 1971; Sallan, 2014). Phylogenetic analysis of *Tanyrhinichthys* is difficult because the available material is flattened and thus lacks many of the internal features that have proven the most informative for determining phylogenetic structure in prior analyses (Sallan, 2014; Giles *et al.,* 2015; Pradel *et al.,* 2016; Argyriou *et al*., 2018; Latimer & Giles, 2018; Wilson *et al.,* 2018; Coates & Tietjen, 2019; Figueroa *et al.,* 2019). Also, the relationships of Permo-Carboniferous actinopterygians are poorly defined and relatively under-examined; most prior analyses involved either Mississippian and Late Permian taxa and/or focused on a subset of Late Paleozoic species belonging to one region or family (Lowney, 1980; Dietze, 2000; Sallan, 2014; Elliott, 2015; Elliott, 2018). Lastly, most other actinopterygians of the same age from North America have only been briefly described. Thus, phylogenetic placement of *Tanyrhinichthys* will require a detailed examination of many Pennsylvanian and Early Permian taxa at KBQ and elsewhere that is outside of the scope of the present work. Therefore, we do not attempt to determine the placement of *Tanyrhinichthys* within the "paleonisciformes". Instead, we compare *Tanyrhinichthys* to other long-rostrumed Paleozoic actinopterygians to determine the possibility of shared evolutionary pathways or close relationships and to examine the early evolutionary history of elongate rostra in ray-finned fishes.

The Paleozoic *Trawdenia planti* (Coates and Tietjen, 2019) and *Illinichthys cozarti* (Schultze & Bardack, 1987) both possess prominent snouts that extend beyond the gape

(Schultze & Bardack, 1987; Coates, 1999; Coates & Tietjen, 2019). These are formed primarily from a bulbous, inflated rostral bone, with contributions from the nasal and premaxilla (Schultze & Bardack, 1987; Coates, 1999; pers. observ.). Although these structures are not as elongate as the snout of *Tanyrhinichthys*, they may represent precursor states. Most of the other features of these genera are common to a broader range of Permo-Carboniferous actinopterygians, thus the degree of relatedness is otherwise difficult to determine as above.

While the Late Devonian *Tegeolepis* and *Tanyrhinichthys* both bear elongate rostra, there are several morphological distinctions between these fishes. Principally, unlike *Tanyrhinichthys*, the rostrum of *Tegeolepis* is composed entirely of an inflated, pointed rostral bone (Dunkle & Schaeffer, 1973). This is distinct from the rostrum of *Tanyrhinichthys*, which also composed of a lengthened median rostral but has contributions from the paired frontals, nasals, premaxillae, and parietals. Additionally, unlike *Tanyrhinichthys*, the pectoral fins of *Tegeolepis* contain deeply-branched fin rays and the median fins lack fringing and basal fulcra (Gardiner, 1963).

Differences in body size, body shape, and dentition between *Tanyrhinichthys* and *Tegeolepis* indicate divergent ecologies. While *Tanyrhinichthys* is a relatively small fish (approximately 15 cm in total length), *Tegeolepis* is huge for a Paleozoic actinopterygian, between 60 cm to 1 meter in total length (Dunkle & Schaeffer, 1973). Additionally, *Tegeolepis* has two series of teeth (marginal and internal) that include large, recurved laniaries (Dunkle & Schaeffer, 1973). This differs considerably from the single set of small, peg-like teeth of *Tanyrhinichthys*. The body form and fin positions of *Tegeolepis* are decidedly more esociform-like, including the presence of small, mirrored median fins near the tail (Dunkle and Schaeffer, 1973). While *Tanyrhinichthys* was most likely a bottom-feeder that inhabited an estuarine environment, *Tegeolepis* has been interpreted as a fast-swimming, pelagic predator that inhabited a marine environment (Gardiner, 1963; Dunkle and Schaeffer, 1973; Long, 2011). Therefore, the superficially-similar rostral forms of these fishes appear to have evolved independently and for completely divergent uses.

The Saurichthyiformes were an extremely successful group of long-rostrumed fishes whose earliest recorded representative, *Eosaurichthys*, is known from the latest Permian (Changhsingian) of Zhejiang, China (Liu & Wei, 1988; Argyriou *et al*., 2018). Saurichthyiformes like *Eosaurichthys* are very distinct from *Tanyrhinichthys* in general body form. While Saurichthyiformes have a homocercal tail and mirrored median fins, *Tanyrhinichthys* has a heterocercal tail and median fins that are not mirrored (see Kogan & Romano, 2016 and refs. therein). Additionally, while the rostrum of *Tanyrhinichthys* is built primarily from lengthened dermal bones of the skull roof (frontals) and dermal bones associated with the ethmoid region (rostral, nasals, and premaxillae), the rostrum of *Eosaurichthys* is formed primarily from lengthened elements that comprise the jaw margin (premaxillae, dentaries) (Liu & Wei, 1988; Kogan & Romano, 2016). While dermal skull roof bones (frontals) and dermal bones associated with the ethmoid region (nasals) are also lengthened in *Eosaurichthys*, its rostrum is very distinct in overall form from that of *Tanyrhinichthys* (Liu & Wei, 1988; Kogan & Romano, 2016). Also, *Tanyrhinichthys* has an extended snout-like structure while *Eosaurichthys* has a lengthened mouth (Fig. 15). The distinctions between the elongate rostra of these fishes are most likely to due to the difference in their inferred ecologies. Unlike the inferred bottom-roving feeding strategy of *Tanyrhinichthys*, the needlefish or barracuda-like forms of *Eosaurichthys* and other Saurichthyiformes indicate that they were likely pelagic, ram-feeding ambush predators (Kogan *et al.,* 2015). The elongate jaws of *Eosaurichthys* and other Saurichthyiformes appear to be convergent on extant taxa (notably pike, needlefish, gar, and barracuda) whose lengthened jaws are well suited for high velocity closure to capture of fast-swimming fishes (Porter & Motta, 2004; Kogan *et al.,* 2015; Kogan & Romano, 2016). Thus, the distinction in the form of the elongate rostra of these fishes, together with other morphological differences, are likely due to *Eosaurichthys* being more ecologically similar to pike and possibly *Tegeolepis* than *Tanyrhinichthys.*

While some morphological distinctions between *Tanyrhinichthys* and *Eosaurichthys* appear to be due to divergent ecologies, a recent study of the internal cranial anatomy of *Saurichthys* sp. found that it is likely part of a clade that is an immediate sister group to crown actinopterygians, while *Tanyrhinichthys* is difficult to distinguish from the mass of Carboniferous forms that fall lower down along the stem (but see discussion of phylogenetic status above) Argyriou *et al*., 2018). Although this topology is weakly supported, phylogenetic study has consistently placed Saurichthyiformes with Triassic taxa (see Argyriou *et al*., 2018 and refs therein). This (along with the considerable temporal gap between these taxa) indicates that *Eosaurichthys* is part of a younger lineage of ray-finned fishes than *Tanyrhinichthys*. Therefore, the available data indicate that elongate rostra evolved independently in *Tanyrhinichthys* and *Eosaurichthys*.

Phanerorhynchus is the most well-known long rostrumed actinopterygian that is contemporaneous with *Tanyrhinichthys* (Gill, 1923; Fig. 16). Our comparison is based on the original description (Gill, 1923), examination of latex peels (P.34421-2 and P. 50023-4, NHM) taken from the holotype (L. 8585), microCT scans of L. 8585 (provided by Matthew Friedman), and the reconstruction and description of *Phanerorhynchus* from Gardiner (1967), which is unfortunately highly idealized (pers. observ.). Like *Tanyrhinichthys*, *Phanerorhynchus* superficially resembles sturgeon, as noted by D.M.S Watson in Gill (1923) and Gardiner (1967).

Both *Tanyrhinichthys* and *Phanerorhynchus* possess a pronounced rostrum, posteriorly placed median fins, and a subterminal mouth (Gill, 1923; Gardiner, 1967; Miller, 2004; Vecsei & Peterson, 2004; Peterson *et al.,* 2007). These shared features suggest that like *Tanyrhinichthys*, *Phanerorhynchus* was a small, bottom-cruising predator (Gill, 1923; Gardiner, 1967).

Much of the skull of the lone specimen of *Phanerorhynchus*, particularly its rostrum and skull roof, are not well-enough preserved for an in-depth comparison to *Tanyrhinichthys* (Gill, 1923; "sk" in Fig. 16), with the exception of the jaws, dermal cheek bones, and orbit. The rostrum of *Phanerorhynchus* is thicker and more conical than that of *Tanyrhinichthys* (Gill, 1923), presenting a marked difference despite the undefined contributions of the fused dermal snout bones in *Phanerorhynchus*. Additionally, the frontals of *Phanerorhynchus* make up a much larger portion of the skull roof and are larger relative to the parietals than those of *Tanyrhinichthys*.

In many respects the skull of *Phanerorhynchus* is distinct from *Tanyrhinichthys* and is more similar to the haplolepids, a group of Carboniferous actinopterygians known from both the UK and North America (Lowney, 1980; Elliott, 2015; Elliott, 2018). The skull bones of *Phanerorhynchus* were ornamented with thick, concentric ridges and tubercles, similar to haplolepids yet distinct from the lightly ornamented or unornamented skull bones of *Tanyrhinichthys* (Gill, 1923; Westoll, 1944; Lowney, 1980). Also, the maxilla of *Phanerorhynchus* is very broad and expanded posteriorly relative to what is typical of other "paleoniscoids" (Gill, 1923; Gardiner, 1967), similar to the Haplolepidae excluding *Microhaplolepis* (Westoll, 1944; Lowney, 1980). In contrast, the maxilla of *Tanyrhinichthys* is narrower and more boomerang-shaped, and thus more typical of the "paleoniscoids". Additionally, the preopercular of *Phanerorhynchus* is wider and much broader dorsally than the preopercular of *Tanyrhinichthys* (Gill, 1923). Other distinctions between the skulls of these fishes lie in the construction of the orbit and the surrounding bones. Unlike *Tanyrhinichthys*, *Phanerorhynchus* lacks a separate jugal and lacrimal (Gardiner, 1967). Instead, *Phanerorhynchus* has a single infraorbital that occupies the same region as the lacrimal and jugal of *Tanyrhinichthys*, a feature that is also present in the Haplolepidae (Westoll, 1944; Gardiner, 1967; Lowney, 1980).

The post-cranial morphology of *Phanerorhynchus* is not complete, but is well-enough preserved for a detailed comparison. The construction of the fins of *Phanerorhynchus* differs considerably from *Tanyrhinichthys* (Gill, 1923; Fig. 16). The lepidotrichia of *Phanerorhynchus* are thick, few in number, and are generally spaced far apart from one another, as in haplolepids (Gill, 1923; Westoll, 1944; Gardiner, 1967; Lowney, 1980). This is very different from the thin, closely packed, and numerous fin rays of *Tanyrhinichthys* aside from the pectoral fin. Additionally, the thick, unjointed lepidotrichia of the anterior portion of the ventral lobe of the caudal fin in *Phanerorhynchus* are distinct from the corresponding thin, jointed fin rays in the caudal fin of *Tanyrhinichthys* (Gill, 1923; "cf" in Fig. 16). Finally the pelvic fin of *Phanerorhynchus* appears much longer relative the short and rounded pelvic fin of *Tanyrhinichthys* ("pe" in Fig. 16).

The squamation of *Tanyrhinichthys* differs from what has been observed in *Phanerorhynchus* (Gill, 1923; Gardiner, 1967). The dorsal, anal, and pelvic fins of *Phanerorhynchus* are preceded by ridge scales and fulcra that are much larger and more pronounced than those preceding the respective fins of *Tanyrhinichthys* (Gill, 1923; Gardiner, 1967). The dorsal ridge scales of *Phanerorhynchus* ("dr" in Fig. 16) grade into dorsal basal fulcra that are relatively large spines (Gill, 1923). These differ considerably from the small, unpointed dorsal basal fulcra in *Tanyrhinichthys*. Furthermore, the scales of *Tanyrhinichthys* are much straighter than those of *Phanerorhynchus*, which have distinctly curved anterior and posterior margins (Gill, 1923). Additionally, the middle flank scales of *Phanerorhynchus* each bear a tubercle on both their dorsal edge and about two thirds of the way between their dorsal and posterior edges (Gill, 1923). There is no evidence of such tubercles being present in *Tanyrhinichthys*.

Tanyrhinichthys is distinctly unlike *Phanerorhynchus* in the construction of its skull, its fins, and its scales. This indicates that *Phanerorhynchus* and *Tanyrhinichthys* are separate long-rostrumed lineages that evolved these features due to convergence on a bottom-cruising lifestyle. *Phanerorhynchus* more closely resembles members of the Haplolepidae in the construction of its skull and fins, particularly haplolepids from the same region of Northern England (Lowney, 1980).

Tanyrhinichthys is most similar to the unnamed long-rostrumed actinopterygian from the Logan Quarry of Indiana. Unfortunately, this taxon is known from an isolated and relatively incomplete skull that offers little morphological information for comparison (PF 2289; Poplin, 1978, Figure 1). Additionally, we could not locate PF 2289 at the FMNH (pers. observ.). However, the skull roof of this taxon appears to be very similar to that of *Tanyrhinichthys* in general morphology. In particular, PF 2289 as illustrated by Poplin (1978, Fig. 6) closely resembles the skull of NMMNH P-51192 (which is also crushed dorsoventrally). Both of these specimens have narrow skull roofs with long, thin, and pointed rostra. Additional material from the Indiana taxon is needed to make a more complete assessment of its relationship to *Tanyrhinichthys.*

Elongate rostra, broadly defined in actinopterygians as extensions of the bones of the skull or the jaws past the orbit or nares, are extremely common amongst both extinct and extant ray-finned fishes (pers. observ.). Based on our comparisons, elongate rostra evolved at least four separate times amongst Paleozoic actinopterygians, once in the Devonian (*Tegeolepis*), at least twice in the Pennsylvanian (*Tanyrhinichthys* and *Phanerorhynchus*, potentially a third time in the Indiana taxon), and finally in the Permian (*Eosaurichthys*). This demonstrates that although elongate rostra are most common in extant ray-finned fishes (pers. observ.), cranial elongation evolved as early as the Late Devonian and appeared independently in several lineages before the end of the Paleozoic.

Although each of the long-rostrumed fishes we examined are distinct in rostral structure, there is a broader pattern in cranial elongation. The rostra of *Tanyrhinichthys*, *Phanerorhynchus*, the Indiana taxon, and *Tegeolepis* are built primarily from bones of the skull roof and bones associated with the ethmoid region that have been lengthened to produce an elongate snout above the mouth (Figure 15A). However, the elongate rostrum of *Eosaurichthys* (like other Saurichthyiformes) is built primarily (not entirely, see discussion above) from elongations of the jaws, giving this fish a lengthened mouth (Figure 15B). It seems that elongate rostra of at least two distinct forms evolved amongst several lineages of Paleozoic actinopterygians (Figure 16). This suggests that lengthened rostra in ray-finned fishes may fall into several distinct general forms or types. A broader survey of long-rostrumed ray-finned fishes that is beyond the scope of this study is required to adequately address this possibility.

Post-Hangenberg convergence and morphological innovation

The Late Pennsylvanian *Tanyrhinichthys* converged on a sturgeon-like bottom-cruising ecomorphology, representing one of the earliest actinopterygians to exhibit these features. *Tanyrhinichthys* appeared almost simultaneously with two other bottom-dwelling freshwater forms with elongate rostra, *Phanerorhynchus* from Lancashire, England, and the elasmobranch chondrichthyan *Bandringa* (Zangerl, 1969) from Mazon Creek, Illinois, Linton, Ohio, and Cannelton, Pennsylvania (Gardiner, 1967; Sallan & Coates, 2014), both Moscovian in age. Another isolated actinopterygian rostrum comes from similarly aged rocks in Indiana (Poplin, 1978), suggesting the widespread appearance of a then-novel form. In these taxa, the snout is constructed from an extended central element (the rostral bone in the actinopterygians, the cruciform rostral cartilage in *Bandringa*), supported by paired struts (the nasals in the actinopterygians, selinoid rostral cartilages in *Bandringa*; Sallan & Coates, 2014). The rostra of these taxa are marked by an increase in the sensory apparatus, as shown by expansion of pores or extension of the lateral line itself towards the distal snout. This excludes *Phanerorhynchus*, because L. 8585 is not well-enough preserved for rostral sensory organs to be present. In *Tanyrhinichthys* and *Bandringa,* the flattened rostral extension (like that of the unnamed Indiana actinopterygian) is separated from the gape by a rounded element surrounding a fenestra of unknown purpose, which may have contained additional sensory tissues (as above; Sallan and Coates, 2014, Fig. 4; Fig. 3A/B; Fig 4).

The degree of convergence in these distantly-related, long-rostrumed fishes is remarkable, especially considering the novelty of their ecomorphologies in the Carboniferous and their overlapping or near-overlapping age estimates in the Late Pennsylvanian. The timing may not be a coincidence given that *Phanerorhynchus, Bandringa,* and the Indiana taxon are found in coal measures, including river settings containing abundant plant matter (Gill, 1923;

Gardiner, 1967: Poplin, 1978; Sallan & Coates, 2014). The murky bottom waters of Carboniferous river systems, choked with decaying, carbon-rich leaves, may have provided abundant food while presenting challenges for visual hunting (Baird, 1997; Sallan & Coates, 2013). While *Tanyrhinichthys* is not found in coal deposits, its rarity at KBQ suggests that it may have come from such, much as *Bandringa* is also found in nearshore marine settings at Mazon Creek (Sallan & Coates, 2014). Alternatively, the estuarine setting of KBQ may have generated enough sediment to also favor less visual modes of prey detection. These novel environments and the challenges they presented to visual hunting may have forced the evolution of snout-based detection systems, as has been hypothesized for both the American paddlefish *Polyodon spathula* (Walbaum, 1792) and sturgeon (Harkness & Dymond, 1961; Jørgensen *et al.,* 1972; Grande & Bemis, 1991; Wilkens *et al.,* 1997; Peterson *et al.,* 2007). These modern analogs suggest that the simultaneous appearance of elongate rostra bearing sensory organs amongst Carboniferous fishes was driven by the challenges to visual predation that arose in novel environments.

The long-rostrumed Pennsylvanian fishes are one example of a repeated pattern of convergent innovation within the diversification of vertebrates following the end-Devonian Hangenberg event (359 Ma; Sallan & Coates, 2010; Sallan, 2014). There are several other simultaneous or near simultaneous first appearances of ecotypes among both actinopterygians and chondrichthyans (especially holocephalans) during the Carboniferous, sometimes in the same ecosystem (Sallan & Coates, 2010, 2013; Sallan *et al.,* 2011; Sallan, 2012). One example is the Mississippian origination of deep-bodied, laterally flattened “reef” fishes among multiple lineages of actinopterygians e.g. Eurynotiformes such as *Cheirodopsis* (Traquair, 1881) and platysomids such as *Platysomus* (Traquair, 1881) from the Visean of Glencartholm, Scotland, *Frederichthys* (Coates, 1993) from the Serpukhovian of Bearsden, Scotland, *Proceramala*

(Poplin & Lund, 2000) and *Discoserra* (Lund, 2000) from the Serpukhovian of Bear Gulch, Montana, and *Adroichthys* (Gardiner, 1969) from the Visean of South Africa (Traquair, 1881: Moy-Thomas & Bradley Dyne, 1938; Gardiner, 1969; Coates, 1993; Lund, 2000; Poplin & Lund, 2000; Hurley *et al.,* 2007; Sallan & Coates, 2013)). Examples of deep-bodied forms also occur among chondrichthyans (the petalodont *Belantsea* (Lund, 1989) and *Echinochimaera* (Lund, 1977)) and even coelacanths (*Allenypterus* (Lund & Lund, 1984)) from Bear Gulch (Lund, 1977; Lund & Lund, 1984; Lund, 1989). Nearly all of these fishes are durophages, presaging later, deep-bodied stem-teleost pycnodonts and modern teleost durophages (sparids, wrasses, parrotfish, and tetraodoniforms) and are coincident with a large number of durophagous chondrichthyans, lungfishes, and actinopterygians with other body types (Bellwood, 2004; Sallan *et al.,* 2011; Sallan & Coates, 2013).

Another example of convergent innovation in Carboniferous fishes is axially-elongated “eels” with reduced paired fins and continuous median-caudal fins. This body form has been observed in actinopterygians from Glencartholm (*Tarrasius* (Traquair, 1881)) and Bear Gulch (*Paratarrasius* (Lund & Melton, 1982; Sallan, 2012)), chondrenchelyid holocephalans from Glencartholm (*Chondrenchelys* (Traquair, 1888)) and Bear Gulch (*Harpagofututor*; Lund, 1982; Lund & Melton, 1982; Finarelli & Coates, 2014), elasmobranch chondrichthyans from the Permian of Europe and North America (*Orthacanthus* (Agassiz, 1843)) and Bear Gulch (*Thrinacoselache*; Zangerl, 1981; Grogan & Lund, 2008; Sallan, 2012), and possibly coelacanths ("Apholidotos", an undescribed but named taxon previously attributed to the polyphyletic actinopterygian family "tarrasiidae" but excluded by more recent work, LS pers. observ., Frickhinger, 1991; Lund & Poplin, 2002; Sallan, 2012).

The convergent taxa mentioned above, including *Tanyrhinichthys*, are only the most extreme and noticeable examples of duplicated, coincident innovations among Late Paleozoic fishes (Fig. 17). The repeated appearance of convergent forms suggests that shared environmental pressures and functional demands existed across Carboniferous marine and freshwater ecosystems. The novel morphologies that first occur among multiple Carboniferous lineages mirror the morphological diversity of later fish clades, such as neopterygians and teleosts in the Mesozoic and Cenozoic (Sallan & Friedman, 2012). However, chondrichthyans after the Paleozoic seem to have become incapable of generating some of the more specialized "reef" forms such as eels and deep-bodied "angelfish," in line with a dramatic loss in relative holocephalan diversity and richness (Friedman & Sallan, 2012).

A global shift in the relative evolvability and viability of fish ecotypes seems to have occurred in the Carboniferous. This was perhaps contingent on the new dominance of actinopterygians and chondrichthyans after the end-Devonian extinction and/or a coincident change in the basic structures of aquatic vertebrate ecosystems or their environments (Sallan & Galimberti, 2015). This new state of fish faunas appears to have lasted to the present day, even as one of the two dominant groups, chondrichthyans, stopped producing the more extreme forms.

CONCLUSIONS

Our revision of the morphology of *Tanyrhinichthys* indicates that it was most likely a bottom-cruising predator similar in general ecomorphology to modern sturgeon, as these taxa share a set of features associated with a benthic lifestyle. Our examination of *Tanyrhinichthys* and broadly contemporaneous long-rostrumed ray-finned fishes demonstrates that elongate rostra evolved independently in several lineages of Paleozoic actinopterygians, as well as at least one chondrichthyan. The bottom-cruising ecomorphology of *Tanyrhinichthys* evolved within the context of widespread, often simultaneous and coincident convergence on then-novel ecomorphologies amongst disparate lineages of actinopterygians and chondrichthyans in the wake of the end-Devonian Hangenberg extinction, a phenomenon that appears to have extended into the Late Pennsylvanian and lasted until today.

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FIGURE CAPTIONS

Figure 1. The holotype of *Tanyrhinichthys*, KUVP 83503 (anterior is to the right). A, specimen photo. B, specimen drawing. Scale bar equals 1 cm.

Figure 2. The most complete specimen of *Tanyrhinichthys*, CM 30737 (anterior is to the right). A, specimen photo (color inverted). B, specimen drawing. Scale bar equals 1 cm.

Figure 3. Skull of the holotype of *Tanyrhinichthys*, KUVP 83503, preserved in lateral view (anterior is to the right). A, specimen photo. B, specimen drawing. Scale bar equals 1 cm.

Figure 4. Most complete skull of *Tanyrhinichthys*, CM 30737, preserved in lateral view (anterior is to the right). A, specimen photo (color inverted). B, specimen drawing. Scale bar equals 1cm.

Figure 5. Skull of *Tanyrhinichthys*, NMMNH P-70413, preserved in lateral view (anterior is to the right). A, specimen photo. B, specimen drawing. Scale bar equals 1 cm.

Figure 6. Skull of *Tanyrhinichthys*, NMMNH P-51192, crushed ventrally (anterior is to the left). A, specimen photo. B, specimen drawing. Scale bar equals 1 cm.

Figure 7. The rostrum of *Tanyrhinichthys*, CM 30737 (anterior is to the right). A, specimen photo. B, specimen drawing. Scale bar equals 0.5 cm.

Figure 8. Pectoral fins of *Tanyrhinichthys* (anterior is to the right). A, NMMNH P-70413 pectoral fin. B, CM 30737 pectoral fin (color inverted in specimen photo). Scale bars equal 1 cm.

Figure 9. Pelvic fin of *Tanyrhinichthys*, CM 30737 (anterior is to the right). A, specimen photo (color inverted). B, specimen drawing. Scale bar equals 1 cm.

Figure 10. Dorsal fin of *Tanyrhinichthys*, CM 30737 (anterior is to the right). A, specimen photo (color inverted). B, specimen drawing. Scale bar equals 1 cm.

Figure 11. Anal fin of *Tanyrhinichthys*, CM 30737 (anterior is to the right). A, specimen photo (color inverted). B, specimen drawing. Scale bar equals 1 cm.

Figure 12. Caudal fin of *Tanyrhinichthys*. A, CM 30737 (anterior is to the right, color inverted in specimen photo). B, NMMNH P-51192 (anterior is to the left). Scale bars equal 1 cm.

Figure 13. Squamation along the ventral margin of the anterior lateral flank of *Tanyrhinichthys*, NMMNH P-70413. A, specimen photo (anterior is to the right). B, specimen drawing. Scale bar equals 1 cm.

Figure 14. A, reconstruction of *Tanyrhinichthys*, based primarily on CM 30737. B, life restoration. Scale bar equals 1 cm.

Figure 15: Comparison of the two broad structural forms of elongate rostra in Paleozoic actinopterygians. A, *Tanyrhinichthys*, which bears an elongate rostrum that is a lengthened snout-like structure above the mouth B, a representative saurichthyiform (*Saurichthys*

madagascariensis (Piveteau, 1945)), which bears an elongate rostrum that is a lengthened mouth (after Kogan and Romano, 2016, Figure 11B).

Figure 16: A, Photograph of a latex peel (P. 34421-2) of the holotype *Phanerorhynchus*, scale bar equals 1 cm. B, Specimen drawing of the holotype of *Phanerorhynchus* (L. 8585), after Gill (1923). Anterior is to the left. Figure 17: Convergent morphological innovation in post-Hangenberg fishes. A, Occurrence of deep-bodied and eel-like actinopterygians, chondrichthyans, and coelacanths in the Mississippian: 1, *Discoserra*; 2, *Thrinacoselache*; 3, *Aesopichthys*; 4, *Allenypterus*; 5, *Paratarrasius*; 6, *Belantsea*; 7, *Echinochimaera*; 8, *Proceramala*; 9, *Harpagofututor*; 10, *Adroichthys*; 11, *Platysomus*; 12, *Tarrasius*; 13, *Paramesolepis*; 14, *Frederichthys*; 15, *Chondrenchelys*; 16, *Amphicentrum*. B, Occurrence of long-rostrumed actinopterygians and chondrichthyans in the Pennsylvanian: 17, *Tanyrhinichthys*; 18, undescribed long-rostrumed taxon from Logan Quarry, Indiana; 19, *Bandringa*; 20, *Phanerorhynchus*. Fishes not to scale. Maps (Key Time Slices of North America, 308 MA and 345 MA) were created by Ron Blakey at Colorado Plateau Geosystems Inc., used under License #61019, ©2013 Colorado Plateau Geosystems Inc.