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A new pachyrhizodontid fish (Actinopterygii: Teleostei) from the Tarrant Formation (Cenomanian) of the Upper Cretaceous Eagle Ford Group of Texas, U.S.A.

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**A new pachyrhizodontid fish (Actinopterygii: Teleostei) from the Tarrant Formation
(Cenomanian) of the Upper Cretaceous Eagle Ford Group of Texas, U.S.A.**

A Thesis Presented in
Partial Fulfillment of the
Requirements for the Degree of
Master of Science

Summer 2019

By

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ABSTRACT

SMU 76938 is a fossil skeleton of a large, nearly complete actinopterygian bony fish housed in Southern Methodist University in Dallas, Texas, USA. It was collected from the Upper Cretaceous Tarrant Formation (middle Cenomanian; ~96 Ma) of the Eagle Ford Group in Tarrant County, Texas, an area where it was near the western margin of the East Texas Embayment during the Late Cretaceous. Although parts of the skull and dorsal fin are damaged, SMU 76938 is relatively complete, especially in the preservation of the caudal fin with its soft tissue outline. The fish has a fusiform body and measures about 93, 109, and 119 cm in standard length, fork length, and total length, respectively, and about 17 cm in maximum body depth. Several features of SMU 76938 are reminiscent of Cretaceous crossognathiforms, yet many features, such as the villiform dentition, have yet to be seen in any taxa within the order. My phylogenetic analysis indicates that SMU 76938 is a pachyrhizodontid crossognathiform fish. The combination of villiform teeth and fused infraorbital 1 and 2 in SMU 76938 is unique, suggesting that the specimen belongs to a new genus and species within the family Pachyrhizodontidae. With a fusiform body, a large symmetrical caudal fin, and a mouth with numerous small conical teeth suited for grasping, the new taxon represented by SMU 76938 was most likely a fast swimming, open-ocean predator capable of high propulsion and quick bursts of speed, that likely pursued smaller, quick swimming animals, such as squid, crustaceans, and other fishes. Although the individual represented by SMU 76938 was about 14 years old at the time of its death, my vertebra-based theoretical growth model indicates that the species could have reached up to about 1.8 m TL and lived up to 37 years old in age.

INTRODUCTION

One of the fundamental quests in science is to determine the total number of species on Earth (Mora et al., 2011) which is estimated to be at least 1 to 6 billion extant species (Larsen et al., 2017), and possibly as many as upwards of 1 trillion when counting microbial species alone (Locey and Lennon, 2016). Although vertebrates represent a small fraction of these total biodiversity estimates, fishes alone consist of over 34,000 species described to date (Froese and Pauly, 2019), not counting numerous extinct species that are known from the fossil record. What allows the communication about such vast biodiversity of life is taxonomy, a field of science in which organisms are described, named, and classified (Linnaeus, 1758; Simpson, 1961). Recognition of species or different taxonomic groups also form the basis of phylogenetic systematics, the science of elucidating the origin and evolutionary interrelationships of organisms, often through cladistics or the forming of phyletic groups based on shared derived characteristics (Hennig, 1950; Wiley and Lieberman, 2011).

Fossils are evidence of the history of life. Although taxonomy and systematics of fossil species are typically based only on morphological characters (Wiens, 2004; Lee and Palci, 2015), fossils are important to help deciphering the evolutionary history of Earth's biodiversity (Donoghue et al., 1989; cf. Patterson, 1981), where the presence of the rich diversity today is due to the immense change of ecosystems in the past. During the Cretaceous period, which lasted for approximately 80 million years (from 145 to 65 million years ago [Ma]), the Earth experienced dynamic changes in geography and climate (Kauffman, 1984). One particular geologic record is the so-called Gulf Series strata that accumulated under a major epicontinental sea, the Western Interior Seaway, that developed over North America during the Late Cretaceous. The Upper

Cretaceous Gulf Series ranges in age from 117 to 85 Ma and includes strata, such as the Woodbine Formation, Eagle Ford Group, and Austin Group, distributed in north and central Texas (Fig. 1A). One of the Eagle Ford strata is the Tarrant Formation (middle Cenomanian) that is interpreted to have formed about 96 Ma through multiple regressions and transgressions in an area near the western margin of the Late Cretaceous 'East Texas Embayment' directly connected to the Western Interior Seaway (Welton and Farish, 1993; Jacobs et al., 2005a, 2005b). The accumulation of the Gulf Series sediments represents a warm climatic period, where Jacobs et al. (2005b) inferred the seawater temperature to be between approximately 20 and 30 °C. With a warm climate and ocean, came a variety of organisms in and along the Western Interior Seaway, including various macroinvertebrates, cartilaginous fishes, bony fishes, and marine reptiles (such as turtles and aquatic squamates) as well as dinosaurs and mammals that were washed into the sea (Jacobs et al., 2013; Everhart, 2017). Using such fossils as clues, one can examine the dynamics of extinct species and gain insight into their evolutionary history.

In the 1980s, a nearly complete fossil fish skeleton (SMU 76938 in Southern Methodist University [SMU], Dallas, Texas) was recovered from the Tarrant Formation (Fig. 1A) by Michael J. Polcyn (SMU) in Tarrant County, Texas, USA (Fig. 1B). At least superficially, the morphology of the vertebrae and caudal fin in SMU 76938 is reminiscent of fishes in the crossognathiform family Pachyrhizodontidae commonly found in Late Cretaceous marine deposits worldwide (Applegate, 1970; Wiffen, 1983; Cavin, 1995; Blanco and Cavin, 2003). However, the exact taxonomic identity of SMU 76938 is uncertain because of some unique features observed in its skull and dentition.

The aim of my study is four-fold. First, I describe the skeletal anatomy of SMU 76938 in detail. Second, based on my skeletal data from SMU 76938 and those taken from published

literature, I conduct a phylogenetic analysis to determine the systematic position of SMU 76938. Specifically, I test whether or not SMU 76938 belongs to Pachyrhizodontidae. Third, based on the systematic position of the SMU 76938, I elucidate its taxonomic identity where I determine whether or not SMU 76938 represents a new species. Fourth, based on the observed skeletal anatomy, I infer the body form and lifestyle of the fossil fish represented by SMU 76938. If the specimen is found to be a form new to science, this study adds another piece of information to the ecological and evolutionary dynamics of the Late Cretaceous Western Interior Seaway of North America.

MATERIALS AND METHODS

Material

SMU 76938 (Fig. 2) is a nearly complete fossil skeleton of a large bony fish that belongs to the Shuler Museum of Paleontology at Southern Methodist University in Dallas, Texas. It is preserved in a plaster jacket, initially exposing only the left lateral side of the skeleton. The skeleton is overall well-articulated in left lateral view except for some missing or damaged elements, such as part of the cranial roof and much of the dorsal fin. The vertebral column at the mid-region of the trunk is rather disorganized, possibly as a result of the formation of gas through post-mortem decomposition.

Preparation and Skeletal Description

Fossil preparation was conducted prior to the detailed examination of SMU 76938. Using a HW-10 Pneumatic Air Scribe Tool (The Stone Company, Boulder, Colorado), rock matrix was removed to expose skeletal parts of SMU 76938. Mechanical preparation was chosen over chemical preparation because of the large size of the specimen as well as the physical state of SMU 76938 where the matrix is relatively soft.

Following preparation of the left side of SMU 76938, I drafted illustrations (photographs and line drawings) of the fish skeleton and later digitally processed the images using Adobe Photoshop CC 2018 (e.g., Fig. 2). A transparent plastic sheet was placed over the entire specimen, and skeletal elements were identified and traced using a permanent marker that formed the basis of my line drawings. Upon the completion of my skeletal analysis based on the left lateral side, I determined that some cranial elements critical for taxonomic diagnosis were not well preserved or missing (Fig. 3A, B). Therefore, the head was removed, coated with a plaster jacket, flipped to make the right lateral side up, and mechanically prepared to expose the right lateral side. The cranial features on the right side was then photographed and illustrated (Fig. 3C, D). A caliper and ruler were used for measuring skeletal elements of SMU 76938 in addition to describing anatomical features.

For the purpose of this study, I followed the osteological terminology and abbreviations of Schultze (2008) and Arratia (2015). For comparisons, osteological data of crossognathiforms were collected from various sources (e.g., Forey, 1977; Maisey, 1991a, 1991b; Cavin, 2001; Arratia, 2008; Murray and Cumbaa, 2015; Shimada, 2015). If SMU 76938 is determined to have

unique characteristics not found in any known species of fishes, it is assumed to represent a new species.

Comparative Specimens

Other fossil fish specimens in the following four museum collections in the United States were examined for comparisons and to check for accuracy of previously reported genus-level anatomical characteristics in literature: American Museum of Natural History (AMNH), New York, New York; Fort Hays State University's Sternberg Museum of Natural History (FHSM), Hays, Kansas; Field Museum of Natural History (FMNH), Chicago, Illinois; and University of Kansas Museum of Natural History (KUVV), Lawrence, Kansas. Some representative examined specimens by genera include (specific species and locality in parentheses): *Apsopelix*—FHSM VP-435 (*A. anglicus*: Kansas), FHSM VP-6245 (*A. sp.*: Kansas), FMNH PF 3328 (*A. "syllaemus"*: Kansas), KUVV 49528 (*A. anglicus*: Kansas), KUVV 309 (*A. anglicus*: Kansas?), KUVV 49402 (*A. anglicus*: Kansas); *Elopopsis*—AMNH FF uncatalogued (*E. haueri*: Dalmatia); *Goulmimichthys*—AMNH FF 19667 (*G. arambourgi*: Morocco); *Notelops*—AMNH FF 11865 (*N. sp.*: Brazil), AMNH FF 2616 (*N. sp.*: Brazil), AMNH FF 2611 (*N. brama*: Brazil), FMNH PF 9620 (*N. brama*: Brazil), FMNH PF 10777 (*N. brama*: Brazil), FMNH PF 10778 (*N. brama*: Brazil); *Pachyrhizodus*—AMNH FF 1756 (holotype of *P. leptopsis*: Kansas), AMNH FF 1881 (holotype of *P. caninus*: Kansas), AMNH FF 1900 (*P. caninus*: Kansas), AMNH FF 8151 (*P. minimus*: Kansas), AMNH FF 8325, (*P. sp.*: Kansas), AMNH FF 8386 (holotype of *P. kingii*: Kansas), AMNH FF 8612 (*P. sp.*: Wyoming, U.S.A.), AMNH FF 8614 (*P. minimus*: Wyoming), AMNH FF 19274 (*P. minimus*: Kansas), AMNH FF 19729 (*P. caninus*: Kansas), FHSM VP-

2189 (*P. caninus*: Kansas), FHSM VP-2281 (*P. "latimentum"*: Kansas), FHSM VP-2282 (*P. minimus*: Kansas), FHSM VP-7312 (*P. minimus*: Kansas), FMNH PF 1696 (*P. minimus*: Alabama, U.S.A.), FMNH PF 3326 (*P. caninus*: Kansas), FMNH PF 5402 (*P. minimus*: Canada), FMNH UF 972 (*P. sp.*: Kansas), KUVVP 300 (*P. minimus*; holotype of *Thrissopater intestinalis*: Texas), KUVVP 12080 (*P. minimus*: Kansas?), KUVVP 27836 (*P. sp.*: Kansas); *Rhacolepis*—AMNH FF 1492 (*R. sp.*: Colombia), AMNH 4617 (*R. buccalis*: Brazil), AMNH FF 11977 (*R. sp.*: Brazil), AMNH FF 13106 (*R. buccalis*: Brazil), FMNH PF 10770 (*R. buccalis*: Brazil), and FMNH PF 10766 (*R. buccalis*: Brazil).

Phylogenetic Analysis

After the determination of its taxonomic identity based on my skeletal data, a phylogenetic analysis was conducted in order to determine the systematic position of the fish taxon represented by SMU 76938. I based my phylogenetic analysis on the study conducted by Arratia and Tischlinger (2010) who presented a data matrix that consisted of 52 taxa (not counting their 'hypothetical common ancestor') and 193 characters. In my study, I used 42 of the 52 taxa, specifically all the taxa included in the monophyletic assemblage united by a clade denoted 'A' in Arratia and Tischlinger's (2010:fig. 12) phylogenetic tree. They comprised of *Pholidophorus*, *Leptolepis*, *Tharsis*, and *Ascalabos*, as well as members of Osteoglossomorpha, Euteleostei, Ostarioclupeomorpha, Elopiformes, Ichthyodectiformes, and Crossognathiformes, where I chose *Pholidophorus* as an outgroup for my study. A total of 49 Arratia and Tischlinger's (2010) characters were deleted for this present study because of ambiguous coding (“?” or “-”) in the outgroup (characters 55–61, 78, 79, 84, 88, 113, 117, 126, 145, 147, 150, 160, 167–169, 187,

and 192) or because all ingroup taxa have the same plesiomorphic coding as the outgroup or the same plesiomorphic coding overall but may also include one or more uninformative coding such as “?” (Arratia and Tischlinger's characters 3, 4, 44, 53, 68, 77, 108, 110, 112, 140, 141, 146, 152, 153, 156, 159, 162, 163, 166, and 170–176). Furthermore, two additional characters in which only one ingroup taxon was found to be apomorphic (i.e., autapomorphy that is not phylogenetically informative) were removed (Arratia and Tischlinger's characters 154 and 189). Of the 142 characters remained, the polarity of eight characters needed to be realigned because of the use of *Pholidophorus* as an outgroup that received coding of "0" for all 142 characters in this present study (Arratia and Tischlinger's characters 30, 47, 116, 133, 136, 151, 165, 185). Fifteen of the 142 characters resulted in the reduction of the number of character states because not all states were represented in the taxa examined (Arratia and Tischlinger's characters 30, 31, 43, 46, 47, 102, 106, 116, 118, 122, 130, 133, 143, 144, 165). All 142 characters and their coding are listed in Appendix 1 with a new set of character numbers for the purpose of this study. Appendix 2 lists the data matrix by taxa used in this study. The character matrix NEXUS file was created using the program Mesquite Version 3.51, a modular system for evolutionary analysis, and was then analyzed using PAUP* (Phylogenetic Analysis Using Parsimony* and other methods) Version 4.0a165.

Arratia and Tischlinger's (2010) study represents the most extensive phylogenetic study of Crossognathiformes available to date, but it should be noted that it is not comprehensive. For example, *Goulmimichthys* and *Rhacolepis* were the only taxa representing Pachyrhizodontidae in their study where the family also includes the following ten genera: *Apricenapiscis*, *Aquilopiscis*, *Elopopsis*, *Greenwoodella*, *Michin*, *Motlayoichthys*, *Nardopiscis*, *Pachyrhizodus*, *Platinx*, and *Tingitanichthys* (Taverne, 2013; Arratia et al., 2018). Therefore, the intent of my phylogenetic

analysis is to determine the family-level affinity of SMU 76938, and not necessarily to determine the phylogenetic interrelationships of SMU 76938 among taxa at the genus or species level.

RESULTS

Skeletal Description

General Anatomy—SMU 76938 is a rather large and nearly complete fossil fish specimen (Fig. 2). SMU 76938 has a standard length of 87 cm, a fork length of 103 cm, and a total length of 119 cm. The fish has a fusiform body plan with a maximum body depth of approximately 18 cm. The base and posterior surface of the neurocranium (e.g., occipital complex and parasphenoid except the basioccipital) are poorly preserved or covered with other cranial bones, but the overall shape of the skull is triangular in lateral view (Fig. 3). Measuring from the anterior end of the premaxilla, the head length is 17 cm to the posterior end of the basioccipital (or 'occipital condyle'), and 29 cm to the end of the operculum. The maximum head depth measures 14 cm at the level of the basioccipital, and the head width is estimated to be 5 cm. SMU 76938 is likely an adult fish due to its massive size and the presence of some fused skull bones. The remains of thin, circular scales that range from 6 mm to 8 mm in maximum diameter, are preserved as 'patches' throughout SMU 76938 (Fig. 4A). Their exact surface texture is difficult to discern, but they are of cycloid type.

Skull—The paired parietal bones (= frontal bones of traditional terminology) are elongated and rectangular, individually measuring 6 cm in length and 1.5 cm in maximum width. The paired postparietal bones (= parietal bones of traditional terminology) are damaged on the

posterior end, but nevertheless are rectangular, each measuring 2 cm in both length and maximum width. The parietal bones and postparietal bones are independent from each other with no indication of fusing or the presence of sutures. The supraoccipital lays medially in skull roof, posterior to the post-parietal bones, and is only partially preserved. Likewise, the exact morphology of the pterotics and epiotics are unknown due to poor preservation. Anterior to the parietal bones are paired nasals, they are damaged, each measuring 2 cm in length and 1 cm in maximum width. Potentially visible in left lateral view is the partial right dermosphenotic in addition to a partially preserved bone that is most likely the anterior portion of the vomer.

The orbit is located within the anterior region of the head and has an estimated diameter of 5.5 cm (Fig. 3). It is considered small, measuring less than 20% of the total anteroposterior skull length (i.e., up to the posterior margin of the opercle). It is completely enclosed by six circumorbital bones that collectively have a maximum anteroposterior length of 14 cm and a dorsoventral height of 8 cm. Infraorbital 4 is the largest in size, followed by infraorbital 3, infraorbital 5, the dermosphenotic, infraorbital 1 + 2, and the supraorbital. The infraorbitals are expanded posteriorly overlapping at least the anterior margin of the preopercle. Positioned ventrally to the orbit are relatively small, fused infraorbitals 1 and 2. The dermosphenotic is damaged yet would have been large and well-developed. The supraorbital is the smallest element of the circumorbital ring and has an expanded anteroventral portion. Suborbitals and antorbital bones are absent in SMU 76938.

The jaws are elongate bearing numerous villiform teeth. The mandible, in its entirety, is 18.5 cm in anteroposterior length with an estimated depth of 3 cm. At the most anterior region of the head, the right and left premaxilla meet, each 2 cm in anteroposterior length with an estimated height of 2 cm and both appear to have been mobile prior to fossilization. Posterior to

the premaxilla, the maxilla is elongate and in lateral view measures 13.5 cm in length with a height of 2 cm. The dentition is represented by many small (i.e., no more than 1.5 mm in height) conical teeth, each with a lingual curvature (Fig. 4B, C). Along with the numerous villiform teeth, acrodontous alveoli are preserved along the oral margin of both the maxilla and premaxilla. The ventral margin of the maxilla is almost straight, whereas the posterior margin is somewhat sharp. Dorsal to the dorsal margin of the maxilla, each upper jaw contains a single elongate supramaxilla, measuring 7.5 cm in length with a height of 1 cm. The supramaxilla is long and narrow, covering a length equivalent to ca. 50 % of the maxilla length.

The most anterior region of the dentary meets approximately the same point as the upper jaw. The dentary is postoroventrally broad with collectively villiform, densely distributed teeth along the inner edge of the mouth. The articular bone is fused with the angular and is within the posterior region of the dentary. The angular-articular articulates with the quadrate and the post-articular process is well developed, extending posterior to the articular facet for the quadrate.

The hyomandibula is partially preserved, separated medially at the lateral plane and broken posteriorly. It is 9 cm in visible maximum height, reaching infraorbital 5 at the dorsal-most point. The quadrate is triangular, oriented ventrally, about 5 cm in maximum dorsoventral height, and 5 cm at the maximum width. The upper margin of the quadrate is almost straight and is extending anterodorsally, meeting at the level of the ectopterygoid. The quadrate-mandibular articulation is placed posterior to the posterior margin of the orbit. The symplectic is partially preserved and does not appear to articulate with lower jaw. The metapterygoid, and entopterygoid are all partially visible in the left lateral side of the head, the full size is unknown due to incomplete preservation. The ectopterygoid is skinny in left lateral view, anterior to the

supramaxilla it is 7 cm in length and less than 0.5 cm in maximum height. The dermopalatine is directly anterior the ectopterygoid and is 1.5 cm in length and 0.5 cm in maximum height.

The opercle is large with a maximum anteroposterior length of 8 cm and a dorsoventral height of 6.5 cm. The anterior portion is covered by the expanded infraorbital bones. Anterior to the opercle, the preopercle is 2 cm in length and 10 cm in height whereas the ventroposterior region of preopercle is broadly expanded. The subopercle is 7 cm in length and 3 cm in maximum height and is positioned ventrally to the opercle and anteriorly to the preopercle.

In right lateral view of the head, paired ossified hypohyals and paired ceratohyals are visible ventrally to the dentary. The ceratohyals are positioned posteriorly to the hypohyals and partial preservation of both has made it difficult to obtain an accurate measurement of size. Partially visible in left lateral view are broken branchiostegal rays. The branchiostegals are positioned posterior to the ceratohyals and are much more well-preserved on the right lateral side. At least 17 branchiostegal rays are visible and they all have a gradual ventroposterior curve.

Vertebral Column and Ribs—SMU 76938 has a nearly complete vertebral column beginning posterior to the occipital condyle with a count of at least 54, but no more than 58 vertebrae. The vertebral centra have a dorsoventral height of 2.5 cm and an anteroposterior length of 1 cm and do not deviate from the size along the vertebral column. The axial skeleton is relatively well-articulated, but it is more-so articulated along the posterior half (Fig. 5A–C). Each vertebra of SMU 76938, where observable, exhibits numerous concentric growth rings on each articular surface. Several of them, particularly towards the periphery of each centrum, are particularly prominent and occur as low ridges. A closer examination reveals that there are several additional similar, but weaker, low ridges also present towards the center of each

centrum. I identify 14 such annuli that are interpreted to be annually growth bands (e.g., Newbrey and Wilson, 2005), meaning that the fossil fish was 14 years old at the time of its death.

The ribs, haemal spines, and neural spines are present throughout the specimen. However, they are all broken or partially preserved, so an accurate measurement of size is not obtainable. Located ventrally along the vertebral column, the fragmented ribs are more concentrated between 19th and 40th vertebrae, with another concentration between 45th and 51st vertebrae. The ribs display varying degrees of fragmentation, some of which still articulating with their respective vertebrae. Although broken, they appear long with a gentle curvature with the longest fragment measures 9 cm in length and complete ribs could have potentially reached 15 cm in length.

Caudal Fin Skeleton—The caudal fin begins posterior to the 54th vertebra and is exceptionally well preserved, retaining its soft tissue outline (Fig. 5D). The overall shape of the tail is forked with the dorsal and ventral lobes measuring the same size with a combined vertical height of 33 cm. There are 19 principle rays, with nine in the lower lobe, and more than 16 branched rays within the caudal fin. The marginal principle caudal rays are segmented and display a step-like, Z-shaped articulation.

The base of the caudal fin is just as well preserved. Discernible are six or less uroneurals (the first being forked anteriorly), six or less hypurals with a fusion between hypurals 1 and 2, and the presence of a hypurapophysis. Both the preural vertebrae and the parhypural appear to be laterally fused with their respective autocentra (Fig. 5E, F). Although difficult to determine due to overlapping elements, there are at least one, no more than two independent ural centra.

Other Fins and Girdles—First found as a float to SMU 76938 was the dorsal fin which is damaged due to erosion (Fig. 5G). Although broken and incompletely preserved, at least 20 fin

rays are visible. It is interpreted that the position of the dorsal fin is anterior to that of the pelvic fin. The pectoral fin base begins at the level of the 12th vertebra with a large, well-developed extrascapular bone extending caudally close to the posterior margin of opercle. Slightly damaged, the fin is at least 19 cm in length with five visible fin rays (Fig. 5H). A large cleithrum dorsal to the pectoral base curves ventroposteriorly with a maximum width of 5 cm and a height of 15 cm. The origin of the pelvic fin occurs at the level of the 26th vertebra. There are at least eight visible rays, although damaged, the longest of the broken rays is at least 7 cm long (Fig. 5I). The origin of the anal fin is at the level of the 46th vertebra, 25 cm posterior to the pelvic fin base. Preservation is partial with at least eight visible rays, longest being at least 11 cm long (Fig. 5J).

Phylogenetic Analysis

Appendix 2 lists my character state coding of SMU 76938 along with that of other fishes based on Arratia and Tischlinger's (2010) morphological characters used for their phylogenetic analysis (see Appendix 1 for all the 142 characters and their states). With parsimony as the optimality criterion, my character matrix yielded 20,013 trees that were rooted using a user-specified outgroup (i.e., *Pholidophorus*). Because this analysis was used only to determine the phylogenetic placement of SMU 76938 and not an overall reevaluation of the order, I searched for only the trees that were supported by previous studies (Arratia, 2008; Arratia and Tischlinger, 2010). This resulted in only one tree (Fig. 6: tree length = 492 steps; consistency index = 0.3801; retention index = 0.6352) with a well-resolved monophyly of Crossognathiformes that is sister to the clade that includes Osteoglossomorphs, Euteleostei, Ostarioclupeomorpha, Elopiformes, and

Ichthyodectiformes, and all the aforementioned groups form a clade that is sister to *Ascalabos*. Within Crossognathiforms, the polytomy within Varasichthyidae (*Domeykos*, *Luisichthys*, *Varasichthys*, and *Protoclupea*) that was present in Arratia and Tischlinger (2010:fig. 12) tree is resolved in my tree in which *Luisichthys* and *Varasichthys* are sisters and the clade that unites them is sister to *Protoclupea* (Fig. 6). Varasichthyidae is sister to the monophyletic group that includes *Chongichthys* (Chongichthyidae), *Bavarichthys* (Family indet.), *Notelops* (Notelopidae), Pachyrhizodontidae, and Crossognathidae. *Chongichthys* is the basal-most crossognathiform of that monophyletic group and it is sister to a clade that includes: *Bavarichthys*, Notelopidae, Crossognathidae, and Pachyrhizodontidae. *Bavarichthys* is sister to the ‘Cretaceous crossognathiform’ assemblage consisting of notelopids, crossognathids, and pachyrhizodontids. Notelopidae is sister to the group that includes the crossognathids and pachyrhizodontids. *Crossognathus* and *Apsopelix* (crossognathids) form a sister group to the pachyrhizodontid clade consisting of *Goulmimichthys*, *Rhacolepis*, and SMU 76938. Within Pachyrhizodontidae, *Rhacolepis* and SMU 76938 show closer affinity relative to *Goulmimichthys*.

DISCUSSION

Systematic Position and Taxonomy of SMU 76938

SMU 76938 exhibits several notable anatomical features with figure 7A showing my cranial reconstruction of the fish taxon represented by SMU 76938. The orbit is relatively small, occupying ca. 19% of the head length (measuring to the end of the opercle), and the quadrate-mandibular articulation is located posterior to the posterior margin of the orbit. The infraorbitals

of the circumorbital series expand posteriorly, reaching not only the preopercle, but the opercle as well. Infraorbitals 1 and 2 appear fused in SMU 76938. The supramaxilla is relatively long, about 50% of the length of the maxilla. Additional noteworthy characteristics include numerous villiform teeth on the maxilla and premaxilla as well as on the elongate lower jaws (Fig. 4B, C). Additionally, the first uroneural reaches anteriorly, at most reaching preural centrum number 2 (Fig. 5E, F).

By including the aforementioned anatomical characteristics, my phylogenetic analysis strongly suggests that SMU 76938 is a pachyrhizodontid of the monophyletic order Crossognathiformes (Fig. 6). Several unique characters of SMU 76938 directly support its placement within this clade. The head of SMU 76938 is similar in shape to other pachyrhizodontids, being triangular with nearly equal sides (Arratia et al., 2018). The parietals of SMU 76938 are long and large, similar to those seen in Pachyrhizodontidae, specifically *Pachyrhizodus* where they are described as very broad with the maximum width located just before the orbit (López-Horgue et al., 2014). The circumorbital ring of SMU 76938 is completely closed without any gaps between the bones, which is a crossognathiform trait (Arratia, 2008; Arratia and Tischlinger, 2010). The presence of a total of five infraorbital bones is also a crossognathiform trait although it differs among genera in which specific bones are fused. There is a fusion between infraorbitals 1 + 2, which is unique to SMU 76938; yet, it displays the trait found in notelopids and pachyrhizodontids where the infraorbitals expands posteriorly over the anterior region of the preopercle, as seen in the genera *Notelops* and *Rhacolepis*, in addition to expanding over the opercle with *Pachyrhizodus* and *Goulmimichthys* (Arratia et al., 2018). The dermosphenotic is partially preserved, yet it is interpreted to be large. This is also a feature found in *Chongichthys* and *Bavarichthys*, but it is now considered a

homoplastic character because it can also be seen in ichthyodectiform and some elopiform fishes (Arratia and Tischlinger, 2010). The antorbital is absent in SMU 76938 which is a trait of Pachyrhizodontidae where the antorbital is lost or completely fused with the first infraorbital (Nelson et al., 2016).

The number of supramaxillary bones may be one or two in crossognathiforms where two supramaxillae are considered a more basal trait seen in the Jurassic forms, and having only one supramaxilla is a pachyrhizodontid and notelopid trait (Arratia and Tischlinger, 2010). SMU 76938 has a single, elongate supramaxilla that is roughly 50% the length of the maxilla. The posterior margin of the maxilla is somewhat sharp in SMU 76938, a character that differs among crossognathiforms. The dentition of SMU 76938 is unique where the teeth are villiform, as opposed to being aligned in a single linear row as typically seen in pachyrhizodontids (Stewart and Bell, 1994; Bartholomai, 2012; Shimada, 2015; Arratia et al., 2018). Another pachyrhizodontid feature is the presence of an internal premaxillary tooth or teeth, but this is difficult to determine in SMU 76938 because its premaxilla can only be viewed laterally (Alvarado-Ortega et al., 2008; Giersch et al., 2010).

The mandible of SMU 76938 is overall elongate, and the quadrate-mandibular articulation is positioned posterior to the posterior margin of the orbit—a feature seen in some pachyrhizodontids (Arratia et al., 2018). The retroarticular bone being excluded from the joint facet of the quadrate is a pachyrhizodontid trait that is seen in SMU 76938. However, this is different for *Notelops* where it is included in the joint facet (Cumbaa and Murray, 2008; Arratia and Tischlinger, 2010; Murray and Cumbaa, 2015). The quadrate of SMU 76938 has an almost straight upper margin extending anteriorly which is a character of pachyrhizodontids and notelopids, but it does not extend dorsally above the ectopterygoid as seen in *Bavarichthys* and

Elops (Arratia and Tischlinger, 2010). Additionally, the symplectic does not articulate with the lower jaw in SMU 76938, a trait that is shared among crossognathiforms (Arratia and Tischlinger, 2010).

It is uncertain if the vertebral count has any taxonomic significance because the total number of vertebrae varies widely across crossognathiforms, especially pachyrhizodontids ranging 40–65 vertebrae (Arratia and Tischlinger, 2010). However, the exceptionally well-preserved caudal skeleton of SMU 76938 shares many unique characteristics with pachyrhizodontids. For instance, whereas the total number of hypurals varies across crossognathiforms, SMU 76938 has six or less, a trait of Pachyrhizodontidae, and its fused hypurals 1 + 2 are also a pachyrhizodontid characteristic. Additional unique features of pachyrhizodontids present in SMU 76938 are the presence six or less uroneurals (the first being forked anteriorly) and the presence of a hypurapophysis. The first uroneural reaching the second preural centrum in SMU 76938 is a trait that varies across crossognathiforms (Arratia and Tischlinger, 2010).

The retained tree from the phylogenetic analysis shows that SMU 76938 is nested within the family Pachyrhizodontidae (Fig. 6). This is more evident when examining the character traits of SMU 76938, sharing the most with *Rhacolepis* and *Goulmimichthys* among the taxa examined by Arratia and Tischlinger (2010). Between the two pachyrhizodontid genera, SMU 76938 is more closely related to *Rhacolepis* than *Goulmimichthys*. However, it should be noted that *Goulmimichthys* has more unknown character states compared to *Rhacolepis*, and such missing data could have impacted the results of the phylogenetic analysis (e.g., see Grande and Bemis, 1998).

Overall, there are many characters that are difficult to compare among pachyrhizodontids because many are incompletely known. Therefore, the phylogenetic analysis among all members of Pachyrhizodontidae is beyond the scope of this paper. Nevertheless, SMU 76938 is considered to represent a new genus and species within Pachyrhizodontidae. Table 1 lists seven selected characters and their condition in each of the 12 known pachyrhizodontid genera and in SMU 76938 (Fig. 7): 1) orbit small (<20% of total skull length); 2) infraorbital plate expanded; 3) infraorbitals 1 and 2 fused; 4) upper and lower jaws equally elongate; 5) villiform teeth present; 6) quadrate-mandibular articulation posterior to orbit; and 7) first uroneural reaching preural centrum 2. The combination of these characters sets SMU 76938 apart from all other pachyrhizodontids, but the presence of villiform teeth and that of fused infraorbital 1 and 2 are particularly decisive. Although I refrain from naming a new genus and a new species in this present work, I here provide the diagnosis for this new taxon:

Order Crossognathiformes Taverne, 1989

Family Pachyrhizodontidae Cope, 1872

Undescribed new genus and species

The following characters are collectively considered to be a diagnosis for the new genus and species (autapomorphies identified with an asterisk in brackets): orbit small, approximately 19% of skull length; infraorbital plate expanded posteriorly, reaching both preopercle and opercle; infraorbitals 1 and 2 fused [*]; supramaxilla long, about 50% of maxilla; elongate maxilla bearing numerous villiform teeth [*]; premaxilla bearing numerous villiform teeth [*];

elongate lower jaw bearing numerous villiform teeth [*]; quadrate-mandibular articulation positioned posterior to orbit; and first uroneural reaching preural centrum 2.

Paleobiological Inferences

SMU 76938 was discovered within the Tarrant Formation (middle Cenomanian), represented by buff muds (sandy clay) and shales with thin interbedded limestone. The stratigraphy is indicative of a marine, near shore environment (no more than 10 km offshore) of the East Texas Embayment that connected to the Western Interior Seaway where the shorelines experienced multiple regressions and transgression during the Late Cretaceous (Welton and Farish, 1993; Jacobs et al., 2005b).

Figure 8A shows my restoration of SMU 76938 in life that measured approximately 1.2 m in total length (cf. Fig. 2). The exact swimming speed and extent of maneuverability are difficult to ascertain from skeletal morphology alone. However, the caudal fin of SMU 76938 is large, symmetrically forked, and homocercal with a wide surface area (Fig. 5D) that suggests that the fish was likely capable of powerful thrusts that passes directionally through the vertebral axis with potential for quick maneuverability (Lauder, 1989, 2000). Therefore, SMU 76938 was likely a fast open-ocean swimmer capable of quick bursts of speed in order to successfully feed and support its large size.

No visible remains that can be interpreted to represent stomach content was found in SMU 76938 (Fig. 2). However, numerous small villiform teeth observed in SMU 76938 (Fig. 4B, C) are reminiscent of teeth in some fast-swimming extant bony fishes, such as scombrids and billfishes that feed on smaller, fast swimming prey such as fishes, squids, and shrimp (Collette

and Nauen, 1983; Nakamura, 1985). Given the predator-like mouth and size of SMU 76938, it must have occupied the Cenomanian ocean with a plethora of smaller fishes. Although SMU 76938 was a relatively large fish, the oceans at that time were home to apex predators of enormous sizes. Large contemporaneous marine predators that could have sought the fish represented by SMU 76938 as prey include aquatic reptiles such as plesiosaurs, large fishes such as *Xiphactinus*, and a variety of sharks such as *Cretoxyrhina* and *Cretodus* (Cumbaa et al., 2010; Jacobs et al., 2013). Whereas SMU 76938 was likely a mesopredator capable of predating fast-moving prey, its fusiform body with a large caudal fin likely allowed the fish a fast swimming ability (e.g., Webb, 1982) that also likely aided in avoiding being consumed by larger predators.

To examine the ontogenetic pattern based on the vertebrae in SMU 76938, I measured the distance of each of the 14 major annuli (growth rings: Fig. 8B) from the center of the vertebra, the centrum radius (CR), that formed the basis of my TL extrapolation when each annulus formed (Table 2). I also measured the distance between each annulus and its immediately previous annulus (i.e., AI: Table 2). I then assumed that the outer-most 14th annulus formed when the individual was 119 cm TL. Next, the CR value for the 14th annulus, 11.2 mm, was considered 100%, and the percent distance of all other annuli, each from the center of the vertebra (pCR), was obtained (Table 2). Then, the estimated TL (eTL) of the fish at each annulus position (or at the time of each annulus formation) was calculated according to each respective pCR value (Table 2). The TL and eTL, along with each of their corresponding annuli, were applied to the von Bertalanffy growth function (VBGF: Bertalanffy, 1938), a common quantitative method used to describe the growth of fishes (e.g., Chen et al., 1992; Quinn and Deriso, 1999; Newbrey and Wilson, 2005; Khan et al., 2019).

The VBGF parameters for SMU 76938 were obtained through the Desmos Inc. graphing software (www.desmos.com) using the following form of VBGF describing the length (L) as a function of the age of the fish (t): $L(t) = L_{\infty} (1 - e^{-k(t-t_0)})$, where L_{∞} is the estimate of asymptotic maximum length, k the rate constant with units of reciprocal time (i.e., time it takes for a fish in a population reaching near its mean maximum length), and t_0 the theoretical time at zero length. Strictly speaking, data for the VBGF analysis must be taken from multiple specimens that are randomly sampled from a population for independent measurements. Measurements taken from one vertebra here provide dependent measurements, so the statistical operations in my study must be viewed experimental with a hypothetically supposition that the 14 annulus-TL pairs (Fig. 8B; Table 2) were obtained from 14 different, randomly sampled individuals. With this supposition, Figure 8C shows the VBGF experimentally fitted to the data to correlate the annulus numbers (= age in years) with TL values using the least squares method (non-linear regression: $R^2 = 99.9\%$). Parameter estimates for the function are 180.753 cm TL for L_{∞} , and 0.0817 yr^{-1} for k . The function would yield an unrealistic (i.e., -7.066 cm TL) length at birth (L_0) that is commonly calculated for elasmobranchs (e.g., Cailliet and Goldman, 2004; Goldman, 2004). However, if the value along with the other two VBGF parameter estimates are applied to Natanson et al.'s (2006) equation for the estimated age at 95% of L_{∞} , $Longevity = (1/k)\ln\{(L_{\infty} - L_0)/[L_{\infty}(1 - x)]\}$ where $x = L(t)/L_{\infty} = 0.95$, the estimated longevity for SMU 76938 is calculated to be about 37 years. Whereas my growth model suggests that the species could have theoretically reached up to about 180 cm TL based on L_{∞} , such large, old individuals must have been exceptionally rare, if any.

CONCLUSION

The goals of this study were to describe SMU 76938, determine its phylogenetic affinity and taxonomic identity, and elucidate its lifestyle. After mechanical preparation of the specimen, photographs and line drawing illustrations of SMU 76938 provided a clear interpretation of skeletal elements and formed the basis for comparison to other fossil fishes. My phylogenetic analysis was based on 142 of the 193 morphological characters used in Arratia and Tischlinger's (2010) study on the systematic relationships of crossognathiforms. *Pholidophorus* was used as the outgroup to the ingroup that consisted of *Leptolepis*, *Tharsis*, *Ascalabos*, the Osteoglossomorphs, Euteleostei, Ostarioclupeomorpha, Elopiformes, Ichthyodectiformes, and Crossognathiformes; including Varasichthyidae, *Chongichthys* (Chongichthyidae), *Bavarichthys* (Family indet.), *Notelops* (Notelopidae), *Crossognathus* and *Apsopelix* (Crossognathidae), and *Goulmimichthys* and *Rhacolepis* (Pachyrhizodontidae) and SMU 76938.

My phylogenetic analysis shows that SMU 76938 belongs to the family Pachyrhizodontidae (Fig. 6). SMU 76938 has villiform dentition and a fusion between infraorbitals 1 and 2. These features are not seen in any other pachyrhizodontids, strongly supporting its assignment as a new genus and species within Pachyrhizodontidae. As of now, SMU 76938 is the only known specimen and representative of this new taxon.

SMU 76938 was likely an open-ocean swimmer, capable of maneuverability and powerful thrusts of speed based on its caudal fin morphology. When comparing the size of SMU 76938 to fauna of its time, it can be considered a mesopredator (predator of smaller organisms yet was also preyed upon). For this reason, SMU 76938 would have needed to be capable of high propulsion for not only food capture, but predator avoidance as well (Webb, 1982). The dental

morphology of SMU 76928 is like that of similar extant fishes, indicative of a grasping-like mechanism for acquiring quick-swimming prey. No stomach content is preserved, but it most likely fed upon smaller fishes, squid, and crustaceans of its time. Whereas the individual represented by SMU 76938 was about 1.2 m TL and 14 years old, my vertebra-based growth model suggests that the species could have lived up to about 1.8 m TL and 37 years old in age.

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TABLE 1. List of selected characters and their condition in each of the 12 known genera of the family Pachyrhizodontidae and in SMU 76938. Characters (Char.): A, orbit small (<20% of total skull length); B, infraorbital plate expanded; C, infraorbitals 1 and 2 fused; D, upper and lower jaws equally elongate; E, villiform teeth present; F, quadrate-mandibular articulation posterior to orbit; G, first uroneural reaching preural centrum 2. Abbreviations: Apr, *Apricenapiscis*; Aqu, *Aquilopiscis*; Elo, *Elopopsis*; Gre, *Greenwoodella*; Gou, *Goulmimichthys*; Mic, *Michin*; Mot, *Motlayoichthyys*; Nar, *Nardopiscis*; Pac, *Pachyrhizodus*; Pla, *Platinx*; Rha, *Rhacolepis*; Tin, *Tingitanichthys*; SMU, SMU 76938. Sources: Taverne, 1973; Taverne, 1991; Cavin, 2001; Alvarado-Ortega et al., 2008; Arratia, 2008; Cumbaa and Murray, 2008; Taverne, 2008; Taverne, 2013; Murray and Cumbaa, 2015; Arratia et al., 2018; this study for SMU 76938.

Char.	Apr	Aqu	Elo	Gre	Gou	Mic	Mot	Nar	Pac	Pla	Rha	Tin	SMU
A	No	No	No	No	Yes	Yes	Yes	No	No	No	Yes	No	Yes
B	No	Yes	No	Yes	Yes	Yes	Yes	Yes	Yes	No	Yes	No	Yes
C	No	?	No	No	No	No	No	No	No	No	No	?	Yes
D	Yes	Yes	Yes	?	Yes	No	No	?	Yes	Yes	Yes	No	Yes
E	No	No	No	?	No	No	No	No	No	No	No	No	Yes
F	Yes	No	Yes	Yes	Yes	Yes	Yes	No	Yes	No	Yes	Yes	Yes
G	?	Yes	Yes	?	No	Yes	?	?	No	No	No	No	Yes

TABLE 2. Raw measurements (annuli, CR, and BI) taken from vertebra of SMU 76938 and derived measurements (pCR and TL; see text for explanation). Abbreviations in listed sequence: CR, centrum radius at each annulus; AI, annulus interval from previous annulus; pCR, percent centrum radius from center of vertebra; eTL, estimated total length of entire fish, except value in asterisk (*) that is raw TL measurement.

Annulus	CR (mm)	AI (mm)	pCR (%)	eTL (cm)
1	0.8	-	7.1	8
2	2.1	1.3	18.8	22
3	3.2	1.1	28.6	34
4	4.2	1.0	37.5	45
5	5.1	0.9	45.5	54
6	6.0	0.9	53.6	64
7	7.0	1.0	62.5	74
8	7.9	0.9	70.5	84
9	8.7	0.8	77.7	92
10	9.3	0.6	83.0	99
11	10.0	0.7	89.3	106
12	10.4	0.4	92.9	111
13	10.8	0.4	96.4	115
14	11.2	0.4	100	119*

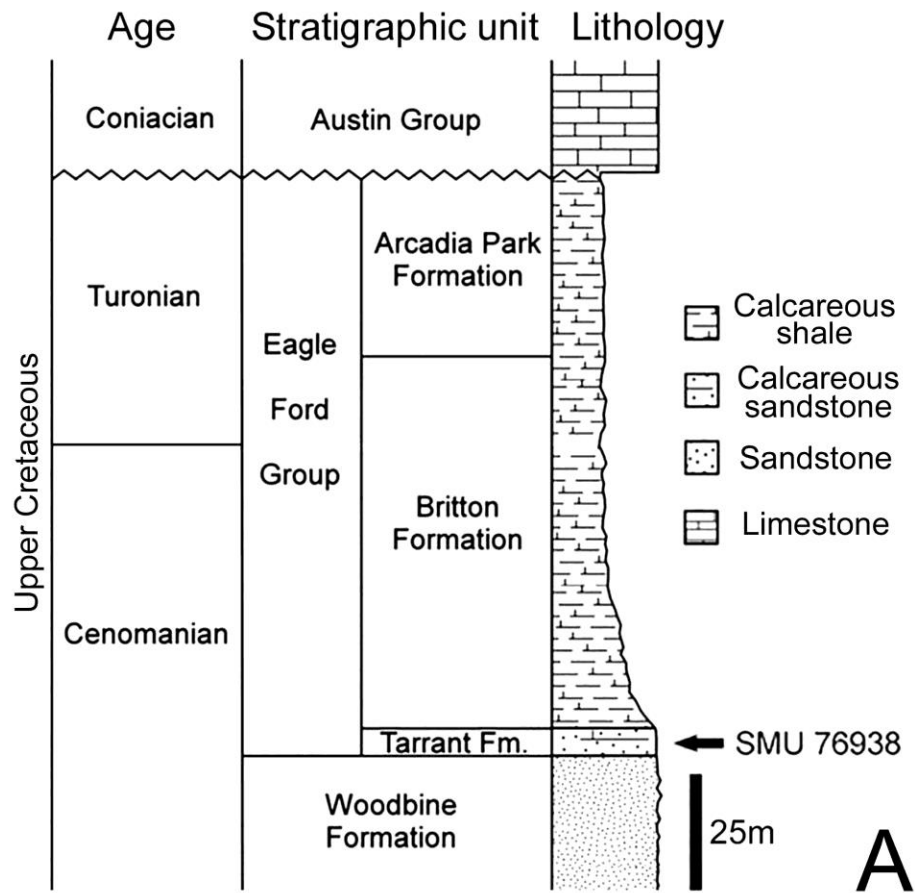
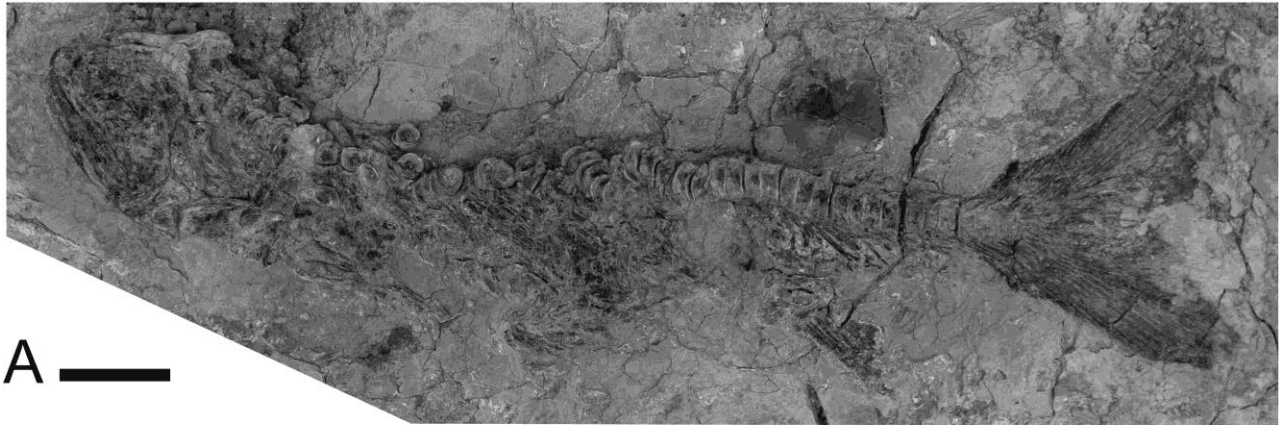
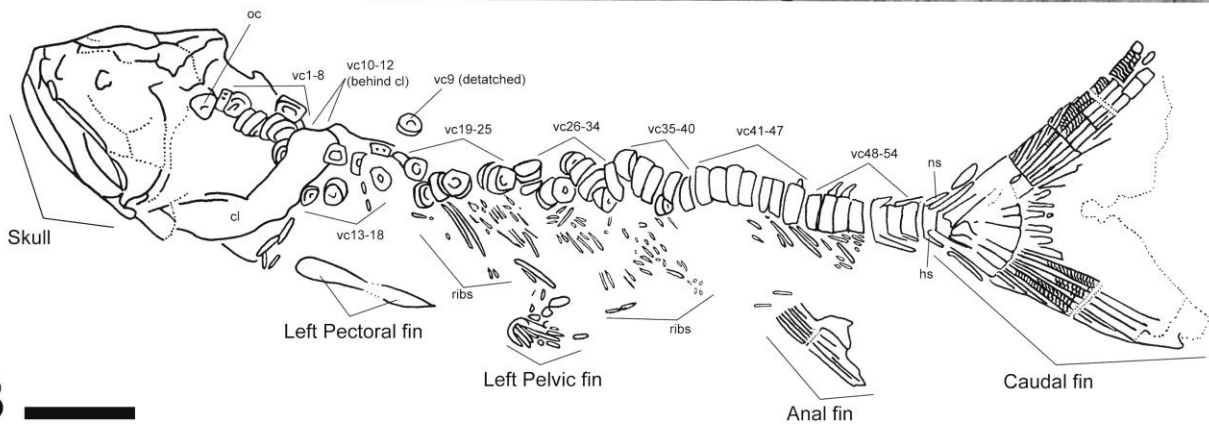


FIGURE 1. Stratigraphy and locality of the fossil fish specimen (SMU 76938) discussed in this study. A, stratigraphic column showing the Tarrant Formation of the Upper Cretaceous Eagle Ford Group in Texas (after Myers, 2010); B, map of the United States highlighting Texas (gray area) and the locality of SMU 76938.



A



B

FIGURE 2. Nearly complete bony fish skeleton (SMU 76938) from Upper Cretaceous Tarrant Formation in Tarrant County, Texas, U.S.A. A, photograph of the entire specimen; B, line drawing of the entire specimen showing identified skeletal elements (cf. Figure 2A). Abbreviations: cl, cleithrum; hs, haemal spine; ns, neural spine; oc, occipital condyle; vc, vertebral centra. Scale bars = 10 cm.

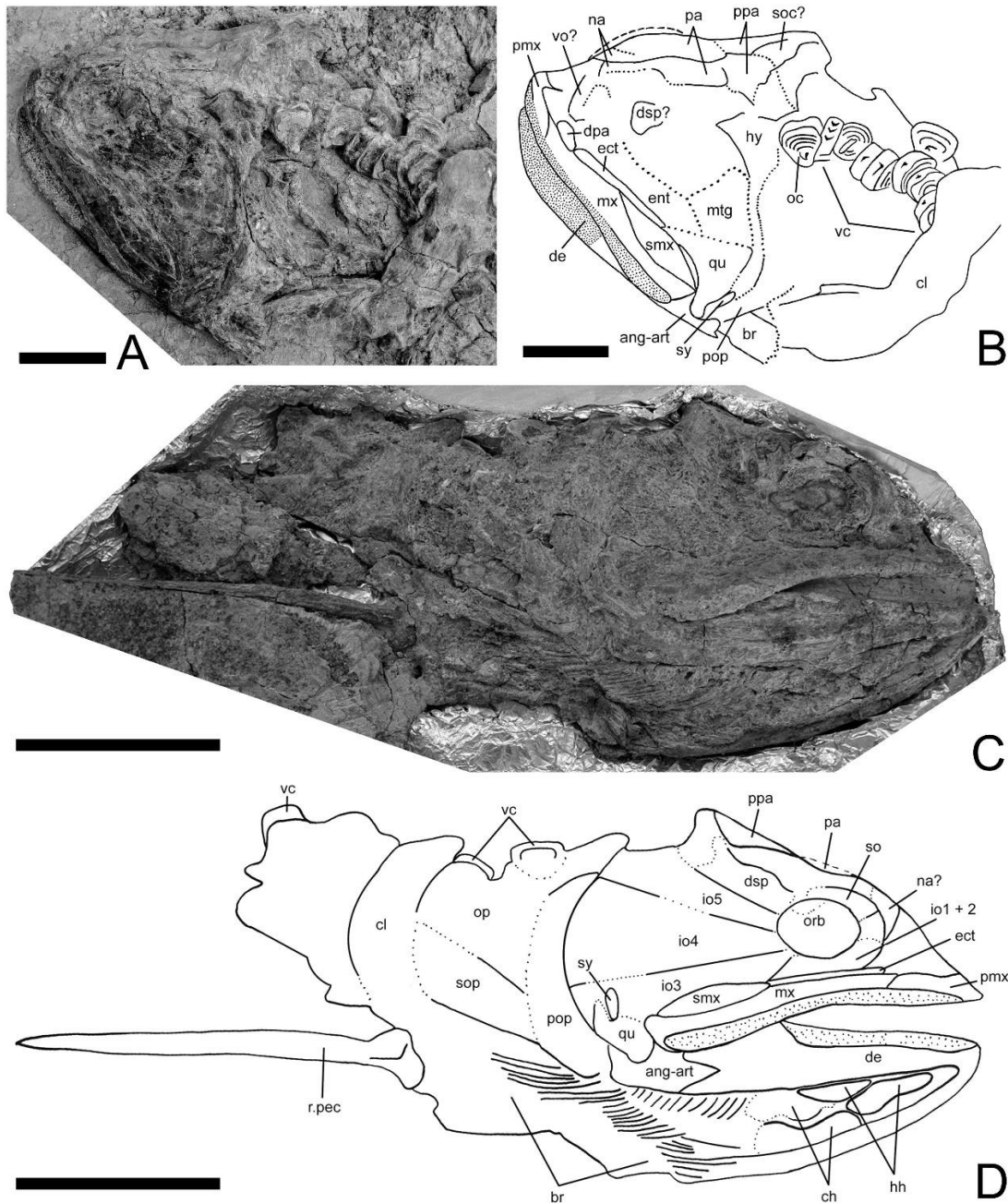


FIGURE 3. Cranial region of SMU 76938. A, photograph in left lateral view; B, line drawing of left lateral view showing identified anatomical features; C, photograph in right lateral view; D, line drawing of right lateral view. Abbreviations: ang-art, angular-articular; br, branchiostegals; ch, ceratohyals; cl, cleithrum; de, dentary; dpa, dermopalatine; dsp, dermosphenotic; ect, ectopterygoid; ent, entopterygoid; hh, hypohyals; hy, hyomandibula; io 1–5, infraorbital 1–5; mtg, metapterygoid; mx, maxilla; na, nasals; oc, occipital condyle; orb, orbit; op, opercle; pa, parietals; pmx, premaxilla; pop, preopercle; ppa, postparietals; qu, quadrate; r.pecf, right pectoral fin; smx, supramaxilla; so, supraorbital; soc?, supraoccipital(?); sop, subopercle; sy, symplectic; vc, vertebral centra; vo?, vomer(?). Scale bars = 5 cm in A, B; 10 cm in C, D.

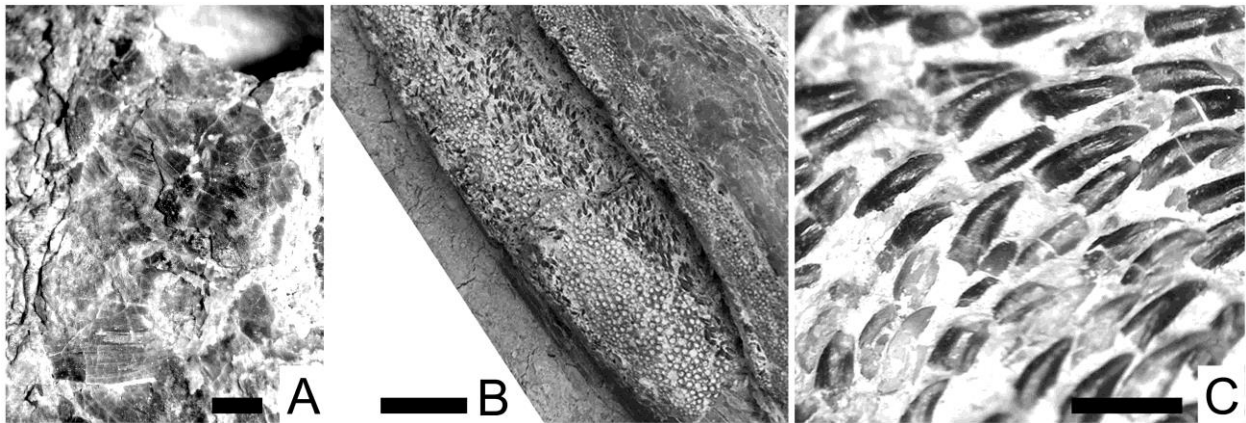


FIGURE 4. Close-up views of scales and dentition in SMU 76938. A, cycloid scales throughout the body; B, the jaws in left lateral view; C, numerous small conical teeth and acrodontous alveoli of the left jaws. Scale bars = 2 mm in A, C; 10 mm in B.

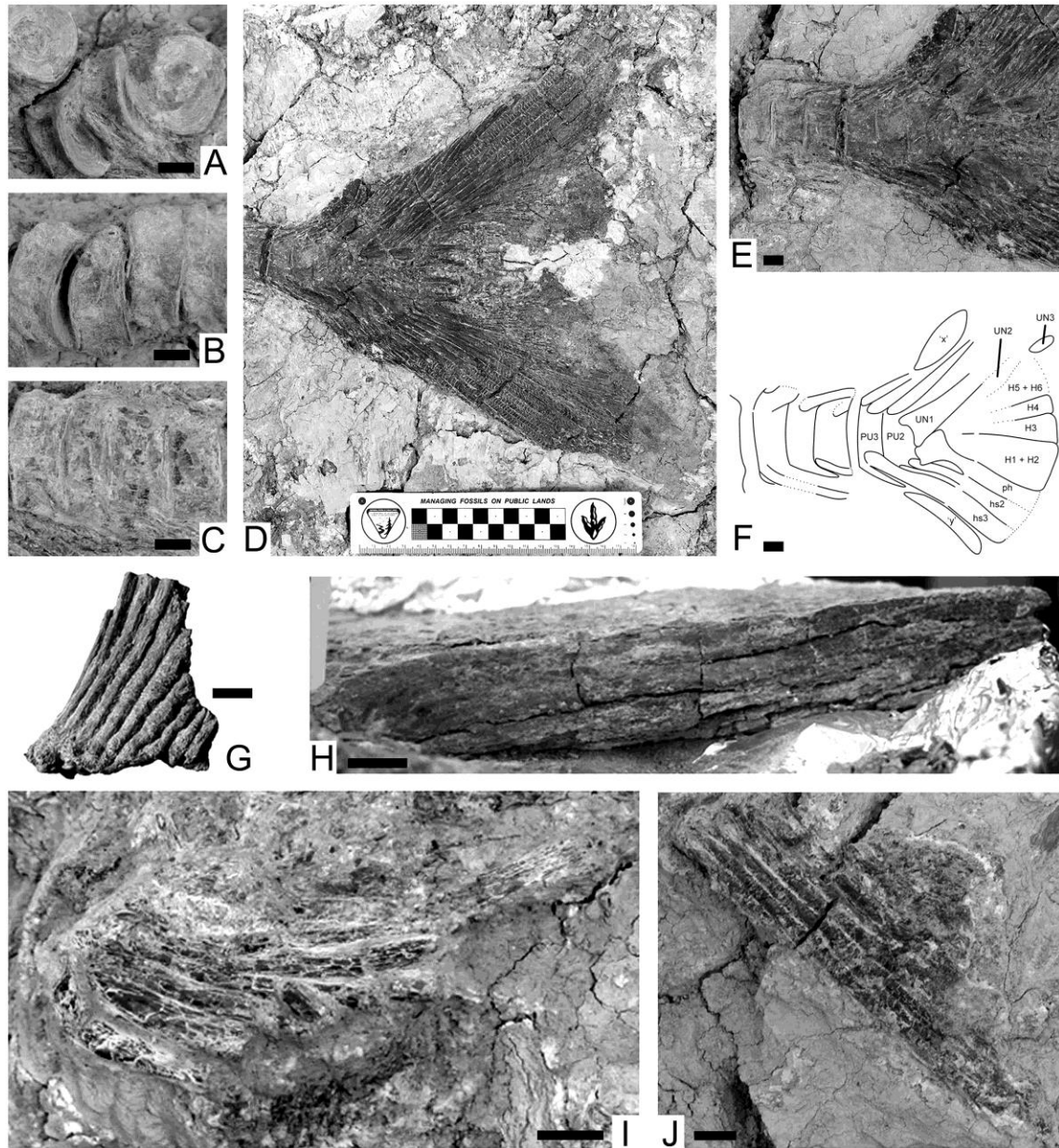


FIGURE 5. Vertebrates and fins of SMU 76938. A, anteriorly-located (20th–23rd) vertebrae showing articular view; B, medially located, (39th–42nd) vertebrae showing lateral-dorsal view; C, posteriorly located, non-caudal (48th–51st) vertebrae showing lateral view; D, full view of caudal fin (note soft tissue outline along its posterior edge); E, close-up view of caudal fin base; F, line drawing of caudal fin base showing identified skeletal elements; G, partial dorsal fin (float) in lateral view; H, right pectoral fin in lateral view; I, left pelvic fin in lateral view; J, anal fin in lateral view. Abbreviations: H1–6, hypural 1–6; hs 2–3, haemal spine of preural centrum 2–3; ph, parhypural; PU 2–3, preural centrum 2–3; UN 1–3, uorneural 1–3; ‘x’, unidentified ossification ‘x’; ‘y’, unidentified ossification ‘y’. Scale bars = 10 mm in 6A–C, E–J.

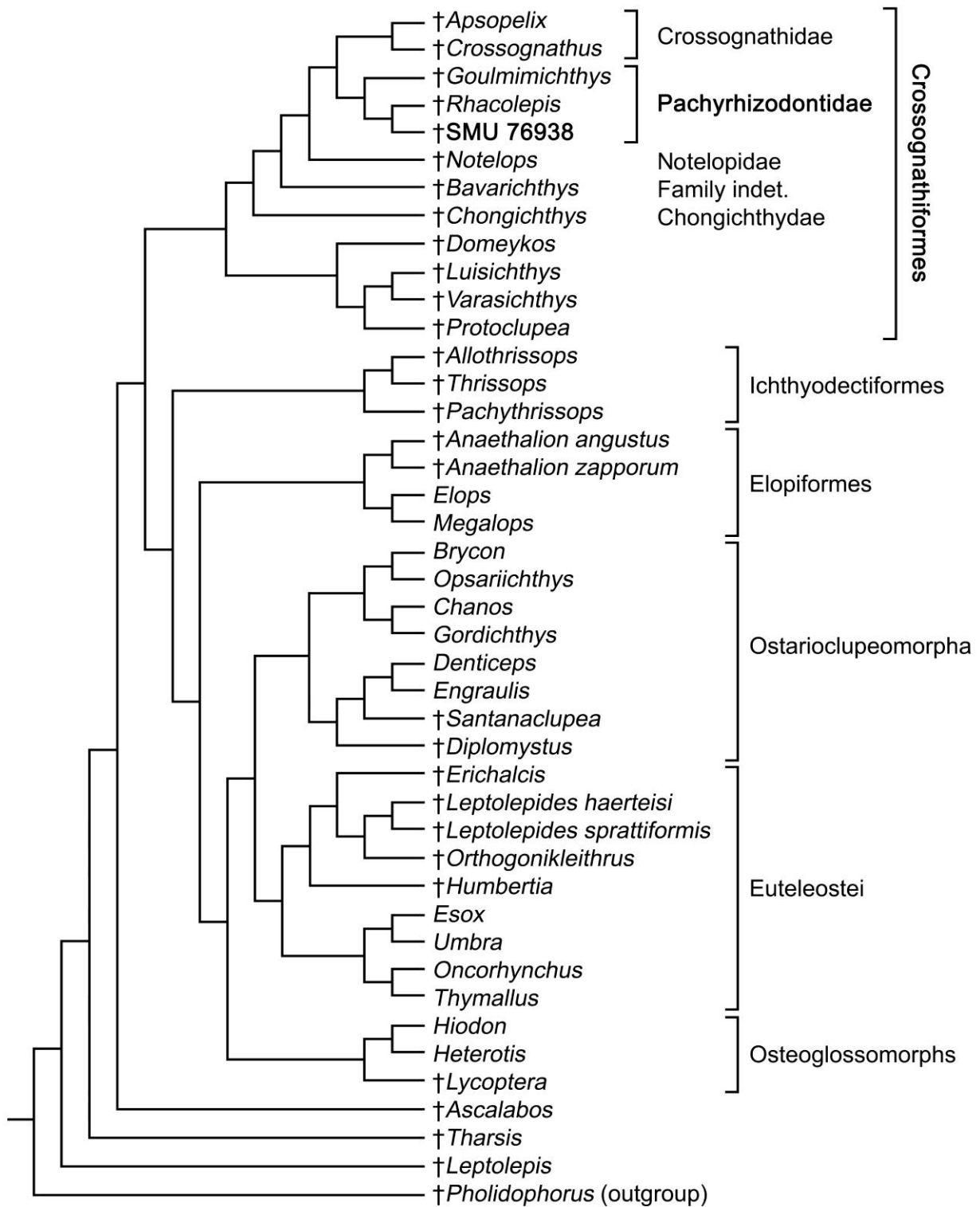


FIGURE 6. Tree displaying phylogenetic relationship of SMU 76938 and other teleost fishes. Made with Mesquite: a modular system for evolutionary analysis, Version 3.51; and PAUP* (Phylogenetic Analysis Using Parsimony* and other methods) Version 4.0a165.

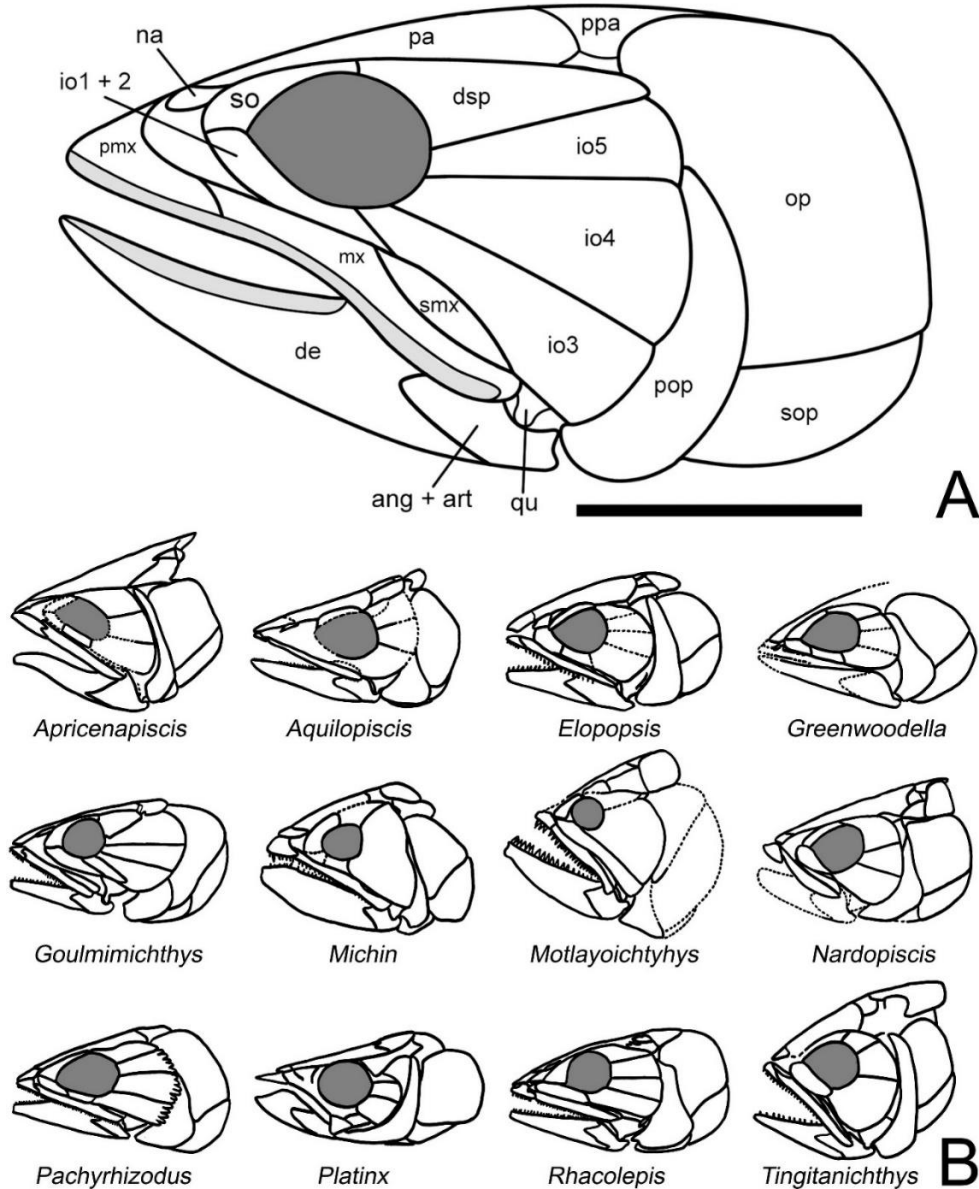


FIGURE 7. Pachyrhizodontidae heads in left lateral view. A, cranial reconstruction based on SMU 76938 in left lateral view; B, cranial reconstruction of other 12 Pachyrhizodontidae genera in left lateral view (skulls not to scale): *Apricenapiscis* (from Taverne, 2013:fig. 3), *Aquilopiscis* (from Cumbaa and Murray, 2008:fig. 7), *Elopopsis* (from Cavin, 2001:fig. 13), *Greenwoodella* (from Taverne, 1991:fig. 1), *Goulmimichthys* (from Arratia et al., 2018:fig. 10), *Michin* (from Alvarado-Ortego et al., 2008:fig. 2), *Motlayoichthys* (from Arratia et al., 2018:fig. 5), *Nardopiscis* (from Taverne, 2008:fig. 3), *Pachyrhizodus* (from Arratia et al., 2018:fig. 10), *Platinx* (from Cavin, 2001:fig. 13), *Rhacolepis* (from Arratia et al., 2018:fig. 10), *Tingitanichthys* (from Cavin, 2001:fig. 13). Abbreviations: ang-art, angular-articular; de, dentary; dsp, dermosphenotic; io 1–5, infraorbital 1–5; mx, maxilla; na, nasal; op, opercle; pa, parietal; pmx, premaxilla; pop, preopercle; ppa, postparietal; qu, quadrate; smx, supramaxilla; so, supraorbital; sop, subopercle. Scale bar = 10 cm in 7A.

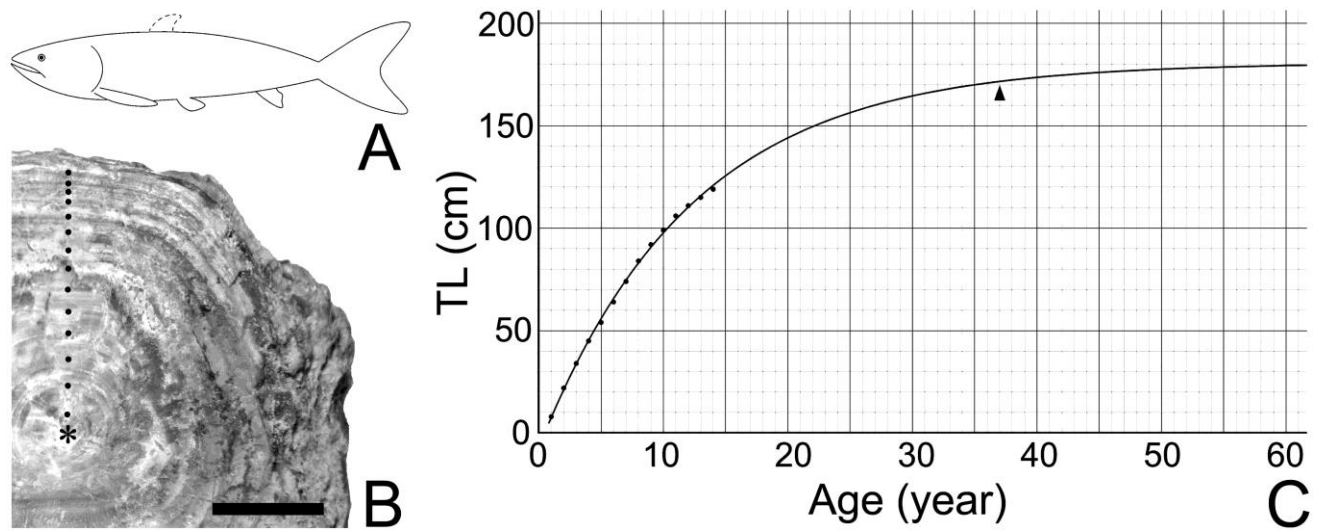


FIGURE 8. Full body restoration and growth analysis of SMU 76938. A, full body outline restoration of a new 1.2-m-long pachyrhizodontid fish in left lateral view based on SMU 76938; B, vertebra of SMU 76938 with interpreted annual growth annuli marked by dots (asterisk indicates center of centrum); C, von Bertalanffy growth function model of SMU 76938 based on vertebral growth annuli (Fig. 8B; Table 2) where calculated theoretical longevity of the fossil fish is indicated by triangle; see text.

APPENDIX 1. List of 142 of 193 morphological characters from Arratia and Tischlinger (2010) study, where [0] represents the plesiomorphic character state and [1], [2], [3], and [4] the apomorphic character states (see text for excluded characters and their rationales). Number in parentheses immediately after each character number indicates original character number used by Arratia and Tischlinger (2010), where each asterisk (*) signifies character in which its original coding needed to be modified because of the use of *Pholidophorus* as outgroup that received coding of "0" for all 142 characters in the present study. Double asterisks (**) indicate characters involved in deletion of one or more character states.

1. (1) Ethmopalatine ossification in the floor of the nasal capsule articulating with autopalatine: absent [0]; present [1].
2. (2) Two paired endoskeletal ethmoidal ossifications: absent [0]; present [1].
3. (5) Basisphenoid: present [0]; absent [1].
4. (6) Sutures between cartilage bones in the braincase retained throughout life, rather than being lost ontogenetically: absent [0]; present [1].
- 5 (7) Suture between parietal bones (= so-called frontals) smooth (sutura armonica): present [0]; absent [1].
6. (8) Orbitosphenoid bone: reduced or absent [0]; large [1].
7. (9) Orbitosphenoid partially or completely reaching the parasphenoid ventrally: absent [0]; present [1].
8. (10) Parasphenoid: with small teeth [0]; toothless [1]; with large teeth [2].
9. (11) Parasphenoid long, extending posterior to basioccipital: absent [0]; present [1].
10. (12) Ossified aortic canal: present [0]; absent [1].
11. (13) Canals for occipital arteries in basioccipital bone: present [0]; absent [1].
12. (14) Spiracular canal: well developed [0]; greatly reduced [1]; absent [2].
13. (15) Posterior myodome: bone-enclosed [0]; opens posteriorly [1].
14. (16) Recessus lateralis: absent [0]; present [1].
15. (17) Otophysic connection involving a diverticulum of the swimbladder that penetrates the exoccipital and extends into the prootic within the lateral wall of the braincase: absent [0]; present [1].
16. (18) Pre-epiotic fossa: absent [0]; present [1].
17. (19) Foramen for glossopharyngeal nerve in exoccipital: absent [0]; present [1].
18. (20) Foramen for vagus nerve placed in posterolateral face of exoccipital alone: absent [0]; present [1].
19. (21) Cephalic sensory canal components: continuous [0]; interrupted between them [1].
20. (22) Cephalic sensory canals with: branched tubules [0]; simple tubules [1]; reduced or no tubules [2].
21. (23) Antorbital bone: carrying a portion of the infraorbital canal [0]; without sensory canal [1].
22. (24) An ethmoidal commissure that penetrates and passes through the whole width of a broad mesethmoid: absent [0]; present [1].
23. (25) Middle pit-line groove crossing the dermopterotic (or pterotic): present [0]; absent [1].
24. (26) Supratemporal commissure (primitively) passing through postparietals or through postparietals (= so called parietal) and supraoccipital: absent [0]; present [1].

25. (27) Ankylosis or fusion between the mesial extrascapula and postparietal alone or postparietal (= so-called parietal) and supraoccipital; absent [0]; present [1].
26. (28) A narrow tube-like infraorbital 1 or a broad antorbital plus infraorbital 1 combined with enlarged bone(s) representing the third and fourth and/or fourth and fifth of other teleosts: absent [0]; present [1].
27. (29) Fourth and fifth infraorbital bones: separate [0]; fused forming an expanded bone [1].
28. (30*) Suborbital bone(s): one [0]; two or three [1]; none [2].**
29. (31) Supraorbital bone(s): more than two [0]; two [1]; one [2].**
30. (32) Large supraorbital bone with expanded anteroventral portion: absent [0]; present [1].
31. (33) Comma-shaped antorbital bone: absent [0]; present [1].
32. (34) Toothed dermopalatine bone(s): present [0]; absent [1].
33. (35) Autopalatine bone: ossifies late in ontogeny [0]; ossifies early in ontogeny [1].
34. (36) Elongation of suspensorium: “normal”, no special elongation [0]; parasagittal elongation due to separation between quadrate and hyomandibula and elongation of symplectic [1]; partial elongation due to enlargement of quadrate and symplectic and the separation between the long and narrow ventral part of the hyomandibula and symplectic [2].
35. (37) Elongation of the suspensorium due to the ventroposterior inclination of the hyomandibula: absent [0]; present [1].
36. (38) Hyomandibular bone with a preopercular process at its posterior margin: absent [0]; present [1].
37. (39) Elongate lower jaw bearing numerous villiform teeth: absent [0]; present [1].
38. (40) Upper and lower jaws: with teeth [0]; without teeth [1].
39. (41) Very broad, concave-convex premaxilla: absent [0]; present [1].
40. (42) Articular process of maxilla very long and irregularly shaped: absent [0]; present [1].
41. (43) Dentated maxilla: present [0]; absent [1].**
42. (45) Quadrate-mandibular articulation: posterior to orbit [0]; placed below the posterior half of orbit [1]; below anterior half of orbit [2]; anterior to orbit [3].
43. (46) Retroarticular bone: included in the joint facet for quadrate [0]; excluded from the joint facet for quadrate [1].**
44. (47*) Articular bone: fused with both angular and retroarticular bones [0]; fused with angular [1]; not fused to angular and retroarticular [2].**
45. (48) Postarticular process of lower jaw: poorly developed [0]; well developed, extending posterior to the articular facet for quadrate [1].
46. (49) Characteristic notch (so-called leptolepid notch) in the deep dorsal ascending margin of the dentary: absent [0]; present [1].
47. (50) Posterior opening of the mandibular sensory canal: placed medial or posterior to angular portion of the jaw [0]; placed lateral to the angular portion of the jaw [1].
48. (51) Posterior section of the mandibular canal: present [0]; absent [1].
49. (52) Mandibular canal enclosed in bone along the whole lower jaw: present [0]; or mandibular canal partially running in a tube bone and a groove [1].
50. (54) Gular plate: present [0]; absent [1].
51. (62) Suprapreopercle: absent [0]; present [1].
52. (63) Ventroposterior (excluding dorsal limb) region of preopercle: narrow or slightly expanded [0]; broadly expanded [1].
53. (64) Preopercular sensory canal with many tubules in ventral limb reaching ventral and ventroposterior margin of the bone: absent [0]; present [1].

54. (65) Preopercular sensory canal with four or fewer short and simple tubules placed in the ventral limb of the bone: absent [0]; present [1].
55. (66) Distinctively enlarged preopercle with a long ventral arm: absent [0]; present [1].
56. (67) Irregular parallelogram, or oval, or kidney-shaped opercular bone: absent [0]; present [1].
57. (69) Each vertebral centrum of the caudal region of adult individuals formed by: mineralized chordacentrum and arcocentra [0]; chordacentrum and basal part of arcocentra surrounded by autocentrum [1]; basal part of arcocentra surrounded by autocentrum [2].
58. (70) Vertebral autocentra: absent [0]; present: thin and smooth [1]; or thick and sculptured [2]; or thick and smooth [3].
59. (71) Vertebral autocentrum: absent [0]; present: without cavities for adipose tissue [1]; with cavities for adipose tissue [2].
60. (72) Vertebral autocentra: absent [0]; not constricting the notochord [1]; strongly constricting the notochord [2].
61. (73) Neural arches of the abdominal region: not fused to the centra [0]; fused, except for the first five or six [1].
62. (74) Dorsomedial portions of the anterior neural arches expanded and abutting against each other and the posterior margin of the exoccipital; absent [0]; present [1].
63. (75) Neural arches of most abdominal vertebrae: with separate halves of the neural arch [0]; with fused halves of the neural arch forming a median neural spine [1].
64. (76) Anterior pleural rib, on third vertebra, is distinctly larger than the next few ribs: absent [0]; present [1].
65. (80) In adult individuals, elongate, solid epineural processes of neural arch of abdominal vertebrae: absent [0]; present [1]; another condition: a separate bone joined to the neural arch by a ligament [2].
66. (81) Epipleural intermuscular bones: absent [0]; few bones in the anterior caudal region only [1]; many bones developed in the abdominal and anterior caudal region [2].
67. (82) Complex epipleural bones: absent [0]; present [1].
68. (83) Series of dorsal intermuscular bones throughout caudal region: absent [0]; present [1].
69. (85) Postsupracleithrum(ra): absent [0]; present [1].
70. (86) Postcleithra: one to three [0]; four or more [1]; none [2].
71. (87) Coracoid bone enlarged ventrally meeting its fellow in a midventral coracoid symphysis: absent [0]; present [1].
72. (89) Pectoral axillary process: absent [0]; present; formed by small bony elements [1]; present; formed by an elongate bony element [2]; present; formed by modified scales [3].
73. (90) Pelvic axillary process: absent [0]; present; formed by an elongate bone [1]; present; formed by a combination of bony element(s) and modified scales [2]; present; formed by modified scales [3].
74. (91) Dorsal and anal fins posteriorly placed: absent [0]; present [1].
75. (92) Dorsal fin origin anterior to that of pelvic fin: absent [0]; present [1].
76. (93) Dorsal fin acuminate: absent [0]; present [1].
77. (94) Anal fin long, falcate, opposed by a short, remote dorsal fin: absent [0]; present [1].
78. (95) First anal pterygiophore placed posterior to fourth or fifth haemal spine: absent [0]; present [1].

79. (96) Preural vertebrae (without preural centrum 1) of adult individuals with haemal arches; autogenous [0]; laterally fused to their respective autocentra [1]; not fused laterally to their autocentra [2].
80. (97) Parhypural (in adults) with haemal arch: autogenous [0]; laterally fused to its autocentrum [1]; laterally not fused to its autocentrum [2].
81. (98) Hypurapophysis: absent [0]; present [1].
82. (99) Neural spine of vertebrae 5–3 distally expanded by fine anterior and posterior membranous outgrowths; absent [0]; present [1].
83. (100) Neural spines of at least preural vertebrae 4–2 with membranous outgrowths and leaf-like: absent [0]; present [1].
84. (101) Neural spine of preural vertebra 3: inclined toward the horizontal at an angle of less than 45 degrees in relation to the dorsal margin of the centra [0]; inclined toward the horizontal at an angle of over 45 degrees [1].
85. (102) Neural spine of preural centrum 2: shorter than neural spine of preural centrum 3 [0]; as long as neural spine of preural centrum 3 [1].**
86. (103) Neural spine of preural centrum 1: rudimentary or short [0]; long, close to, or reaching the dorsal margin of the body [1]; absent [2].
87. (104) Neural arch on preural centrum 1: present [0]; absent or atrophic [1].
88. (105) Neural spine of ural centra 1 and 2 or 'first' ural centrum: present [0]; absent [1]; other condition: preural centrum 1 fused with ural centrum(ra) [2].
89. (106) Neural arch of ural centra 1 and 2 or 'first' ural centrum: present [0]; absent [1].**
90. (107) Neural arch over 'first' ural centrum: complete [0]; reduced [1]; other condition: fusion of elements [2].
91. (109) A compound neural arch formed in a mass of cartilage over preural centrum 1 and ural centra: absent [0]; present [1].
92. (111) Number of epurals: four or more [0]; three [1]; two [2]; one [3]; none [4].
93. (114) Six or seven uroneurals, the first three or four extending anteroventrally to cover the entire lateral surface of the first, second and third preural centra: absent [0]; present [1].
94. (115) Uppermost uroneurals (= 5 to 7 of primitive teleosts) forming a series that overlaps and lies at an angle to, longer anterior ones: [0] absent; present [1].
95. (116*) First uroneural reaches: preural centrum 4 or 3 [0]; preural centrum 2 [1]; preural centrum 1 [2]; no uroneural present [3].**
96. (118) Number of hypurals in adult individuals: eight or more than eight [0]; seven [1]; six or less [2].**
97. (119) Only hypural 2 (between the lower set of hypurals) fused with 'first' ural centrum (diural terminology): absent [0]; present [1].
98. (120) Hypurals 1 and 2: independent from each other [0]; fused at their bases only [1]; fused to each other along their length [2].
99. (121) Both hypurals 1 and 2 associated by fusion or articulation with a 'compound centrum', apparently formed by preural centrum 1 and ural centrum(a): absent [0]; present [1].
100. (122) A space or diasteme between hypurals 2 and 3: absent [0]; present [1].**
101. (123) First uroneural (pleurostyle) fused with a 'compound centrum' apparently formed by preural centrum 1 and ural centrum(a): absent [0]; present [1].
102. (124) Stegural: absent [0]; present [1].
103. (125) Membranous outgrowth of stegural covering laterally the ventral tips of epurals: absent [0]; present [1].

104. (127) Small ‘urodermals’ associated with the uppermost principal caudal fin ray(s): none [0]; two or three [1]; one [2].
105. (128) Fringing fulcra preceding the first principal caudal fin ray: many [0]; one to five [1]; absent [2].
106. (129) Epaxial basal fulcra on the dorsal margin of the caudal fin: present [0]; absent [1].
107. (130) Proximity of the basal fulcra or dorsal precurrent (or procurrent) rays to: epurals and posterior uroneurals [0]; neural spines, epurals, and posterior uroneurals [1].**
108. (131) Long dorsal segmented precurrent (or procurrent) ray(s); absent [0]; present [1].
109. (132) Number of principal caudal rays: twenty or more [0]; nineteen [1]; less than nineteen [2].
110. (133*) Lower lobe of the caudal fin with: more than nine principal rays [0]; nine principal rays [1]; less than nine principal rays [2].**
111. (134) Branched rays of the caudal fin: more than 16 [0]; 16 or less [1].
112. (135) Bases of the dorsalmost principal rays of the caudal fin crossing obliquely over the entire upper hypural series (save the last); present [0]; absent [1].
113. (136*) Dorsal processes of the bases of the innermost principal caudal rays of upper lobe: present [1]; absent [0].
114. (137) Marginal principal caudal rays with: Z-like or step-like segmentation [0]; straight segmentation [1].
115. (138) One or more abdominal scutes, each of a single element, which crosses the ventral midline of the fish: absent [0]; present [1].
116. (139) Dorsal scute(s) preceding caudal fin: present [0]; absent [1].
117. (142) Cycloid scales: absent [0]; present [1]; other condition: without scales [2].
118. (143) Cycloid scales posterior to the pectoral girdle with circuli crossed by transverse lines in the middle field: absent [0]; [present [1]].**
119. (144) Cycloid scales with crenulate posterior margin: absent [0]; present [1].**
120. (148) Adipose fin: absent [0]; present [1].
121. (149) Primary bite between parasphenoid and basihyal: absent [0]; present [1].
122. (151*) Posterior margin of maxilla: convexly rounded or straight [0]; concave or at least notched [1]; sharp [2].
123. (155) Number of ossified ural neural arches: more than two [0]; two [1]; one or none [2].
124. (157) Number of independent ural centra (in adults): more than two [0]; two or one [1]; no ural centra [2].
125. (158) First two hypurals supported by a single centrum: absent [0]; present [1]; fusion of elements [2].
126. (161) Urohyal formed as an unpaired tendon-bone: absent [0]; present [1].
127. (164) Surangular bone in lower jaw: present [0]; absent [1].
128. (165*) Posterior myodome: extending in basioccipital [0]; not extending into basioccipital (e.g., in prootic) [1].**
129. (177) Large, roofed posttemporal fossa framed by the epiotic, pterotic, exoccipital, and intercalar: absent [0]; present [1].
130. (178) Large, well-developed extrascapular bone extending caudally close to the posterior margin of opercle: absent [0]; present [1].
131. (179) Circumorbital ring: incompletely closed [0]; completely closed ring, no space left between bones [1].
132. (180) Dermosphenotic: small [0]; very large, well-developed bone [1].

133. (181) Independent antorbital bone: present [0]; absent [1].
134. (182) Posterior infraorbital bones: small and not overlapping or slightly overlapping the anterior margin of preopercle [0]; expanded posterior infraorbitals overlapping the anterior margin of preopercle [1].
135. (183) Condition of skull roof: mediopostparietal [0]; lateropostparietal [1].
136. (184) Elongate maxilla bearing numerous villiform teeth: absent [0]; present [1].
137. (185*) Maxilla with a ventral margin: slightly convex [0]; straight or almost straight [1]; slightly concave [2].
138. (186) Quadrate with an almost straight upper margin extending anterodorsally above the ectopterygoid: absent [0]; present [1].
139. (188) Reticulated scales: absent [0]; present [1].
140. (190) Scaphium: absent [0]; present [1].
141. (191) Tripus: absent [0]; present [1].
142. (193) Uroneurals cover the lateral faces of the ural centra and first two preural centra: absent [0]; present [1].

APPENDIX 2. Character state values of SMU 76938 and 42 taxa of the 142 morphological characters for the data matrix used in the phylogenetic analysis.

Pholidophorus (outgroup)
00
00
0000000000000000

Apsopelix
00010?0111112?0001101?0100012?101?0000000020010000101000012220?00
12010?1??011001100000001010/000002000001?1111101000110?000??2?1?
1111?1001?0001

Allothrissops
11?100000??210001101101000021001?0010000010210000101000012220000
10000010010110220000100/000110000001000/210111000000100000211110
00110000000001

Anaethalion angustus
000100000??2?000??0101?000021000000?100001?010000000000012220000
12100?00?000001?000000?0??1?00?/01?10002111011011000101000?/1110
?00?0001?00000

Anaethalion zapporum
0001?0000??000??01?1?000021000?0001000010?100000000?0012220000
12000?00000000110000?00100?10?1??101000211101101?00010?00?21111?
?0?????1100000

Ascalabos
00?1?00?0??2?000??01?0?00002?????0000000010?11000100000012220000
110000000001001100000000000100000101000120011100000010?00021111?
?000?000000000

Bavarichthys
?0?1?001?????000??01-?10001211???00?100000??1000010000001222000?
1201000??00100110000?0010001001202010002101011001/00?????00211?1?
?1??1100210000

Brycon
0011-001011210001102101100022001110000001211001101000000?2221010
22110000?????0011000?00021001012200111000211111011100100?00?2-110
000?0010100110

Chanos

0011000101121000110110101002100111000111130001100110001012220111
22110201300000/21000120200030-220011100021111100100010100021-110
00000?10000000

Chongichthys

??01000101???00?1101??100?02?????000000?001210000100000012220000
11000?0?000100?????????????????????????????????????0?100002?????1?
?????11010000?

Crossognathus

00010001???2?0?0??010010001211?1?0??0000011100000/01000012220?00
12010?0?001?001100000001000/000002000001?11111010000100000212?1?
?11111001?0001

Denticeps

000101010112111011011011-002200010000000021110100100000022?21010
?2011000010000110000100101020-2210010000211121011111100000211111
00000010?00000

Diplomystus

00?100010112101111011010?002?00??000000001111?100100000012221000
1201?00000000011000110010?01002110010000211111011?1010000?211?10
00000010000000

Domeykos

00?1?0010??2?0001?01?0100?????????00?0??01?21?000101100012220000
11000101100?001100001000000000000101000??0010000000?111000111?1?
?1?????10000000

Engraulis

0001?00101121111110010111002200010100000001110100100000022221010
12011003?0000012100?100/1-02012?1001100021111101111110000021-110
00000010100000

Elops

000100000112100011000110000210000000100000001000000000012220000
1201010220010022100000000011001100010002211111011000101000111110
00110101110000

Erichalcis

00?10001?????000??01?01000021011?0000000011110100100000012220010
??0?000000??0122?10002011-010?12010001/2211111010100?00?00211?1?
??000?10000000

Esox

010101010112100011121010000210-010000?00101110111100010012220000
?201000001000022000012111-020-2200010100211111011101100000211110
00000010100000

Gordichthys

001??000?????000??010010?0021001?10?0111131101?00110001012?20101
1100000??00000?10000100001020-120001000021111100?10110?000211?1?
?0000010000000

Goulmimichthys

?0?1100101?2100011??-?1000021100?000000000?110?00101000012220000
1?000?0?001?0?111000??0??0?0-020201000?????????001??0?0??2110
111111101?000?

Hiodon

00011102011210001101-01001122000-0000000010210100100000112220010
120000023100001/0000110000030-1100010000211122111001100010111110
00001000101000

Heterotis

00110001011200001101-01001122000-0000000020210100100000111?21010
1200000??1000012000011000004003200010000211122111101100010??1111
00001000101000

Humbertia

0001?101011210001101101000021010?0000001011110100100000012?20000
12010000?0000122101002111-01031200110112211111011100100?00?11110
00000000000000

Leptolepis

000000000/011000000100000001000000010000010001000000000011110000
100000002000001100000000000/000001000001000011000000100000111110
00000000000000

Leptolepides haerteisi

000101100??2?000??0110000002011??200000102??1?100000010013?2000?
1210000000100111010010000001011?01000102210111010100100000211???
?00000000000000

Leptolepides sprattiformis

000100000112?0001?01101000021111?2000001021110100000010013?20000
1100000000100111010000000001011/010001/221011100010010100021111?
?00000000000000

Luisichthys

?0?1100?0112?0?011?1?010000?????00?000001??1??00001100012220000

1100010??0??002200000000010100001?01000?10110000?00011?000111?1?
11???0000?0000

Lycoptera

000100020??2?000??01100001022000-0000000010?10100000000012?20000
1000000??100001/0000110000030-11000100002111221111011000101//?1?
?0000010101000

Megalops

0001000001121000110001100002100000001000000010000000000012220000
1301010220010012100000000011001100010002/11111011000101000111110
00100101000000

Notelops

0001100101?200001101-110001211?0?0000000000210000000000012220000
1000000?0011002100000001??02??2?0200000?21111100?000100002212110
11111100100000

Oncorhynchus

0001010101121000110110100002100010000000001110100110010012220000
11000100200000/2111112111-01011200010110211111011101100100201110
00000010200000

Opsariichthys

0011110101121000110210101002100111000100121110100100000013221010
230100003000001210001000020301220011100021111101100010100122-110
0000-000000110

Orthogonikleithrus hoelli

0001?1110??2?000??01?01000021??1?2000100111100100100010012220000
1?00000??0100112010110011-010112010001022101110111002--?0021111?
?000?000000000

Pachythrissops

???1?0000??2?000??01?0?0000210?0?00?0000010?100000?0000012220000
1200??100101101200001100000/10100/010002001011000000101000?11?1?
?0?0?0?00?0000

Protoclupea

???100010??2?0?0??010?000002?00??000000001?21100010110001222000?
1??00101100000220000000?010100000?01000?2111000?00011100??11?1?
?1??0000000000

Rhacolepis

0001100101?210001101-010000211?1?0000000001110000101000012220000
1000000?001?0011100000010?02??2?0/00000?21011101?00010?002212110
11111110100000

Santanaclupea

00?100010??2?111000???1110?21????01?000000??101001000000?2220?00
1??000???0000011?00010011-0?0-221001000?21011101??1010?00021111?
?0?0?010?00000

Tharsis

00010001011/1000100100100002100000010000010011000000000012220000
1100000000000221000100000010000010000011000110000001000002/1110
00000000000000

Thrissops

1101?00?01?21000??0110100002100??00?000001?210000100000012220000
1000001001011022000000000?0110000001000221011100000010?00021111?
?0110000/00001

Thymallus

0001010101121000110100100002100010000000011110100110010012220000
1100000020000022101102111-01011200010100211111011101100100211110
00000010000000

Umbra

01?100010112100011121010000210-010000?00121100111100010012221000
?20?000001000012000012111-020-220001010021112211110?10000?211110
00?00010100000

Varasichthys

000100011112?000110100000000100??0000000011101000001100012220000
11001101100100120000?10?0103000?0001000110110000?000111001?11?1?
?1??0000000000

SMU 76938

00??1????????????????-??00002110??0001000001110????01??0012220?0?
??0??????01?00111000?????0????12?2?0?00?21?1110??0001??002?12?1?
?11111?110000?