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A New Intriguing Teleost from the Albian Muhi Quarry, Central Mexico, and Early Euteleostean Diversification

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Abstract: The Albian Muhi Quarry of Central Mexico has produced a variety of fishes, among which the teleosts are the most diversified, including representatives of stem groups together with a variety of crown groups. A new genus and species, †*Xeneichthys yanesi*, is described based on a unique combination of characters, such as a dorsoventral elongation and narrowing of infraorbitals 2 and 3, preopercle, opercle, and cleithrum; absence of some bones, such as the infraorbital 5, interopercle, and pelvic plate and fin; presence of an elongated urostyle and a membranous outgrowth or stegural on the first uroneural; and cycloid and ctenoid scales on the flanks. Due to its combination of characters, †*Xeneichthys yanesi* is interpreted as belonging to a new extinct family, †Xeneichthyidae, which is considered as an Euteleostei or Euteleosteomorpha *incertae sedis.* The fish faunas of another Albian quarry, Tlayúa of Tepexi de Rodriguez, Puebla, and Muhi Quarry are compared, and although both contain taxa that can be assigned to stem teleosts (e.g., †ichthyodectiforms and †crossognathiforms), both also contain crown teleosts (e.g., elopomorphs, clupeomorphs, and euteleosts)—all of which are endemic to their respective quarries and make them important centers of diversification of fish faunas during the Early Cretaceous.

Keywords: Lower Cretaceous; El Doctor Formation; Actinopterygii; Euteleostei; morphology; taxonomy

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1. Introduction

The Muhi Quarry is a Lagerstätte that produced and continues to produce an ever-growing diversity of ichthyofauna [1]. During recent years, many new species and genera have been described, and all of them are endemic to this Cretaceous locality [2–5]. However, this is not an isolated finding because other endemic fish faunas are known from other Cretaceous fossiliferous sites in Mexico, for instance, Tlayúa Quarry in Tepexi de Rodríguez, Puebla [2,6–9], El Espinal and El Chango quarries, Sierra Madre Formation in Chiapas [10], San José de Gracia Quarry in Puebla [11], Tzimol, Angostura Formation in Chiapas [12], Vallecillo, Nuevo León, and Múzquiz, Coahuila [3,13,14].

The Muhi Quarry is located outside the town of Zimapán, which is 120 km northwest of Pachuca City in the state of Hidalgo in central México (Figures 1 and 2). The quarry belongs to the municipality of Zimapán and is exploited to obtain rocks that are used for construction. The outcrop consists of a sequence of biomicritic and micritic limestones, with intercalated bedded and/or nodular cherts, and laminae made of siliciclastic clay and calcium carbonate [1,15]. The original exposure was 7.2 m from the top to the bottom with 20 m of lateral extension, but due to the continuous quarrying, the outcrop has increased in depth by about 3 m below the floor, and most of the specimens studied here come from this segment. The lateral extension has also increased by more than 30 m. The quarrying is part of the socio-economic development of the municipality, but it has caused a major deterioration of the outcrop (Figure 1).

Figure 1. Panorama of the Muhi Quarry. (**A**) Photograph of the locality taken in the year 2000 when the exploitation was artisanal; most of the studied material comes from the floor and three meters below the surface of this area. (**B**) Current state due to overexploitation to obtain gravel; the original outcrop in the background is covered by rubble.

The locality belongs to the La Negra facies of the El Doctor Formation (Bravo-Cuevas et al. [1,15]) that was interpreted as Albian–Cenomanian age [16–19]; nevertheless, a recent study of the ammonites recovered from the site has revealed that the outcrop is of Upper Albian age [20]. According to the lithology, the environment corresponded to an outer marine shelf, with well-oxygenated waters, occasionally receiving pulses of pelagic waters and near-shore waters possibly during storms [1,15].

The fossiliferous content of Muhi Quarry recovered up to now includes †ammonites [20,21], crinoids [22], crustaceans [23,24], echinoids [15,23], and fishes. The fish diversity includes a few chondrichthyans, e.g., the sharks †*Squalicorax falcatus* and †*Ptychodus decurrens*, and rays [2,3], while the osteichthyans comprise actinistians [25] and a great variety of actinopterygians, such as neopterygians *incertae sedis* (†Pycnodontiformes, not yet studied [3]), a basal stem teleost (†Aspidorhynchiformes, not yet studied [3]), and numerous teleosts belonging to groups with very different phylogenetic positions, making the quarry an unusual center of teleostean diversification during the Early Cretaceous, which is still poorly understood. Among stem teleost species belonging to †Ichthyodectiformes, there are †*Heckelichthys preopercularis* and an indeterminate †cladocyclid [5], as well as a new species of †Crossognathiformes, *Motlayoichthys sergioi* [4]. Others are Elopiformes (under study) and Albuliformes (†*Nunaneichthys mexicanus* [26]), which are among the most primitive members of crown Teleostei or Teleocephala [27–32], while †*Araripichthys* and †Tselfatiiformes [2,3] are *incertae sedis* among Clupeocephala. New materials of Clupeiformes (Clupeinae) and one indeterminate specimen of Gonorynchiformes [2,3] are assigned to the Otomorpha *sensu* Arratia [33,34] and Betancur-R. et al. [30,31]. The most advanced teleosts or neoteleosts are represented in the locality by species of Aulopiformes (†*Ichthyotringa mexicana* [35] and †*Enchodus zimapanensis* [36], which are considered as primitive neoteleosts) and by new taxa of more advanced neoteleosts, the Acanthomorpha: *incertae sedis* †*Muhichthys cordobai* [37], *incertae sedis* †*Dalgoichthys tropicalis*, and the beryciform †Pseudomonocentrididae [38].

The fish diversity of the Muhi Quarry is great, but in particular, its record of teleostean taxa is outstanding. It is represented not just by new genera and species of stem and crown groups of Teleostei from different orders, but a new extinct family (Pseudomonocentrididae) has been discovered, and it represents the oldest member of the beryciform acanthomorphs [38,39]. Thus, our main goal here is to describe this new fish from Muhi Quarry that displays an unusual combination of anatomical characters (many of them autapomorphic), which makes its study exciting but difficult to interpret anatomically and taxonomically, opening questions on the current understanding of fossil clupeocephalan lineages.

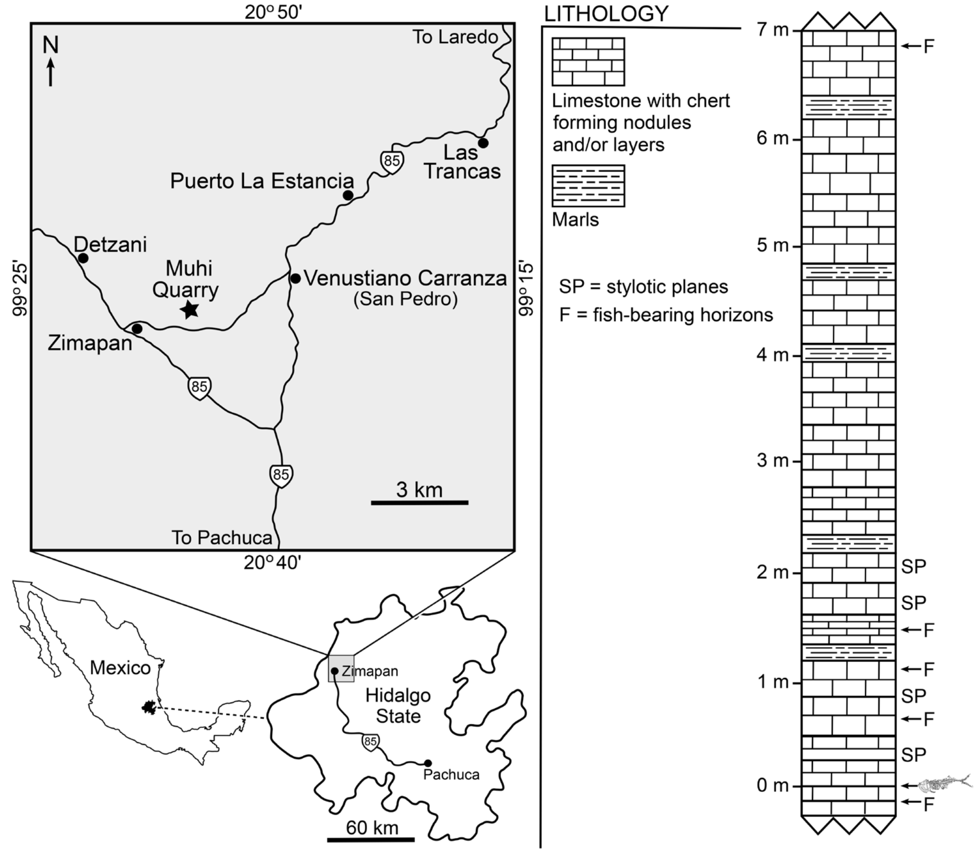

Figure 2. Location of the Muhi Quarry of Zimapán, Hidalgo, central Mexico, and stratigraphic column of the locality. The layer where most of the specimens were collected is indicated with the fish drawing in the stratigraphic column.

2. Materials and Methods

Specimens examined: The studied fossil material is deposited in the Museo de Paleontología (UAHMP), Universidad Autónoma del Estado de Hidalgo, Mexico, and it consist of 22 specimens in various degrees of completeness: UAHMP 973, complete fish; UAHMP 1063, complete fish; UAHMP 2028, skull disarticulated; UAHMP 2226, skull disarticulated; UAHMP 3157, complete fish; UAHMP 3158, nearly complete fish; UAHMP 3159, nearly complete fish; UAHMP 3656, skull; UAHMP 3727, impression of complete fish; UAHMP 3836, skull; UAHMP 3903, impression of skull; UAHMP 3967, skull and anterior vertebrae; UAHMP 3971, disarticulated skeleton; UAHMP 4443, incomplete skull and anterior vertebrae; UAHMP 4672, incomplete skull and some anterior vertebrae; UAHMP 4697, almost complete fish without the anterior portion of head; UAHMP 4698, almost complete fish without caudal fin; UAHMP 4699, impression of almost complete fish without caudal fin; UAHMP 4763, impression of skull and anterior vertebrae; UAHMP 4834, incomplete skull and impression of the vertebrae; UAHMP 4861, almost complete specimen without caudal fin; and UAHMP 4862, skull disarticulated. Other fishes used in comparisons (see Discussion) are listed in Appendix A.

2.1. Methods

Most of the specimens were prepared using paleontological and dental tools, brushes, and dissection needles under a binocular microscope. We used a camera lucida attached to a Leica MZ6 microscope (Leica Microsystems, Wetzlar, Germany) to photograph specimens and perform detailed drawings of specific structures before inking them. A Nikon camera (Coolpix 53700, Nikon Corp, Tokyo, Japan) was used to photograph the specimens.

Measurements were taken with a digital caliper Starret 799. The length of the head, used in description and comparisons, was measured from the anterior border of the dentary to the posterior margin of the opercle. The depth of the head was measured tracing a straight line extending from the back of the skull roof to the base of the subopercle. The preorbital length was measured from the anterior border of the premaxilla to the anterior margin of the orbit. The orbital diameter represents the maximum width of the orbit in its middle region. Other measurements follow standard procedures as closely as possible because of preservation problems.

2.2. Anatomical Terminology

The terminology concerning the skull roof bones is based on the homologization of bones [40–42]. To facilitate comparisons, the traditional terminology is presented in brackets in the text and figures, e.g., parietal bone [=fr] and postparietal bone [=pa]. Terminology concerning vertebrae and associated elements follows Arratia et al. [43], fin rays follow Arratia [44], and caudal skeleton follows Arratia and Schultze [45] and Schultze and Arratia [46]. The terminology of the scales follows Schultze [47,48].

3. Systematic Paleontology

3.1. Teleostei

Infraclass Teleostei Müller, 1845 [49].
Clupeocephala *sensu* Arratia, 2010 [50].
Euteleosteomorpha *incertae sedis.*
Family Xeneichthyidae new.

3.1.1. New Family Xeneichthyidae

Diagnosis: (Based on a unique combination of characters; autapomorphies are identified with an asterisk [*].) Moderately long teleost reaching about 200 mm total length and 170 mm standard length. Head with a characteristic profile, slightly concave in the mid-region of the skull roof, with an almost rounded ventral profile given by a long lower jaw protruding anteriorly to the snout. Notable dorsoventral elongation and narrowing of certain cranial bones, such as infraorbitals 2 and 3, preopercle, opercle, and cleithrum [*]. Reduced circumorbital series including four infraorbitals, dermosphenotic, and one supraorbital. One large supramaxilla present. Preopercle with a narrow triangular ventral region and a long, narrow dorsal region, reaching close to the lateral margin of pterotic [*]. Interopercle absent [*]. Pectoral fin long, extending to the level of the 16th vertebra, almost as long as the length of abdominal region (up to the 19th vertebra) [*]. Pelvic girdle and fins absent [*]. Dorsal fin positioned posterior to the origin of the anal fin, at the level of the 30th vertebra [*]. Long anal fin, almost double the length of the dorsal fin, including about 18 pterygiophores. Preanal length short; the anal fin originates at the mid-line of the body length, making the body cavity characteristically short [*]. About 45 to 47 vertebrae markedly sculptured. Long epineural and epipleural series extending from first abdominal vertebra up to the caudal fin [*]. Seven uroneurals distributed in two series, with the longest one formed by two long elements that reach the anterior border of the urostyle or compound ural region. First uroneural or stegural having a membranous outgrowth dorsomedially [*].

Etymology: the generic name refers to the Otomí Mexican language "Xene" meaning big mouth, combined with "ichthys" (Greek) meaning fish.

Content: only one species known.

†Xeneichthys yanesi gen. et sp. nov.

Zoobank registration of family: **urn:lsid:zoobank.org:act:75DB21FE-6877-4462-84E3-5AA27FBC722C.**

Zoobank registration of species: **urn:lsid:zoobank.org:act:16390C5D-140B-4411-93D2-201FFB62D4D9.**

(Figures 3–11).

Synonyms:
Megalopid, 2009: [51], mention, Figure 4B.
Megalopid-like fish, 2013: [52], p. 27, mention.
Type species: †*Xeneichthys yanesi* gen. et sp. nov.
Diagnosis: same as for family.
Holotype: UAHMP 1063, complete specimen (Figures 3 and 4).
Paratypes: UAHMP 973, UAHMP 1063, UAHMP 2028, UAHMP 2226, UAHMP 3157, UAHMP 3158, UAHMP 3159, UAHMP 3656, UAHMP 3727, UAHMP 3836, UAHMP 3903, UAHMP 3967, UAHMP 3971, UAHMP 4443, UAHMP 4672, UAHMP 4697, UAHMP 4698, UAHMP 4699, UAHMP 4763, UAHMP 4834, UAHMP 4861, and UAHMP 4862 skull disarticulated.
Etymology: the species name refers to Yáñez, the family name of the Muhi Quarry workers.
Locality: Muhi Quarry, Zimapán, State of Hidalgo, Mexico.
Age: El Doctor Formation, Upper Albian [20], Cretaceous.

3.1.2. Description

General features: The standard length (SL) of the largest individuals of †*Xeneichthys yanesi* gen. et sp. nov. averages ca. 170 mm. The fish has an elongated body (Figure 3) with a head that is almost as deep as long; in the largest specimens, the head length is about 23–26% of the SL. The head has a characteristic profile, with the highest point at the posterior tip of the skull roof, which is slightly bent in its middle region; in contrast, the long and protruding lower jaw gives the head a slightly rounded ventral contour. The general shape of the head is reminiscent of the modern teleost *Megalops,* and this partially explains why the fish was described as megalopid-like by González-Rodríguez and Fielitz [51,52]. The orbit is small, about 27–33% of the head length, and it has a dorsal position, as viewed laterally.

The pectoral fins have a low position on the body, near the ventral body margin (Figure 3). Pelvic girdles and fins are not preserved in any of the partial to nearly complete specimens; consequently, pelvic basipterygia and fins are interpreted as absent in this fish. The short dorsal fin (Figure 3) is placed about 68% of the SL in the holotype, which means that this fin is posteriorly placed. In contrast, the origin of the anal fin is positioned forward, at the mid-line of the body length at about 56% of the SL in the holotype; the anal fin, based on the pterygiophore series, is much longer, about double the length of the base of the dorsal fin. The caudal fin (Figure 3) is homocercal and deeply forked. Although fin rays are damaged in most specimens, there is no evidence that basal or fringing fulcra were present.

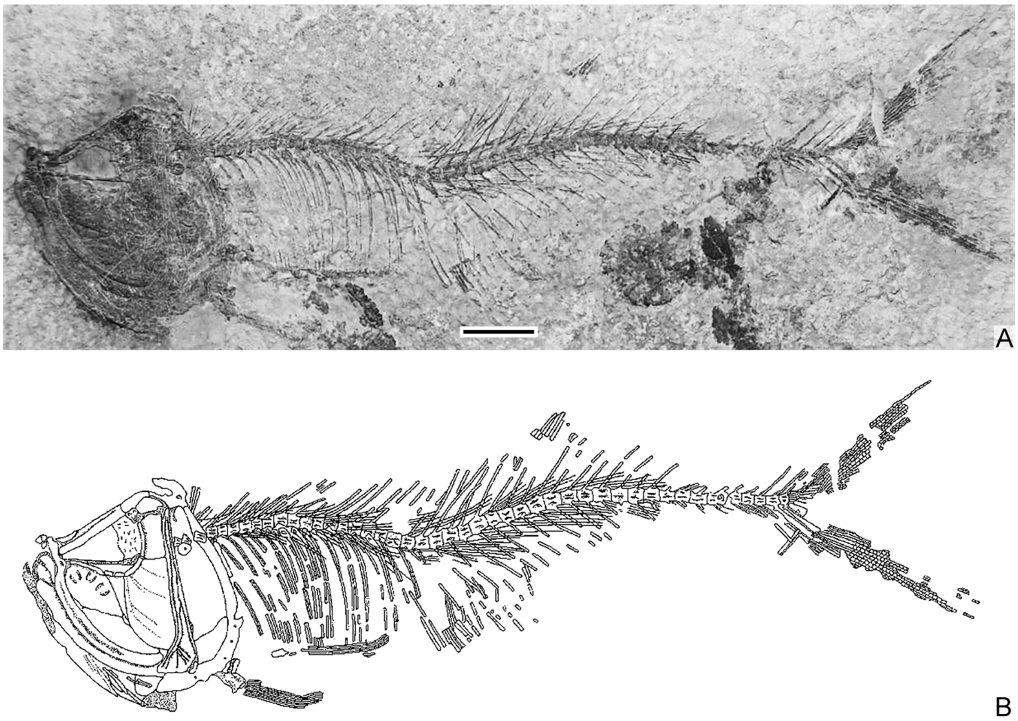

Figure 3. †*Xeneichthys yanesi* gen. et sp. nov. Holotype, specimen UAHMP 1063 in lateral view; (**A**) photograph; (**B**) line drawing, both reversed to the left. Scale bar = 1 cm.

Skull roof: The bones of the skull roof (Figures 4–7) are preserved in lateral view or are slightly displaced dorsolaterally. The anterior, narrow preorbital region of the skull roof is better preserved than the postorbital one, which widens dramatically behind the orbit, a characteristic of the teleostean skull roof [53,54]. Additionally, the parietal region [=frontal region] is long, more than twice the length of the postparietal/pterotic region (Figure 5).

The following description of the mesethmoid corresponds to the information provided by UAHMP 3656 and 4696. The mesethmoid (Figures 4–6) is a wide bone anterolaterally, as wide as the parietal region, with two lateral processes and a rounded and somehow protruding anterior region; its posterior region (Figure 5) has two elongated processes (UAHMP 3656).

The parietal [=frontal] bones articulate with the mesethmoid anteriorly. Both parietals [=frontals] are narrow for most of the anterior portion of the skull roof, and they contact medially by a straight suture (*sutura harmonica*). They then slightly widen at the level of the posterior corner of the orbit where they end. They join the postparietal [=parietal] bones posteriorly by straight sutures. There is no contact between the parietal and the pterotic in the holotype (Figure 4), but additional specimens do not provide more information; the parietal bones are limited mainly to the orbital region (Figure 5).

The postparietal [=parietal] bones are rectangular and meet with the parietal [=frontal] bones anteriorly. An autosphenotic or sphenotic is not preserved in the available material. The pterotic appears to be a moderately large, rectangular bone (UAHMP 3656; Figure 5) suturing with the postparietal medially; other sutures of surrounding bones are unclear due to preservation. The epiotics are not preserved. The supraoccipital is fragmentary or is not preserved. It appears to have been a narrow bone with a low crest, extending posteriorly in UAHMP 4698.

Braincase: In most specimens, the braincase is crushed and/or hidden by the posterodorsal infraorbitals and opercular bones. The anterior end of the vomer is preserved on UAHMP 3656 and UAHMP 1063 and appears to be disarticulated from the parasphenoid and displaced anteriorly (Figure 4). Three conical vomerine teeth are preserved on UAHMP 3656. A section of the parasphenoid (Figures 4–6) is visible in some specimens; it is a narrow bone, with a high, triangular ascending process (UAHMP 1063). No teeth have been observed associated with the parasphenoid. Large remains of the orbitosphenoid are preserved (Figures 5 and 6), indicating that the orbitosphenoid formed a complete orbital septum separating both eyes.

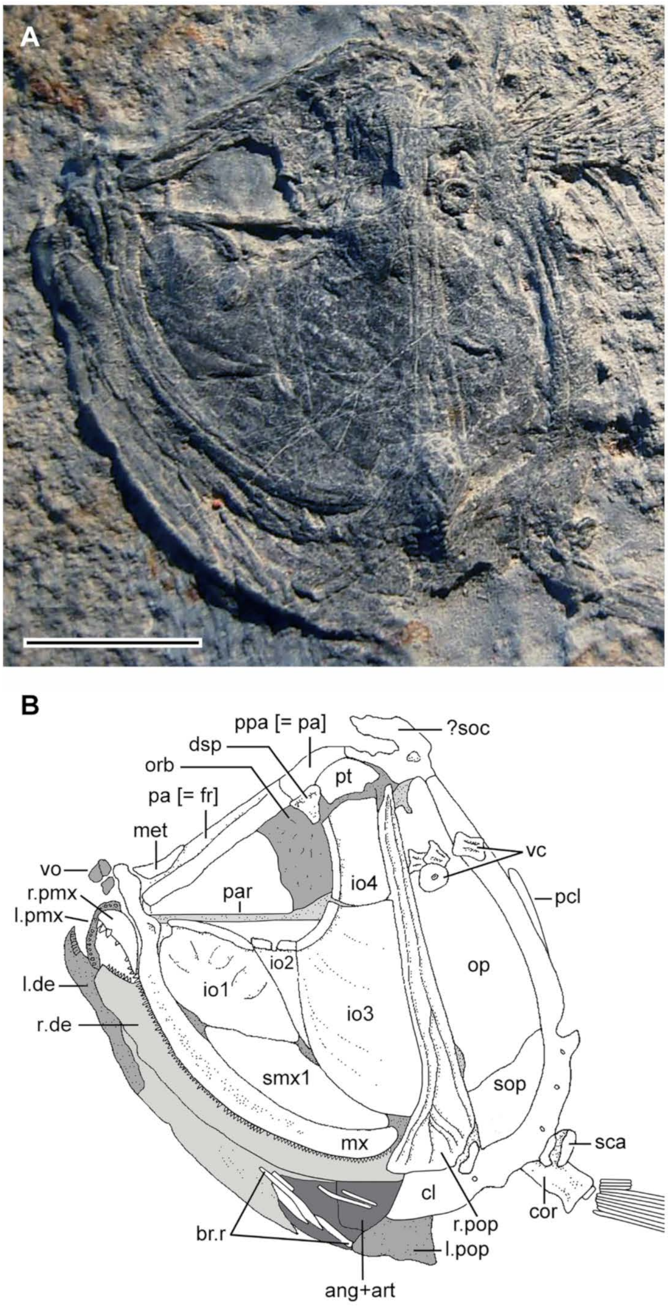

Figure 4. †*Xeneichthys yanesi* gen. et sp. nov. Head of the holotype, specimen UAHMP 1063. (**A**) Photograph; (**B**) line drawing, both reversed to the left. Scale bar = 1 cm. Abbreviations: ang+art, anguloarticular; br.r, branchiostegal rays; cl, cleithrum; cor, coracoid; dsp, dermosphenotic; io1–4, infraorbitals 1–4; l.de, left dentary; l.pmx, left premaxilla; l.pop, left preopercle; met, mesethmoid; mx, maxilla; op, opercle; orb, orbitosphenoid; pa [=fr], parietal [=fr]; par, parasphenoid; pcl, postcleithrum; ppa [=pa], postparietal [=pa]; pt, pterotic; r.de, right dentary; r.pmx, right premaxilla; r.pop, right preopercle; sca, scapula; smx, supramaxilla; soc, supraoccipital; sop, subopercle; vc, vertebral centra; vo, vomer.

The cranial facet for the hyomandibula is observed on the dorsolateral aspect of the braincase in UAHMP 4698. The facet is formed by the autosphenotic and pterotic. It is unclear whether the prootic forms part of the facet.

Circumorbital series: The preserved circumorbital series (Figures 4–6) is formed by a supraorbital, four infraorbital bones, and the dermosphenotic. The circumorbital ring is incomplete dorsally, leaving a space between the posterior tip of the supraorbital and the dermosphenotic. Remains of sclerotic bones have not been observed.

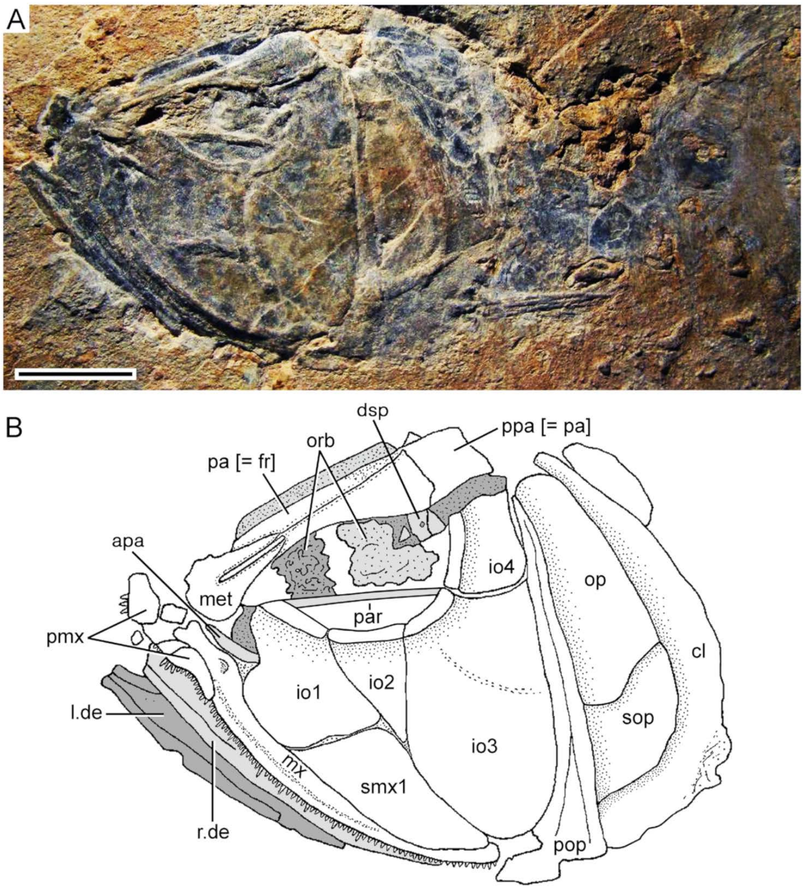

Figure 5. †*Xeneichthys yanesi* gen. et sp. nov. Head of specimen UAHMP 3656 in lateral view. (**A**) Photograph; (**B**) line drawing. Scale bar = 1 cm. Abbreviations: apa, autopalatine; cl, cleithrum; dsp, dermosphenotic; io1–4, infraorbitals 1–4; l.de, left dentary; met, mesethmoid; mx, maxilla; op, opercle; orb, broken orbitosphenoid; pa [=fr], parietal [=frontal]; par, parasphenoid; pmx, premaxilla; pop, preopercle; ppa [=pa], postparietal [=parietal]; pto, pterotic; r.de, right dentary; smx, supramaxilla; sop, subopercle.

The supraorbital is a small, elongated bone placed at the anterolateral corner of the parietal and separated from infraorbital 1 by a very short distance. An antorbital has not been observed in the available material, and it is interpreted here to be absent or very small—an interpretation that is supported by the position of the supraorbital and infraorbital 1. Infraorbital 1 or lacrimal carries the infraorbital canal, bone-enclosed, in its dorsal margin; the main body of infraorbital 1 is represented by a flat, thin, tear-drop-shaped lamina that occupies a significant part of the anterolateral region of the cheek. Infraorbital 2 is an elongated, narrow, triangular laminar bone that carries the bone-enclosed infraorbital canal in its dorsal margin. Narrow sensory branches radiate off ventrally from the main canal. The third infraorbital is the largest and deepest bone of the series, with its posterior margin extending along the anterior border of the preopercle and almost reaching the posterior part of the lower jaw ventrally. Thus, the bone has a plate-like laminar aspect with a short section of the bone-enclosed infraorbital canal at its orbital margin. The fourth infraorbital is a rectangular-shaped laminar bone, extending laterally to the hyomandibula and reaching posteriorly the anterior margin of the preopercle and, possibly, part of the anterior margin of the opercle; it also carries a section of the tubular infraorbital canal at its anterior margin.

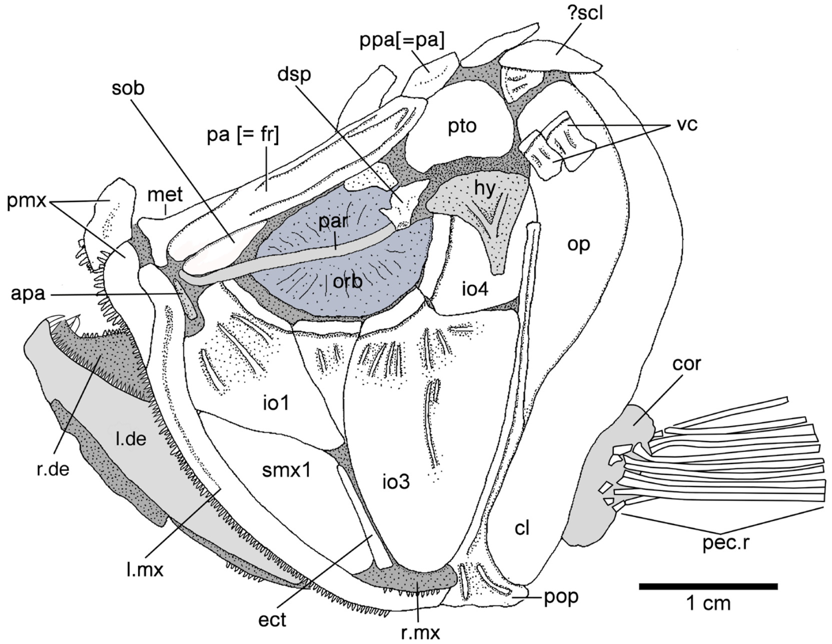

Figure 6. †*Xeneichthys yanesi* gen. et sp. nov. Line drawing of the head and pectoral girdle and fin in lateral view (specimen UAHMP 4698). Abbreviations: apa, autopalatine; cl, cleithrum; cor, scapula–coracoid? dsp, dermosphenotic; ect, ectopterygoid; hy, hyomandibula; io1–4, infraorbitals 1–4; l.de, left dentary; l.mx, left maxilla; met, mesethmoid; mx, maxilla; op, opercle; ors, orbitosphenoid; pa [=fr], parietal [=frontal]; par, parasphenoid; pec.r, pectoral fin rays; pmx, premaxilla; pop, preopercle; ppa [=pa], postparietal [=parietal]; pt, pterotic; r.de, right dentary; r.mx, right maxilla; smx, supramaxilla; sob, supraorbital; vc, vertebral centra.

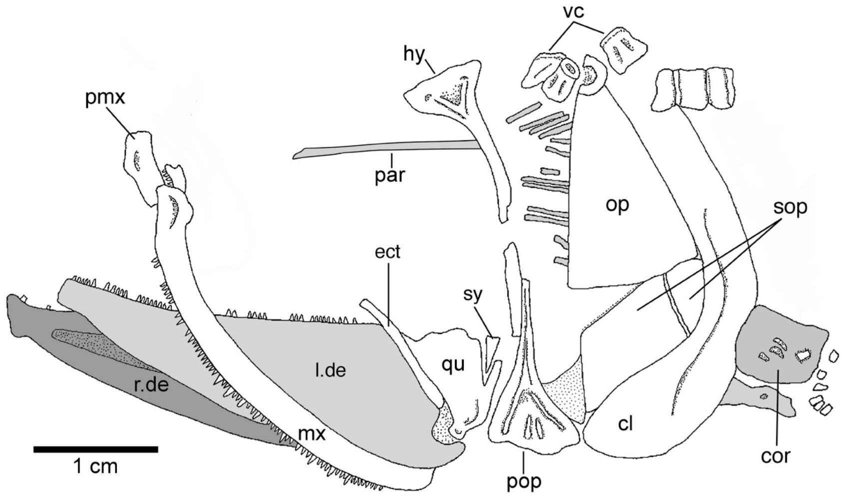

Figure 7. †*Xeneichthys yanesi* gen. et sp. nov. Line drawing of specimen UAHMP 4672 showing part of the suspensorium. Abbreviations: cl, cleithrum; cor, scapula–coracoid? ect, broken ectopterygoid missing its anterior part; hy, broken hyomandibula; l.de, left dentary; mx, maxilla; op, opercle; par, broken parasphenoid; pmx, premaxilla; pop, preopercle; qu, quadrate; r.de, right dentary; sop, subopercle; sy, broken symplectic; vc, displaced vertebral centra.

The dermosphenotic is a small, ossicle-like bone carrying the infraorbital canal. Due to the condition of the preservation of the area and the poor or incomplete preservation of the supraorbital and otic canals, it is unclear whether the infraorbital canal ends in the dermosphenotic or has a connection with other cephalic sensory canals.

Upper jaw: the upper jaw is remarkably long, extending posterior to the posterior margin of the orbit (Figures 4–7); the jaw is composed of the premaxilla, maxilla, and supramaxilla.

The premaxilla (Figures 4–6) is small and half-moon-shaped, with a tiny ascendant process that is observed in UAHMP 3656. It is about a fifth of the length of the maxilla. The three anteriormost premaxillary teeth are conical and longer (ca. 1.5 mm, UAHMP 1063 and UAHMP 3656) than the remaining eleven teeth (ca. 1 mm).

The maxilla (Figures 4–7) is a long, gently curved, narrow bone that changes its angle anteriorly to form the anterior articular process and narrows posteriorly, ending in a rounded posterior margin (Figure 6) that covers laterally the anterior tip of the ventral part of the preopercle. A groove is positioned along most of the lateral surface of the bone, extending into its articular process, which produces an anterodorsal angle in relation to the maxillary blade. The prominent articular process articulates with the mesethmoid region and the autopalatine in other teleosts, but these articulations cannot be checked in the available material. The articular process narrows to form a shallow, ventral concavity to accommodate the premaxilla. Along the entire oral border of the maxilla is a continuation of the small, conical teeth similar to those on the premaxilla. The teeth are densely packed, and there is one slightly longer tooth positioned between five or six smaller teeth along the length of the oral margin. However, this distribution of teeth may vary among specimens or even in the same specimen.

There is one supramaxilla (Figures 4–6), which is large and slightly triangular- or oval-shaped. The supramaxilla is long, taking up about half of the length of the maxilla (UAHMP 1063) or even more (UAHMP 3656). Dorsally, it is bordered by infraorbitals 1–3.

Lower jaw: The lower jaw (Figures 4–7) is long, and its articulatory facet with the quadrate is placed posteriorly to the posterior margin of the orbit. The triangular-shaped jaw has its higher depth closer to its posterior end, at ca. 82% of its total length, but the increase in depth is so gradual that there is not a distinct coronoid process. The higher depth or so-called coronoid process is formed by the dorsal regions of the dentary and angular (UAHMP 4672). Laterally, each jaw (Figures 4–7) is composed of the dentary or dentalosplenial and angular. An anguloarticular is present in the medial aspect of the posterior section of the jaw. This interpretation is based on the holotype with a smooth medial surface, with no distinction between angular and articular ossifications.

The dentary is the largest bone of the jaw, making up about three-fourths of the mandible; although the suture between the dentary and angular is poorly preserved and appears to be V-shaped, the holotype clearly shows that the lower section of the dentary extends close to the posterior end of the jaw. The anterior margin of the dentary forming the mandibular symphysis is narrow, about one-third of the deeper posterior section of the jaw. The ventral symphysial process is low or non-existent. The angular has a short postarticular process (Figure 7), extending slightly posterior to the lower jaw–quadrate articulation (see UAHMP 3159), or no process at all. A separated retroarticular has not been observed in the available specimens. The trajectory of the mandibular canal is usually not discernible or is destroyed, but the posterior opening of the mandibular canal, which is laterally placed on the angular, is visible in UAHMP 3158 and UAHMP 3159.

The dentary bears a single row of teeth observed in UAHMP 1063, UAHMP 3157, UAHMP 3836, UAHMP 3656, UAHMP 4672, and UAHMP 4698. The teeth have the same shape and size as those of the maxilla, except for the first two (Figure 6), which are twice the size of the rest (also observable in UAHMP 4698).

Hyo-symplectic, palatoquadrate, and associated bones: The suspensorium (Figure 7) of the lower jaw includes the hyomandibula and symplectic, the latter one articulating with the quadrate. These structures are rarely observed because the cheek bones are covering them; however, one specimen (UAHMP 4672; Figure 7) has the cheek bones removed so that internal bones are exposed.

The hyomandibula and symplectic (Figure 7) are conspicuously long and narrow and placed in an almost straight angle with respect to the braincase. The cup-like hyomandibula is slightly expanded dorsally and markedly narrow ventrally in a long pedicel. The opercular process is not observed, and an anterior membranous outgrowth seems to be absent. The symplectic is broken, and its lower tip is observed in a notch for the dorsal margin of the quadrate.

The metapterygoid is a large square bone observed in UAHMP 4834 (not illustrated). The quadrate, in different states of preservation, is observed in several specimens (UAHMP 3158, UAHMP 3159, UAHMP 4834, and UAHMP 4672). It is a deep, triangular-like bone with a ventral, broad, and flat surface just posterior to the articular condyle and with a short and broad posterodorsal process that does not reach the dorsoposterior margin of the quadrate. Another bone is visible in UAHMP 3656 and UAHMP 3967. It is narrow posteriorly, followed by a blade-shaped head, which articulates to the palatine process of the maxilla, and it is interpreted here as the autopalatine. A narrow, long, and heavily ossified ectopterygoid (Figure 7) is preserved anterior to the quadrate in specimens UAHMP 2828, UAHMP 4672, and UAHMP 4834. The ectopterygoid does not have teeth.

Hyoid arch and branchiostegal rays: The lower part of the hyoid arch is preserved in UAHMP 2028. It consists of the anterior ceratohyal characterized by a narrow mid-section.

Five branchiostegal rays (Figure 4) are preserved in UAHMP 1063. The two anterior ones are longer and broader, whereas the three posterior branchiostegal rays are slender and shorter. Eleven short and slender branchiostegal rays are preserved in specimen UAHMP 2828.

Urohyal and gular plate: An urohyal is not preserved in any specimen. Evidence of a gular plate has not been found, and the bone is interpreted as absent.

Opercular series: Following the dorsoventral elongation of the cranium, the opercular bones (Figures 4–7) are also much deeper than wide. The characteristically shaped preopercle has a long, vertical dorsal limb and a small ventral limb that widens ventrally equally in both anterior and posterior directions. The tip of the dorsal limb almost reaches the pterotic region. The preopercular sensory canal is represented by a covered ridge that branches in a fan of sensory tubules on the ventral limb. The opercle is about three times deeper than long. Its anterior border is straight, following most of the deepness of the preopercle, and its posterior border is gently curved. The subopercle is somewhat triangular, and its height is about three times shorter than the opercular height. A gently oblique suture joins both bones. The anterior border of the bone is straight, so that the anterodorsal process of the subopercle seems to be missing; the posterior border continues to curve anteriorly. An interopercle has not been observed in any specimen and is interpreted as absent.

Vertebral column and associated elements: There is a total of 45 autocentral vertebrae, including preural centrum 1, and 19 abdominal or precaudal vertebrae in the holotype, but the number ranges from 44 to 46 in other specimens (Figure 3). All centra (Figure 8) are slightly longer than deep and strongly sculptured with a fine elongated crest and two deep grooves extending along their lateral surfaces. All neural arches are fused to the centra; they are narrow and positioned about the midlength of the centra. The neural spines are slightly inclined posteriorly, and they are unfused medially in the abdominal vertebrae and, possibly, the first caudal one. There are about 17 pairs of ribs (Figure 3) preserved in the holotype; they are moderately long, not reaching the ventral body margin. Starting with the fourth rib, they widen proximally where they meet with their respective centrum. The abdominal centra (Figure 8), with well-preserved walls, show at their lateroventral region a small process bearing a small facet where the head of each rib articulates. This means that each parapophysis is fused to its centrum.

There are three series of intermuscular bones: the supradorsal, epineural, and epipleural (Figure 3). The series of elongated and narrow supradorsal bones is incomplete in all specimens due to problems with preservation. As far it can be observed in the holotype, the elongated, fine remains of supradorsals extend in the spaces between neural spines in the abdominal region.

A long series of epineural bones (Figures 3 and 8)—not epineural processes of the neural arch—extends from posterior to the skull up to the preural caudal region. According to the available information, their proximal ends lie lateral to the neural arches, and some of them are so long that they extend over the space of five or six vertebrae. The most posterior ones become shorter than the anterior ones. In UAHMP 1063, the last epineural is observed lateral to the neural arch of preural centrum 5. A long series of epipleurals (Figures 3 and 8) seems to be attached to the proximal end of the ribs in the abdominal region and to the haemal arches in the caudal region, up to the preural region. In UAHMP 1063, the last epipleural is observed lateral to the haemal arch and spine of preural centrum 4.

Pectoral girdle and fin: The pectoral girdle, as in the opercular bones, is dorsoventrally narrow, and the boundaries between bones are difficult to observe. Of the dermal pectoral girdle, the cleithrum is preserved and possibly one or two postcleithra. The identification of a posttemporal—the bone linking the girdle to the cranium—is unclear in the available material, as well as that of a supracleithrum.

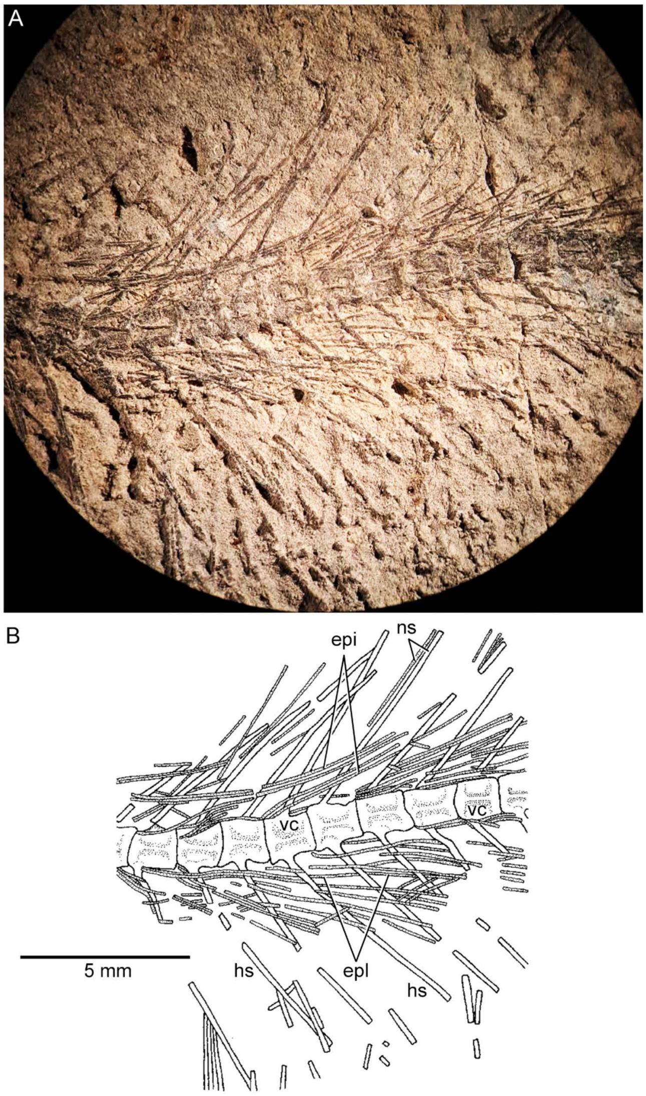

Figure 8. †*Xeneichthys yanesi* gen. et sp. nov. Section of the vertebral column of the holotype, specimen UAHMP 1063, showing the series of intermuscular bones associated with the first caudal vertebrae. (**A**) Photograph; (**B**) line drawing, both reversed to the left. Abbreviations: epi, epineurals; epl, epipleurals; ns, neural spines; hs, haemal spines; vc, vertebral centra.

The cleithrum makes up most of the girdle. It starts about the level of the vertebral column and extends below the opercular region, ending close to the posterior margin of the jaw, according to the holotype (Figure 4). The lower part of the cleithrum is slightly expanded at its anteroventral tip, as shown in specimens UAHMP 1063 and UAHMP 4672 (Figure 7), where the bone is exposed. An independent supracleithrum has not been observed in any specimen, and there is no evidence that it could be fused with the upper part of the cleithrum. An elongated bony splint placed posterior to the cleithrum is interpreted here as a postcleithrum (Figure 4).

The chondral part of the pectoral girdle has preserved remains of the scapula and the coracoid, which are difficult to identify, so the remains are identified as possibly the scapula–coracoid in the illustrations; pectoral radials are not preserved. The scapula (Figure 5) seems to be a small, elongated bone with a central depression and two small openings, and the coracoid is rectangular-shaped.

The pectoral fin (Figure 3) is long, extending to the level of the 16th vertebra in the holotype UAHMP 1063; this means that the fin is almost as long as the body cavity (up to the 19th vertebra; see below). The rays are very thin and segmented distally, but apparently, they do not branch.

Pelvic girdles and fins: Pelvic girdles and fins are not present in any specimen. Previously, in a preliminary report, the pectoral fin of UAHMP 1063 of the left side was interpreted as a badly preserved pelvic girdle and fin, which additionally were interpreted by González-Rodríguez and Fielitz [52] as having an anterior position, closer to the pectoral fins. After revision of all specimens available to this study, we currently interpret this fish as lacking pelvic girdles and fins.

Dorsal fin: The dorsal fin is not well preserved, but according to the available information, it originates at the level of the 30th vertebra (Figure 3; UAHMP 1063, UAHMP 3158, and UAHMP 4697). Ten dorsal fin rays are counted in UAHMP 1063 and UAHMP 4697 and eleven dorsal fin rays in UAHMP 3158. The first four are smaller and thicker than the posterior ones. The distal part of the remaining rays is not completely preserved, but apparently, the rays are segmented but not branched.

Anal fin: The insertion of the anal fin (Figure 3) is positioned at the level of the 20th vertebra in UAHMP 3158 and UAHMP 4697 and the 18th vertebra in UAHMP 1063. Ten anal rays are preserved in UAHMP 3158 and eleven in UAHMP 4697. The rays are very thin and segmented but not branched, and their total number is larger, because there are at least 18 pterygiophores, but they are disarticulated from their correspondent rays or the rays are not preserved. This means that the anal fin was long, longer than the dorsal fin, and according to the series of pterygiophores in the holotype, it started at the level of the 18th vertebra and ended at the level of the 31st vertebra. The most anterior pterygiophores are long and thin and, apparently, lack membranous outgrowths (Figure 3).

Caudal fin and endoskeleton: In general, the caudal fin and its endoskeleton are poorly preserved or not preserved at all. Only two specimens (UAHMP 1063 and UAHMP 3158) provide some information. At least four preural vertebrae support rays in the holotype. These preural vertebrae are slightly longer than deep, but preural centrum 1 is as deep as long. The narrow neural arches of preural centra (Figure 9) are fused to their centra, and they are placed closer to the anterior margin of the centrum than to the posterior one. The neural arch of preural centrum 1 bears a long neural spine, as long as or even longer than the preceding spine, which is also narrow and lacking membranous outgrowths. The arch of the parhypural is fused to preural centrum 1. The parhypural, as well as the haemal spines of preural vertebrae 3–2, has an expanded anterior membranous flange (Figure 10C,D) that tapers ventrally. The main shaft of the haemal spines of preural vertebrae 3–1 widens distally, being the distal portion of the parhypural that is the most expanded.

The ural region is incompletely preserved in UAHMP 1063 and UAHMP 3158. The latter presents a long ural centrum 1 (diural terminology) that is even slightly longer than preural centrum 1 and articulates with the bases of hypurals 1 and 2; this ural centrum is followed by a second ural centrum (of diural terminology) that articulates with the proximal regions of hypurals 3 and 4 (Figure 9A,B). In contrast, Figure 10D shows only one compound ural centrum or urostyle supporting hypurals 1–5, whereas in Figure 10B, the posterior hypurals are displaced and seem to be articulating with the urostyle. There are six or seven hypurals preserved, and all of them are autogenous. Because the distal portions of hypurals 2 and 3 are poorly preserved, it is unclear whether a diastema was present or not; however, according to the size of hypural 3 (Figure 10D), the largest of the series, it seems possible that a hypural diastema was missing. UAHMP 1063 has seven hypurals, five dorsal and two ventral ones (Figure 10D); however, only the space of hypural 2 is left—the bone is not preserved. Mainly the proximal regions of the hypurals are preserved. Seven hypurals are also preserved in UAHMP 3158 (Figure 10C,D); hypural 3 is the broadest element of the series, with a broad articular proximal region. Hypural 1 is the second broadest but is the longest, as long as the parhypural. Hypurals 4–7 are elongated and become progressively smaller.

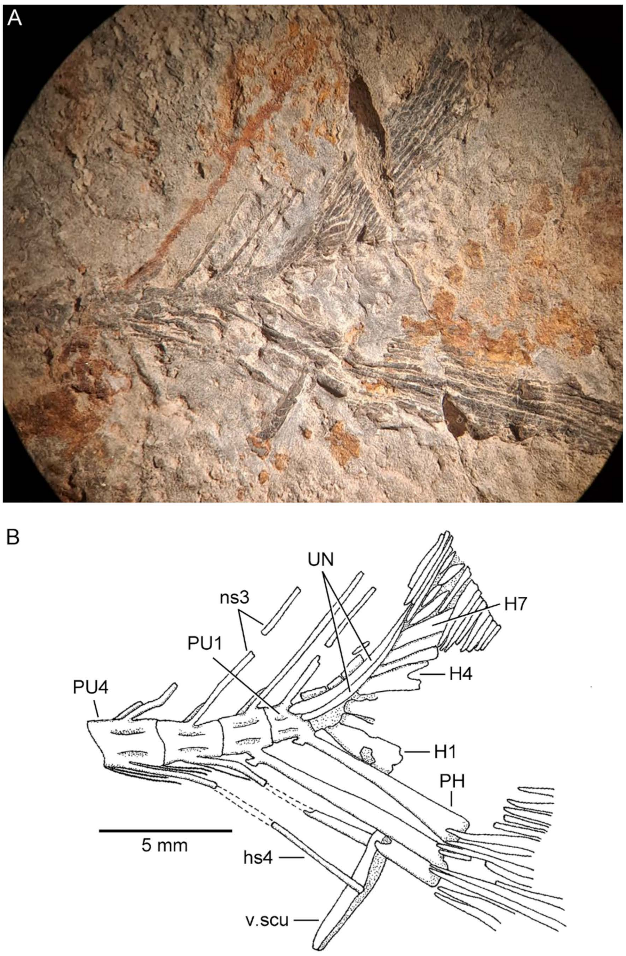

Figure 9. †*Xeneichthys yanesi* gen. et sp. nov. Caudal skeleton of the holotype specimen UAHMP 1063. (**A**) Photograph; (**B**) line drawing, both reversed to the left. Abbreviations: H1, 4, 7, hypural 1, 4, 7; hs4, haemal spine of preural centrum 4; ns3, neural spine of preural centrum 3; PH, parhypural; PU1–4, preural centrum 1–4; UN, uroneurals; v.scu, ventral scute.

The uroneural series is poorly or incompletely preserved in most specimens. In specimens UAHMP 1063 and UAHMP 4697, the series includes six uroneurals distributed in two series—a long, anterior one represented by three uroneurals (Figure 10A,B) and a short, posterior one represented by four uroneurals (Figure 9). Uroneural 1 is an enlarged element bearing a membranous outgrowth dorsally that it is interpreted here as a stegural (Figure 10A,C). This element almost reaches the posterior margin of preural centrum 1, ending in the anterolateral margin of the urostyle. Posterolateral to the stegural is the second uroneural, which is a little shorter and narrower than the stegural, but it also ends at the anterolateral margin of the urostyle (Figure 10C,D). Uroneural 3 is slightly longer than the first two uroneurals. Dorsal to hypural 7 (Figure 9), four more uroneurals are present, which are small and fusiform in shape (UAHMP 1063). There are no epurals preserved.

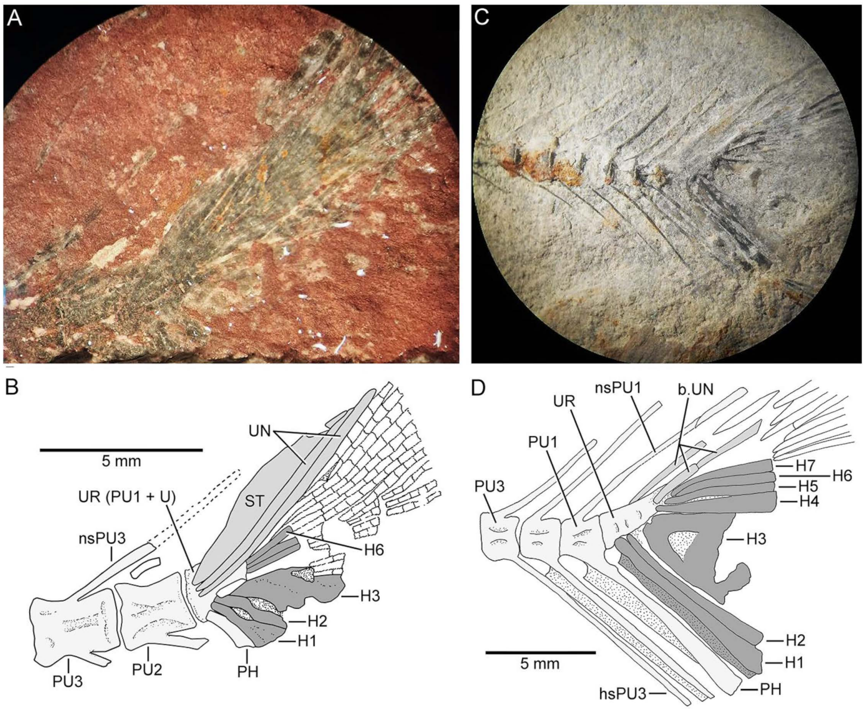

Figure 10. †*Xeneichthys yanesi* gen. et sp. nov. (**A**) Photograph and (**B**) line drawing of the caudal skeleton of specimen UAHMP 4697; (**C**) photograph and (**D**) line drawing of the caudal skeleton of specimen UAHMP 3158. Abbreviations: b.UN, broken uroneural; H 1–7, hypurals 1–7; hsPU3, haemal spine of preural centrum 3; nsPU3, neural spine of preural centrum 3; nsPU1, neural spine of preural centrum 1; PH, parhypural; PU2, 3, preural centrum 2, 3; UN, uroneural; UR (PU1 + U), urostyle (preural centrum 1 + undetermined ural centra); st, stegural.

The homocercal caudal fin is deeply forked. An incomplete ventral scute is preserved on UAHMP 1063 (Figure 9), which is not in situ. It is long, with a rounded posterior region, but it is broken at its anterior end so that its complete length is unknown. The fin rays are segmented and branched, but due to their poor preservation and incompleteness, we avoid providing details on them.

Squamation: In general, scales are poorly preserved or not preserved at all. The few scales observed in three specimens are cycloid and ctenoid. A few cycloid scales (Figure 11A) are preserved on the lateral and dorsal regions of UAHMP 3656, a large specimen which is incompletely preserved, so its SL is unknown. The scales are rounded with incomplete circuli in the anterior field, and no radii are present. Numerous tiny tubercles are observed in the posterior field of the scales. Isolated scales are also preserved in the lateral region of UAHMP 3159 and UAHMP 4698. The scales are slightly rounded and measure between 1.5 and 2.0 mm. Their surface is weathered out, preserving incomplete, parallel furrows and no ornamentation. A few ctenii are observed at their posterior margin (Figure 11B).

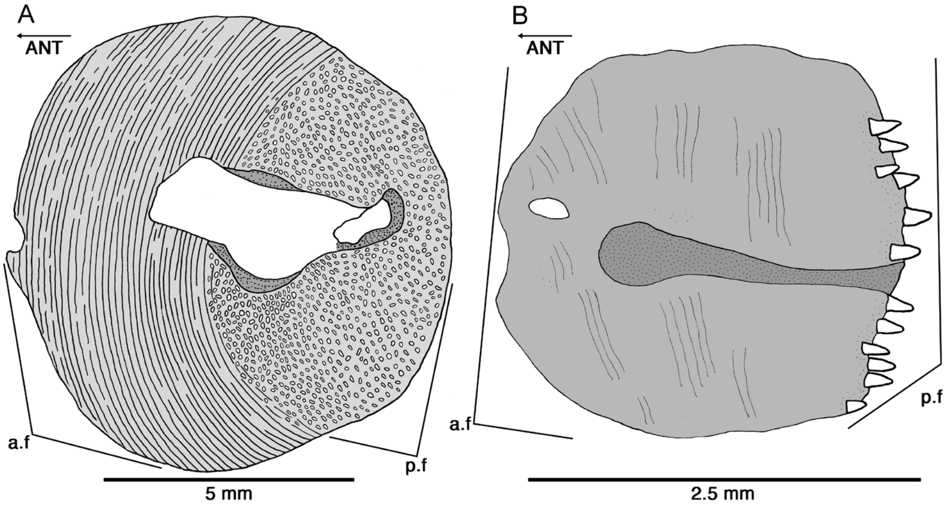

Figure 11. †*Xeneichthys yanesi* gen. et sp. nov. (**A**) lateral line cycloid scale (UAHMP 3656); (**B**) ctenoid scale (UAHMP 3159). Abbreviations: a.f, anterior field; ANT, oriented anteriad; p.f, posterior field.

4. Taxonomic Comments and Assignments

Although this study includes several specimens, their preservation makes it difficult to describe them because of the dark gray color of both the specimen and its matrix (Figure 3). In addition, the delicate fin rays are poorly preserved in comparison to the strong bones of the cranium. Independent of these difficulties, we have no doubt that these specimens represent a new taxon among the fish fauna of the Muhi Quarry because of its unique morphology—even for a Cretaceous teleost.

Preliminarily, the fish was thought to be an elopomorph, a megalopid-like fish, by González-Rodríguez and Fielitz [51,52] mainly because of the presence of a superior mouth, a deep cranium, a long mandible extending behind the level of the orbit, both dentary and maxilla with small conical teeth, and numerous intermuscular bones. This preliminary assignment was also due to the skull resembling a megalopid in its roof curvature, orbital size, and the lower jaw positioned slightly anterior to the upper jaw ([55]: Figure 31; Arratia pers. obs.). However, the preparation of more specimens and comparisons with *Megalops atlanticus* and *M. cyprinoides* (see Appendix A) have shown that beyond the superficial resemblance there are major differences in the morphology of megalopids and the new fish, †*Xeneichthys yanesi* gen. et sp. nov., as described above. Additionally, †*X. yanesi* has a very different cranial morphology from another elopomorph from Muhi Quarry, the albuliform †*Nunaneichthys mexicanus* ([26] and at least two undescribed species).

A broad analysis of the morphological characters of †*Xeneichthys yanesi* furthermore demonstrates that the fish is not an elopomorph or an osteoglossomorph because it has one bone at the posterior part of the lower jaw that is identified as the anguloarticular (Figure 4), and the retroarticular is not included in the articular facet of the lower jaw. The presence of an anguloarticular is a prominent character of Clupeocephala [50,56]. Additional clupeocephalan characters are a neural arch over ural centrum 1 that is reduced or absent and a reduced number of hypurals. As shown in Figures 9 and 10, †*Xeneichthys yanesi* does not have neural arches on preural centrum 1 and ural centra. Extant clupeocephalans consistently have a reduced number of bony hypurals (six or less; for a survey in extant teleosts see [57]) in comparison to some older fossils interpreted as clupeocephalans with more than six hypurals, for instance, the Late Jurassic †*Leptolepides* and †*Orthogonikleithrus* from Europe ([33]: figs. 44 and 53), †*Luisiella* from South America, and †*Cavenderichthys* from Australia ([33] and [58]: Figure 12). †*Xeneichthys yanesi* also has more than six hypurals (Figures 8 and 9).

The cohort Clupeocephala was erected by Patterson and Rosen [59] to contain the subcohorts Clupeomorpha (e.g., engraulids and clupeids) and Euteleostei (e.g., salmonids, galaxiids, and percomorphs). The current interpretation of Clupeocephala—based on both morphological and molecular evidence—includes the Otomorpha or Ostarioclupeomorpha and Euteleostei or Euteleosteomorpha [31,32,50]. Among the clupeocephalan characters, some cannot be verified in the new fossil fish due to preservation, for instance, there is not an early ontogenetic stage of †*Xeneichthys yanesi* to check for the "autopalatine ossified early in ontogeny" [50], and there is no soft anatomy preserved in these fossils to confirm the "hyoidean artery piercing the ventral hypohyal" [50].

The presence of a stegural in the caudal skeleton is interpreted as a synapomorphy of Euteleostei [28,56,59,60]. A stegural is a modified uroneural bearing a membranous outgrowth dorsally [45,50]; however, it is unclear whether the stegural is a modification of the same uroneural among euteleostean clades, making the homology of this structure unlikely [46,50]. However, it was demonstrated that a membranous outgrowth on the first uroneural or stegural also can be found in several fossil clupeocephalans *incertae sedis*, such as the Late Jurassic teleosts *Leptolepides* and *Orthogonikleithrus* and the Cretaceous *Erichalcis* [28,50]. The Cretaceous fish studied here, †*Xeneichthys yanesi,* also has a stegural (Figures 9 and 10), which is another feature supporting its assignment to Clupeocephala, specifically, to Euteleosteomorpha. Other synapomorphies of Euteleosteomorpha, e.g., "pattern 2 supraneurals" and "caudal median cartilages" [55] cannot be checked in the new fossil because of preservation conditions. Additionally, despite its poor preservation, one specimen shows a structure identified as a urostyle in euteleosts (=preural centrum 1 and ural centra fused into one single compound element; Figure 10B,D), while another specimen shows preural centrum 1 separated from the fused ural centra (Figure 10D). These differences may represent differences in ontogeny. The interesting point here is that the so-called urostyle is a feature commonly found in euteleosts, though it does occur in the gonorynchiform *Chanos chanos* (G. Arratia pers. obser.).

To make things more interesting, †*Xeneichthys yanesi* has the scales poorly preserved, but in these specimens where this character can be observed, two kinds are preserved: cycloid (Figure 11A) and ctenoid (Figure 11B). The first one is present in many stem teleosteomorphs [29,47,48] and stands as a teleostean synapomorphy at the phylogenetic level of †*Leptolepis coryphaenoides* plus more advanced teleosts [28,29,33,53], including stem and crown elopomorphs, osteoglossomorphs, and otomorphs, whereas the second one can be found in many euteleosts [61], which have modifications and configurations of the ctenii in the posterior field of the scale that characterize certain clades. The presence of ctenii on the scales, plus the stegural and urostyle in the caudal skeleton, could be interpreted as characters supporting the new family †Xeneichthyidae as a member of the Euteleostei.

The fishes identified here as belonging to the new family †Xeneichthyidae, which currently is known by one genus and species (†*Xeneichthys yanesi* gen. et sp. nov.), are characterized by an unusual combination of unique characters, for example, a head with an almost rounded ventral profile shaped by a long and massive lower jaw protruding anteriorly to the snout into a protractile mouth and the slightly concave profile of the skull roof that reaches its deepest point at the level of the opercular region, giving the head an almost triangular aspect (Figure 4). Additionally, some of the head bones have a notable dorsoventral elongation, such as infraorbitals 3 and 4, the preopercle, and the opercle. The fish is also noteworthy in the reduction in or loss of certain bones, such as the circumorbital series reduced to four bones, one supramaxilla instead of two, interopercle absent, and pelvic plate or basipterygium and pelvic fin absent. Fishes with an especially narrow preopercle and narrow opercle and subopercle are found in some aulopiforms (e.g., *Evermannella*), some pearleyes (Scopelarchidae), and some stomiiforms (e.g., *Gonostomata*); however, independent of the narrow opercular bones, the position of these bones is not similar to those in †*Xeneichthys yanesi* gen. et sp. nov. nor is the structure of other cranial bones.

As reported above, Clupeocephala includes the Otomorpha and Euteleostei or Euteleosteomorpha, which includes the majority of teleostean fishes today, with thousands of recognized families [31,32,62]. We extensively surveyed the literature and are unable to assign †*Xeneichthys yanesi* n. gen. et sp. to any of the existing teleostean families. Furthermore, due to its combination of characters and the difficulties interpreting some soft anatomical synapomorphies, it is difficult to assign †Xeneichthyidae to a specific euteleostean clade, though there is strong evidence supporting the new fish as an euteleost. Considering such arguments, we interpret the extinct †Xeneichthyidae new family as a Euteleostei *incertae sedis* until more specimens become available for study.

5. Early Cretaceous (Albian) Mexican Crown Teleosts

The fossiliferous content on Early Cretaceous teleosts of Mexico, especially from Muhi (El Doctor Formation) and Tlayúa of Tepexi de Rodríguez (Tlayúa Formation) Quarries, is characterized by a variety of crown teleostean clades containing new species belonging to major lineages, especially of euteleosts that coexisted with a variety of stem teleosts. Both of these quarries are currently interpreted as Albian (ca. 100.5–93.9 Ma [20,63]), close to the boundary between the Early and Late Cretaceous.

Teleosts from the Albian of the Tlayúa Formation in Tepexi de Rodríguez include a few stem teleosts interpreted as †Crossognathiformes, such as the †pachyrhizodontid *Michin csernai* [64] and the †ichthyodectiform *Unamichthys espinosai* [65]. A few others are from Muhi Quarry, such as †*Heckelichthys preopercularis*, an indeterminate †cladocyclid species [5], and a new species of †Crossognathiformes, *Motlayoichthys sergioi* [4].

Among Albian teleosts from Mexico are some elopocephalans from the Tlayúa Quarry, for instance, †*Araripichthys weberi* [66] and the elopiform †*Epaelops martinezi* [67]. A new albuliform (†*Nunaneichthys mexicanus* [26]) has recently been described from the Muhi Quarry, and a few other elopomorphs remain undescribed. Among clupeocephalans, several clupeomorphs identified as †Ellimmichthyiformes are represented in the Tlayúa Quarry, for instance, †*Armigatus carrenoae* [68], †*Armigatus felixi* [69], and †*Paraclupea seilacheri* [70]. From Muhi Quarry, one †Tselfatiiformes [3] and one indeterminate gonorynchiform [2] have been reported. Recently, two indeterminate specimens of †Araripichthyidae were also found.

Several euteleosts, belonging to a variety of taxa with different phylogenetic positions, have been discovered in the Albian of Muhi Quarry, for instance, the Aulopiformes †*Ichthyotringa mexicana* [35] and †*Enchodus zimapanensis* [36], the acanthomorph *incertae sedis* †*Muhichthys cordobai* [37], the beryciform †*Handuichthys interopercularis*, and the acanthomorph *incertae sedis* †*Dalgoichthys tropicalis* [38].

The Albian El Doctor and Tlayúa Formations have produced a variety of teleosts, all of them endemic to one or the other of these formations—a fact that opens major questions about these places as origin and diversification centers of teleosts in the crucial times when the Atlantic and Pacific Oceans were connected throughout the Proto-Caribbean Sea. Certainly, the new connection opened new environmental possibilities to the faunas and floras of the region; what is currently Mexico had a strategic position between two big oceans that were connecting, and these new environments gave rise to the various fish faunas of at least the Tlayúa and the El Doctor Formations. These faunas had some stem and crown teleosts, including some advanced euteleosts, which suggest these two quarries were major centers of diversification of teleostean faunas in the Early Cretaceous.

There are no other Albian localities with fishes in Mexico to strengthen the idea of an early diversification of euteleosts in the Proto-Caribbean Sea during the end of the Early Cretaceous; nevertheless, these fish groups already present in the Albian of Mexico diversified during the Late Cretaceous, extending their distribution to the south during the Cenomanian [71,72] and to the north during the Turonian and Maastrichtian [73–75], reaching even the Western Interior Sea.

6. Paleobiological Considerations

The new genus and species †*Xeneichthys yanesi* is one of the most numerous fish taxa found in the Muhi Quarry, following †*Enchodus zimapanensis* [36], the small beryciforms belonging to the family †Pseudomonocentrididae [38], and the †ichthyodectiform *Hecke-*

lichthys preopercularis [5] in abundance. All these fishes have been collected at the base of the outcrop or one meter below it. Some specimens were in the same layer near each other, suggesting that they were living in the same environment at the same time. †*Xeneichthys yanesi* gen. et sp. nov. is not the exception, with at least UAHMP 3157, UAHMP 3158, and UAHMP 3159 having been collected in the same speciose layer, as well as UAHMP 4697, UAHMP 4698, and UAHMP 4699 in two different fieldwork seasons.

According to Bravo-Cuevas et al. [1], the fossil concentration of the Muhi Quarry represents a mixed parautochthonous–allochthonous association that may live at or near the site of the deposit in an outer shelf setting within the warm waters of the western Tethys. †*Xeneichthys yanesi* gen. et sp. nov. could be part of the parautochthonous fauna because of its abundance in the locality. On the other hand, Fielitz and González-Rodríguez [36] proposed that †*Enchodus zimapanensis* and other fishes of the quarry, such as the bericoids, were part of a paleocommunity due to the presence of juvenile or sub-adult specimens of different taxa in the outcrop; the size range of †*Xeneichthys yanesi* gen. et sp. nov. fossils (SL 91–170 mm) also suggests the presence of different growth stages, supporting their interpretation of a community.

Regarding the numerous conical teeth and jaw positions of †*Xeneichthys yanesi* gen. et sp. nov., it is possible to speculate that the species could have been a suction-feeder predator of other small fishes or small invertebrates in the upper part of the water column, as occurs in other taxa with superior or protractile mouths.

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Conflicts of Interest: The authors declare no conflicts of interest.

Appendix A

A.1. Material Studied

The material listed below includes some fossil and extant teleosts used in comparisons to place *Xeneichthys yanesi* gen. et sp. nov. taxonomically. The specimens are listed following a taxonomic arrangement and ordered alphabetically within each taxon. Extinct taxa are identified with the sign "†".

Institutional Acronyms:
AMNH, American Museum of Natural History; New York, USA.
ANSP, Academy of Natural Sciences of Philadelphia; Philadelphia, USA.
CAS, California Academy of Sciences; San Francisco, California, USA. The addition of (ICH), (IUM), and (SU)-ICH refers to special collections within the catalogue of the institution.
DMNH, Denver Museum of Natural History; Denver, USA.
FMNH-PF, Field Museum of Natural History, Paleontology; Chicago, Illinois.
JFBM, James Ford Bell Museum; Saint Paul, Minnesota, USA.
JME SOS and **JME ETT**, Jura Museum; Eichstätt, Germany (SOS and ETT refer to specific collections in Solnhofen and Ettling).

KU:KUI, Museum of Natural History, Ichthyology; University of Kansas, Lawrence, Kansas, USA.
MCZ:Ich, Museum of Comparative Zoology, Ichthyological Collection, Harvard University; Cambridge, Massachusetts, USA.
SIO or SIO CR, Scripps Institution of Oceanography, University of California; LA Jolla, California, USA.
SMNS, Department of Paleozoology, Museum of Natural History; Stockholm, Sweden.
TCWC, Texas A&M University Biodiversity Research and Teaching Collections; Austin, Texas, USA.
UALVP, Laboratory of Vertebrate Paleontology, University of Alberta; Edmonton, Canada.
UAHMP, Museo de Paleontología, Universidad Autónoma del Estado de Hidalgo; Mexico.
UCLA, Department of Biology, University of California; Los Angeles, USA.
UF, Florida Museum of Natural History; Gainesville, Florida, USA.
USNM or **USNM UW**, United States National Museum of Natural History, Ichthyology; Washington, D.C., USA.
VIMS, Nunnally Ichthyology Collection, Virginia Institute of Marine Sciences; Gloucester Point, Virginia, USA.

Abbreviations:

cl&st = cleared and double-stained specimens for cartilage and bone; NL = notochordal length. Skl = skull length; SL = standard length; Sp. = specimens; Uncat = without catalog number.

Teleosteomorpha.

†**Aspidorhynchiformes**. *Vinctifer* sp. UAHMP 1378, UAHMP 3964.

†**Crossognathiformes**. †*Motlayoichthys sergioi*: UAHMP 600.

†**Pachyrhizodontidae indet**. UAHMP 3851, UAHMP 2018.

†**Ichthyodectiformes**. †*Heckelichthys preopercularis*: UAHMP 4437, 252 mm SL.

Elopocephala or Teleocephala (or crown-group Teleostei).

Elopomorpha.

Elopiformes. UAHMP 3852; UAHMP 4855; †*Anaethalion angustus*: JME SOS 2271; JME SOS 2259; and others. †*Anaethalion knorri*: JME SOS 2267a-b; JME SOS 2270; and JME SOS 2282. *Elops affinis*: SIO 69-167, 1 cl&st, 121 mm SL. UCLA W 50-29, 4 cl&st., 121.3, 128.4, 157, and 165 mm SL. *Elops hawaiensis*: CAS(SU) 35105, partially disarticulated skl, braincase of about 90 mm length. *Elops saurus*: ANSP 147401, 2 cl&st, 97.8 and 99.1 mm SL. CAS(SU) 10847, skl, ±395 mm SL. TCWC 0503.1, 5 cl&st, 24.0, 24.0, 26, 30.0, and 35.0 mm SL; TCWC 0782.1, 3 cl&st., 35.7, 43, and 46.4 mm SL; TCWC 2452.2, 5 cl&st, 60.1, 97.3, 107, 110.4, and 154 mm SL. UNC 82/8, 2 cl&st, 57 and 76 mm SL. †*Elopsomolos frickhingeri*: JME SOS 4393. *Megalops atlanticus*: UF 171286, 5 cl&st, 26.3, 27.8, 29.1, 29.8, and 40.5 mm SL; UF 208605, 5 cl&st, 25.5, 31, 32.7, 41.1, and 44.5 mm SL; UF 208780, 3 cl&st, 85, 90.4, and 122.5 mm SL. *Megalops cyprinoides*: CAS 145216, 2 cl&st, 17.5 mm and 34.5 mm SL.

Albuliformes. †*Nunaneichthys mexicanus*: UAHMP 4232. *Albula vulpes:* AMNH 56840, skl, ±292 mm SL; AMNH 56743, skl, ±300 mm SL; and AMNH 56878, skl, ±305 mm SL; UCLA W58-96, 2 cl&st, 195 and 220 mm SL. UCLA W49-122, 5 cl&st, 46.7, 54.6, 63.5, 72.7, and 88.8 mm SL.

Osteoglocephala or Osteoglossocephalai.

Hiodontiformes. *Hiodon alosoides*: JFBM 43312, 1 skl, ±400 mm SL; and JFBM 43306, 1 skl, ±380 mm SL. KU:KUI 7618, 7 cl&st, from 22.0 to 56.0 mm SL; KU:KUI 9618, 7 cl&st, from 22 to 55 mm SL; KU:KUI uncat. 3 cl&st, 68, 70, and 72 mm SL; KU:KUI 9661, 2 cl&st, 59 and 67 mm SL; KU:KUI 13993, 2 cl&st, 200 and 305 mm SL. *Hiodon tergisus*: KU:KUI 9662, 3 cl&st, 48.6, 51.8, and 55.7 mm SL.

Clupeocephala.

Incertae sedis. †*Araripichthys incertae sedis*: UAHMP 3763, ±110 mm SL.

†*Leptolepides haertesi*: JME SOS 2473, JME SOS 2474, and JME SOS 2554. †*Leptolepides sprattiformis*: FMNH-PF 10984 and FMNH-PF 10986; JME SOS 2956; KUVP 60722 and KUVP 96128; SMNH P 1891, SMNH P 1894, SMNS 55106, and SMNS 55928. †*Orthogonikleithrus hoelli*: JME ETT 2301, JME ETT 2632, JME ETT 3954, JME ETT 3955, and JME ETT 3956.

†*Orthogonikleithrus leichi*: JME SOS 2301 and JME SOS 2632. †*Orthogonikleithrus* sp.: JME ETT 30 and JME ETT 216.

†Tselfatiiformes. *Tselfatia formosa*: UAHMP 4656, 250 mm SL.

Otomorpha.

Clupeiformes. Clupeinae indet; UAHMP 2878, UAHMP 3145, and UAHMP 3849, 110 mm SL. *Alosa chrysochloris*: KU:KUI 9634, 2 cl&st, 43.7 and 54.3 mm SL. *Anchoa mitchilli*: KU:KUI 7494, 2 cl&st, disarticulated specimens; KU:KUI 17183, 2 cl&st, disarticulated specimens. *Brevoortia patronus*: KU:KUI 15113, 5 cl&st, disarticulated specimens. *Dorosoma cepedianum*: KU:KUI 12100, 3 cl&st, 30.5, 67, and 71.6 mm SL; KU:KUI 16167, 1 cl&st, 46.9 mm SL; KU:KUI 21801, 169 cl&st (100 sps. from 8 mm notochordal length (NL) to 15 mm SL and 69 sps. from 13.9 to 29.5 mm SL). *Engraulis encrasicolus*: KU:KUI 19941, 8 cl&st, 25 to 50 mm SL. *Ethmidium maculatus*: KU:KUI 19349, 2 cl&st, disarticulated large specimens. *Lile stolifera*: KU:KUI 5411, 3 cl&st, 29.5, 45.6, and 52.2 mm SL; UCLA 58-307, 3 cl&st, 71.7, 80, and 88.1 mm SL. *Sardinops sagax*: KU:KUI 19345, 6 cl&st larvae, 14 to 19 mm SL, and 4 cl&st disarticulated large specimens.

Alepocephaliformes. *Alepocephalus agassizii*: VIMS 6606, 1 cl&st, 100.9 mm SL. *Alepocephalus tenebrosus*: SIO 91-80, 124 and 154 mm SL; USNM UW 042217 #3, 3 cl&st, 87.7, 119, and 150 mm SL; USNM UW 042217 #4, 1 cl&st, 363 mm SL. *Bathylaco nigricans*: SIO 91-19, 1 cl&st partially disarticulated; SIO 64-15-8, 1 cl&st partially disarticulated. *Bajacalifornia burragei*: SIO 53-235, 2 cl&st, 91.7 and 79.6 mm SL; SIO 69-489, 1 cl&st, 133.7 mm SL. *Bathytroctes microlepis*, 1 cl&st, 61.3 mm SL. *Holtbyrnia latifrons*: SIO 71-112, 1 cl&st, 59.6 mm SL. *Mirorichthys caningi*: SIO 66-20, 1 cl&st, 91.5 mm SL. *Mirorichthys taaning*: SIO 82-85, 97.8 mm SL. *Paraholtbyrnia cyanocephala*, SIO 077, 1 cl&st, 126.4 mm SL. *Pellisolus eubranchus*: SIO 60-287, 1 cl&st, 93 mm SL. *Photostylus pycnopterus*: VIMS 15368, 1 cl&st, 49.9 mm SL. *Sagamichthys abei*: SIO 66-468, 1 cl&st partially disarticulated. *Searsia koefoedi*: SIO 77-38, 1 cl&st, 115.9 mm SL; SIO 77-53, 1 cl&st, 117.9 mm SL. *Searsioides multispinus*: SIO 077-21, 1 cl&st, aprox. 100 mm SL. *Talismania aphos*: SIO 72-141, 1 cl&st, 103.8 mm SL. *Talismania bifurcata*: KU:KUI 41394, 1 cl&st, 16.73 mm SL; KU:KUI 41395, 1 cl&st, 28.18 mm SL; SIO 56-68, 4 cl&st, 18.9, 23.2, 25.8, and 30.6; SIO 64-1027, 2 cl&st, 67.44 and 71.4 mm SL. *Xenodermichthys copei*: VIMS 3550, 1 cl&st, 82.1 mm SL.

Ostariophysi.

Gonorynchiformes. Gonorynchiformes indet.: UAHMP 3774 ± 54 mm SL. *Chanos chanos*: CAS(SU) 35075, 1 skl, disarticulated, braincase of 148 mm length; KU:KUI 40365, 4 skl, 370 and 376 mm SL and 4 cl&st, 150, 180, 330, and 400 mm SL.

Euteleostei.

Esociformes. *Esox americanus*: KU:KUI 5227, caudal skeleton only, cl&st; KU:KUI 17864, 4 cl&st, 82.7, 89.5, 112, and 123 mm SL. *Esox lucius*: KU:KUI 19092, disarticulated skull, lower jaw 120 mm length, and caudal skeleton.

Salmoniformes. †*Erichalcis arcta*: UALVP 8598, UALVP 8602, UALVP 8606, and UALVP 8612. †*Humbertia* sp.: DMNH 2518-1. *Oncorhynchus mykiss*: KU:KUI 12463, 7 cl&st, from 28.0 to 43 mm SL; KU:KUI 21936, 20 cl&st, 290 to 300 mm SL; OS uncat., day-to-day ontogenetic series of about 200 cl&st, from 13 mm NL to 73 mm SL. *Prosopium cilindraceous*: KU:KUI 15417, 2 cl&st, 300 and 310 mm SL. *Prosopium williamsoni*: KU:KUI 11817, 13 cl&st, twelve larvae between 20 and 33.6 mm SL and one specimen of 230 mm SL. *Thymallus arcticus*: KU:KUI 15419, 3 cl&st, 151, 166, and 177 mm SL. *Umbra limi*: KU:KUI 10370, 6 cl&st, 22.5, 26.3, 27, 27.8, 52, and 54.4 mm SL.

Argentiniformes. *Argentina sialis*: SIO 66-4, 3 cl&st, 119, 121.2, and 144.2 mm SL; SIO CR 5208, 4 cl&st, four larvae of 9.0 to 14 mm NL, and one specimen of 13.5 mm SL

Aulopiformes. †*Ichthyotringa mexicana*: UAHMP 2067; †*Enchodus zimapanensis* UAHMP 679, 208 SL.

Order Centrarchiformes.

Suborder Percichthyoidei.

Bostockia diagramma: MCZ:Ich: 33108, 2 sp., 34.1 and 34.6 mm SL. *Gadopsis marmoratus*: CAS-ICH 024428, 18 sp., 48 mm to 92.3 mm SL and 1 cl&st, dissected. MCZ:Ich: 27554, 1 sp., 177 mm SL. USNM 308109, 2 cl&st partially dissected; 31.8 mm and 62.7 mm SL. USNM 344900, 1 cl&st, 130.7 mm SL. *Maccullochella macquarensis*: CAS-ICH 20790, 1 sp., 212 mm SL. *Macquaria ambigua* (= *Plectroplites ambiguus*): CAS-ICH 23516, 1 sp., ca. 170 mm SL. CAS-ICH 24429, 2 sp., 167 mm SL. USNM 287450, 1 cl&st, 53.2 mm SL. *Nannoperca australis*: USNM 218843, 2 cl&st, 39.7 mm and 41.5 mm SL. USNM 399435, 2 sp., 38.34 mm and 43.4 mm SL. *Percichthys colhuapiensis*: CAS(SU)-ICH 31614, 2 sp., 224 and 231 cm SL. KU:KUI uncat: 2 cl&st dissected. *Percichthys chilensis*: CAS(IUM) 15559, 2 sp.; CAS 70005, 3 sp., ca. 135 to 185 mm SL; CAS 79013, 3 sp., 61.2 mm, 103.7 mm, and 172 mm SL. CAS-ICH 79015, 1 sp.; CAS-ICH 79019, 2 sp. *Percilia gillissi*: CAS-ICH 70189, 13 sp., 23.7 mm to 62.6 mm SL; CAS-ICH 70185, 10 sp., 31.1 to 55.8 mm SL; CAS-ICH 70190, 10 sp. KU:KUI 19241, 47 sp., 2 cl&st; KU:KUI 19303, 5 cl&st; KU:KUI 19314, 1 cl&st; KU:KUI 19334, 2 cl&st. MVNV 3256, 2 cl&st, 55.9 mm and 62 mm SL. USNM 290487, 4 sp. 51.5 mm, 54.3 mm, 63 mm, and 65.9 mm SL.

Centrarchidae. *Lepomis gibbosus*: KU:KUI 13983, 4 cl&st. *Lepomis megalotis*: KU:KUI 21928, 21 sp. *Pomoxis annularis*: KU:KUI 21463, 8 cl&st.

Percalatoidei.

Percalates colonorum (=*Macquaria colonorum* in Betancur-R et al., 2017): CAS 2913, 2 sp.; CAS 20786, 3 sp., 1 cl&st, 114.8 mm SL, 163 mm. CAS 20787, 4 sp.; CAS 24427, 145 mm SL. *Percalates novemaculeata* (=*Macquaria novaemaculeatus* in Betancur-R et al., 2017): CAS[SU] 20765, 3 sp., 148 mm SL; CAS[SU] 20786, 1 sp., 114.8 mm SL. USNM 312977, 1 cl&st, ca. 115 mm SL.

Order Pampheriformes.

Acropoma japonicus: CAS-ICH 6733. 3 sp., 1 cl&st; CAS-ICH 20776, 2 sp.

Doederleinia berycoides: CAS-ICH 17563, 21 sp., 2 cl&st; CAS-ICH 22631, 2 sp. 210 mm SL; CAS(SU) 23488, 2 sp. *Malakichthys grisseus*: CAS(SU) 17756, 4 sp., 140 mm SL. *Synagrops trispinosis*: CAS 61035, 10 sp., 1 cl&st.

Hollowellidae: Howella broidei: CAS 52432, 1 sp.

Lateolabricidae: *Lateolabrax japonicus*: CAS(SU) 7298, 1 sp.; CAS 9999, 10 sp.; CAS 28746, 1 sp.

Perciformes.

Percidae: *Perca flavescens*: KU:KUI 3741, 10 sp. *Stizostedium vitreum*: KU:KUI 4955, 2 sp.; KU:KUI uncat., 40 cl&st larvae.

Eupercaria, order *incertae sedis.*

Moronidae: *Morone chrysops*: KU:KUI 13147, 3 cl&st, dissected; KU:KUI 9881, 4 sp., 210 mm SL; KU:KUI 22669. 10 sp., ca. 114 to 200 mm SL; KU:KUI 16011, 1 cl&st; KU:KUI 16799, 10 cl&st; KU:KUI 18024, 5 cl&st. *Morone sexatilis*: KU:KUI 18212, 2 sp., 1 cl&st, 71 mm SL.

Acanthomorpha *incertae sedis*? †*Muhichthys cordobai*: UAHMP 2068, 80 mm SL. Acanthomorpha *incertae sedis*, *Dalgoichthys tropicalis* UAHMP 1387.

Beryciformes, Pseudomonocentrididae: †*Handuichthys interopercularis*: UAHMP 1389, ±44 mm SL; †*Pseudomonocentris microspinosus* UAHMP 3721, 37.30 mm SL.

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