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A NEW GENUS AND SPECIES OF PYCNODONT FROM THE CRETACEOUS (ALBIAN) OF CENTRAL MEXICO, TEPEXI DE RODRÍGUEZ, PUEBLA

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ABSTRACT

A new genus and species of pycnodont, *Tepexichthys aranguthyorum* gen. et sp. nov., is described from the Tlayúa quarries, near Tepexi de Rodríguez, Puebla. The specimens were all collected in the middle member of the Tlayúa Formation of middle or late Albian age. *T. aranguthyorum* is characterized by: (1) a diamond-shaped body; (2) a deeply forked tail; (3) a small supraorbital above the orbit; (4) a deep and narrow notch in the maxilla; (5) a dentition containing numerous tooth shapes that occur in irregular rows; (6) 17 dorsal scutes all lacking definite serrations or spines; (7) 14 anterior ventral scutes also lacking serrations or spines; (8) two ventral scutes below the pelvic fin with large serrations; (9) two ventral scutes behind the cloaca with finger-like projections—making a total of 18 ventral scutes; and (10) dermal punctations on the three lower plates of the dermal armor and on some plates of the head.

This genus is considered as an advanced form of pycnodont, related to *Coelodus*; nevertheless, the whole group is in need of revision and, until this is accomplished, the placement of *Tepexichthys* must remain tentative. The large amount of variation, noted in the number and shape of the teeth, raises the question of the validity of using this element alone to define pycnodont genera and species. *T. aranguthyorum*, because of its body shape and dental apparatus, is considered an inhabitant of coral reefs. This is supported by observations of the preserved gut contents and the teeth which show a huge amount of wear, suggesting grazing on corals and algae.

Key words: holostean, pycnodont, paleoecology, taxonomy, Albian, Tlayúa quarry, Tepexi de Rodríguez, Puebla, Mexico.

RESUMEN

Se describe los nuevos género y especie de picnodonte, *Tepexichthys aranguthyorum* gen. et sp. nov., de las canteras Tlayúa, de Tepexi de Rodríguez, Estado de Puebla. Los especímenes provienen del miembro medio de la Formación Tlayúa de edad albiana media o tardía. *T. aranguthyorum* se caracteriza por poseer: (1) un cuerpo en forma de diamante; (2) una cola marcadamente bifurcada; (3) un pequeño supraorbital encima de la órbita ocular; (4) una muesca profunda y angosta en el maxilar; (5) una dentición compuesta por numerosas formas dentales que están presentes en hileras irregulares; (6) 17 escudos dorsales lisos, sin serraciones o espinas; (7) 14 escudos ventrales anteriores también lisos; (8) dos escudos ventrales con grandes serraciones, situados debajo de la aleta pélvica; (9) dos escudos ventrales con proyecciones digitiformes, atrás de la cloaca—totalizando 18 escudos ventrales; y (10) las tres placas inferiores de la armadura dérmica y algunas placas de la cabeza, ornamentadas con un característico puntuado dérmico.

Este género es considerado como una forma avanzada de picnodonte, emparentada con *Coelodus*; sin embargo, todo el grupo taxonómico necesita ser revisado y, hasta que esto haya sido realizado, la posición taxonómica de este nuevo taxón deberá permanecer tentativa. La enorme variación detectada, en cuanto a número y forma de los dientes de estos organismos, pone en duda su aplicación exclusiva para definir géneros y especies de picnodontes. Por la apariencia de su cuerpo y las características dentales, el hábitat de *Tepexichthys aranguthyorum* se interpreta como de arrecife coralino, lo cual está apoyado por el análisis de los contenidos estomacales preservados y por los dientes, mismos que presentan un enorme desgaste, sugiriendo el "mordisqueo" del coral y de las algas.

Palabras clave: holósteo, picnodonte, paleoecología, taxonomía, Albiano, cantera Tlayúa, Tepexi de Rodríguez, Puebla, México.

INTRODUCTION

The first fossil fish to be discovered in the Tlayúa quarries was a pycnodont of unknown affinities. The whereabouts of this specimen are unknown and it has not been seen by the writer.

The specimen was found by Félix Aranguthy in 1959. This discovery coincides with the first year of the operation of the complex. It was only in 1980, with the aid of the Aranguthy family, that the Institute of Geology of the University of Mexico began to collect these fish and to deposit them in the Institute's museum of the Department of Paleontology.

The location of the Tlayúa quarries, near Tepexi de Rodríguez, Puebla, is shown in Figure 1. The work to date in the quarries has been discussed in two field guides and in several other papers (Applegate and Espinosa-Arrubarrena, 1982; Applegate *et al.*, 1984; Applegate, 1987; Seibertz and Buitrón, 1987; Applegate, 1988, Martill, 1989; Pantoja-Alor *et al.*, 1989, among others).

Presently, the Tlayúa complex (Figure 2) may be divided into three areas: (a) the original, or Aranguthy quarry, which includes the sections AA', BB' and CC'. This portion of the quarry has been registered as IGM locality 370; (b) the National

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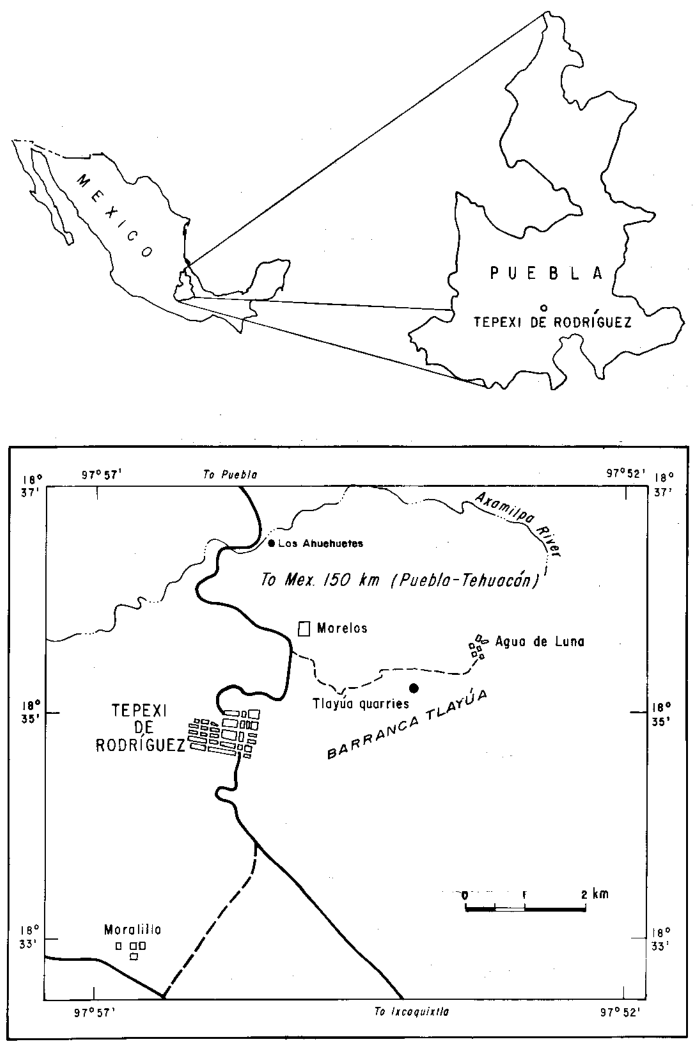

Figure 1.- Location map of the Tlayúa quarries, near Tepexi de Rodríguez, Puebla.

Geographic Society or Alacranes quarry (NGS) to the east, which includes the section DD'. This locality bears the designation IGM locality 1970; and (c) the National Science Foundation quarry (NSF), which underlies the eastern part of the Aranguthy quarry, sections BB' and CC'. Figure 2 shows the physical relationships of all these quarries.

The first quarry (a) was worked from 1959 to the present, the second (b) from 1983 to 1986, and the third (c) was operated from May 1986 to September 1988. More recently, 90 m east of the Alacranes quarry (loc. 1970), a new site has been opened, through the support of the Consejo Nacional de Ciencia y Tecnología (CONACyT grant P221CCON 892313). With this effort, the excavation operation has been significantly increased and in the near future there will be plenty of new material to be included in these studies. The level reached within the CONACyT quarry, in 1990, was 2 m above the productive beds of the Aranguthy quarry.

GEOLOGICAL SETTING

The geology of the Tlayúa quarries and the surrounding area has been the subject of several field investigations (Applegate, 1987; Pantoja-Alor *et al.*, 1989; Martill, 1989; Pantoja-Alor, 1990). The oldest beds in the area are those of the Acatlán Complex, of Paleozoic age (Ortega-Gutiérrez, 1978). According to Ortega-Guerrero (1989), during the Jurassic times, this complex represented a positive land surface, a condition that is thought to have existed also during the Early Cretaceous (Applegate, 1987). Presumably, resting on top of the Jurassic sediments, there is a series of limestones and, among these, there are the beds in which the pycnodonts described in this paper were collected. The carbonated lithostratigraphic unit was informally described by Pantoja-Alor and coworkers, in 1989, as the Tlayúa Formation. These sediments comprise a lower blue-grey massive limestone member, a red laminated middle member, which contains the fossiliferous quarries, and an upper grey-blue dolomitic member.

The lower member of the Tlayúa Formation consists of tightly-folded bioturbated limestones, which in its lower part bears the rudist *Toucasia polygyra*, above which is a distinct bed of bivalves of the genus *Chondrodonta*. The strata of this lower member are capped by an undescribed molluscan fauna, consisting of very small bivalves and gastropods. Also, throughout all these beds, numerous miliolids, that have yet to be described, can be found. The lower part of the middle member of the formation contains isolated undetermined pycnodont teeth. This member varies from 48 to 50 m in thickness, and consists of laminated, honey-colored limestones. The bedding planes show red hematitic layers, which bear a large array of well-preserved fossils. All the specimens of *Tepexichthys* come from beds that are more than 10 m below the top of this middle member. Finally, the upper member of the Tlayúa Formation is dolomitized and barren of fossils.

PALEOECOLOGICAL CONSIDERATIONS

To the east of the Tlayúa complex, there are limestones containing numerous hard corals and it is believed that some of these corals formed large reefs. These limestones are Early Cretaceous in age and therefore some may be contemporaneous to the Tlayúa Formation.

The extent and size of these beds suggest an undescribed large barrier reef at the western edge of the Tethys sea. Behind this reef, there was a large narrow lagoon that may have contained an extensive fauna related to the reef, part of which was found fossilized as an allochthonous element in the middle member of the Tlayúa beds.

Behind the lagoon—towards the land mass—at the time of deposition, it is thought that a definite barrier —perhaps an older reef—existed between the "biorich" lagoon and the Tlayúa deposits—back lagoon. This second barrier created the two most important conditions for the exquisite preservation of the fauna. One was a restricted circulation of water, resulting in an anaerobic and/or hypersaline environment. The second, perhaps a result of the first one, was the lack of an infauna and the absence of scavengers.

Algal mats were formed in the back lagoon. At times—perhaps in extremely dry seasons—this back lagoon was completely desiccated, causing the formation of mud cracks. There were also seasons when there was enough water to support a rich planktonic community, and large quantities of calcareous ooze were produced, resulting in a rapid burial of the organisms.

The fossils themselves, except some Foraminifera, were transported from two different areas to the Tlayúa beds. One was the adjacent land surface and the other was the "biorich" lagoon. The organisms entered the depositional environment of the Tlayúa beds when the barrier was breached, probably during

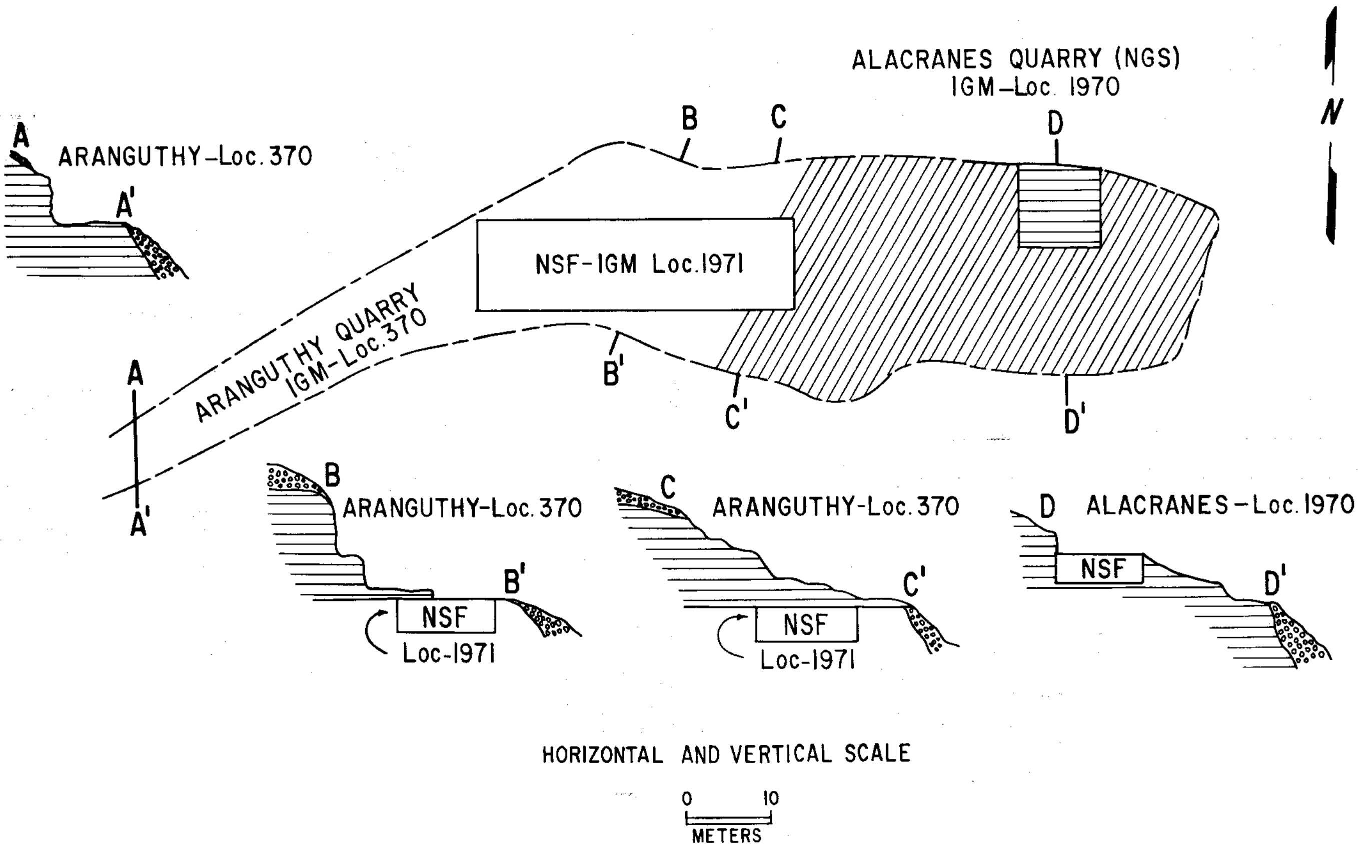

Figure 2.- The relationship of the quarries that exist in the Tlayúa complex.

periods of heavy rains and hurricanes, or during high tides or through a combination of these events.

SYSTEMATIC PALEONTOLOGY

Class Osteichthyes Huxley, 1880
Order Pycnodontiformes Berg, 1940
Family Pycnodontidae Agassiz, 1833

Genus *Tepexichthys* gen. nov.
(Figures 3-10)

TYPE SPECIES

Tepexichthys aranguthyorum sp. nov.

DIAGNOSIS

Body approximately diamond-shaped (Figure 3), with an averaged total length—from the tip of the snout to the tip of the tail—1.70 times the body depth; head twice as high as long. The anterior edge of the head slopes at about 60° from a dorsal-ventral axis perpendicular to the notochordal space.

All fins are pointed, except the pectoral and pelvic ones, which are rounded. The caudal fin is forked and indented, so that the posterior edge almost forms a shallow V-shape. The dorsal fin originates at the apex of the body, well in advance of the pelvic region, and inserts immediately in front of the upper lobe of the tail. This fin is elongated. Its front edge rises to a sharp point behind which it slopes, forming a shallow concave arch posteriorly (Figure 4). The anal fin is the second largest fin. Its length is about 3/4 that of the dorsal. The anterior edge of this fin is about three times deeper than the posterior and its external margin is straight, in contrast to the convex nature of the dorsal fin.

All neural and haemal spines have a supporting function, except the last pair, which is evidently free and supports neither pterygiophores nor caudal fin lepidotrichia. The tail lacks a definite caudal peduncle (Figure 4).

A total of 16 ventral scutes is present before the anal opening and two are behind this structure. The lower external portion of the body is formed by four rows of scutes above the ventrals. The lower rows of the lateral scutes and the ventrals are ornamented with rounded pits—punctations—that tend to be aligned in dorso-ventral rows. The shape of the scutes above the ventrals—first row—is elongated, lenticular and each bears a series of rounded crenulations. Above these, there are three more unornamented and interlocking rows of scutes (Figures 3 and 4). Along the top of the body, there are 17 dorsal scutes. From the first 14, five narrow scales extend to the ventral armor and the three most posterior are unattached, extending only slightly below the notochord. The most posterior dorsal scute has four scales instead of five (Figure 4). Each neural spine has an anterior blade, whose anterior margin is smooth and slightly curved. Similar blades occur on the haemal arches. The bases of all the neural and haemal arches are rounded and lack fluting (Figure 5).

The caudal fin in its lower portion has five haemal spines and a single parhypural. Behind these, there are four hypurals (1 through 4, respectively). The third hypural is the largest, followed by the second. There are six neural spines supporting the upper part of the caudal fin and, at least, one urodermal is present. There are two conspicuous caudal fin fulcra, one ventral and the other dorsal. The caudal fin is supported by 29 articulated and branching lepidotrichia (Figures 6 and 7).

The distinctive characters of the head plates consist of a plow-shaped supraoccipital above the temporal fossa (Figures 8 and 9). Posteriorly, this plate shows a fan-shaped limb with

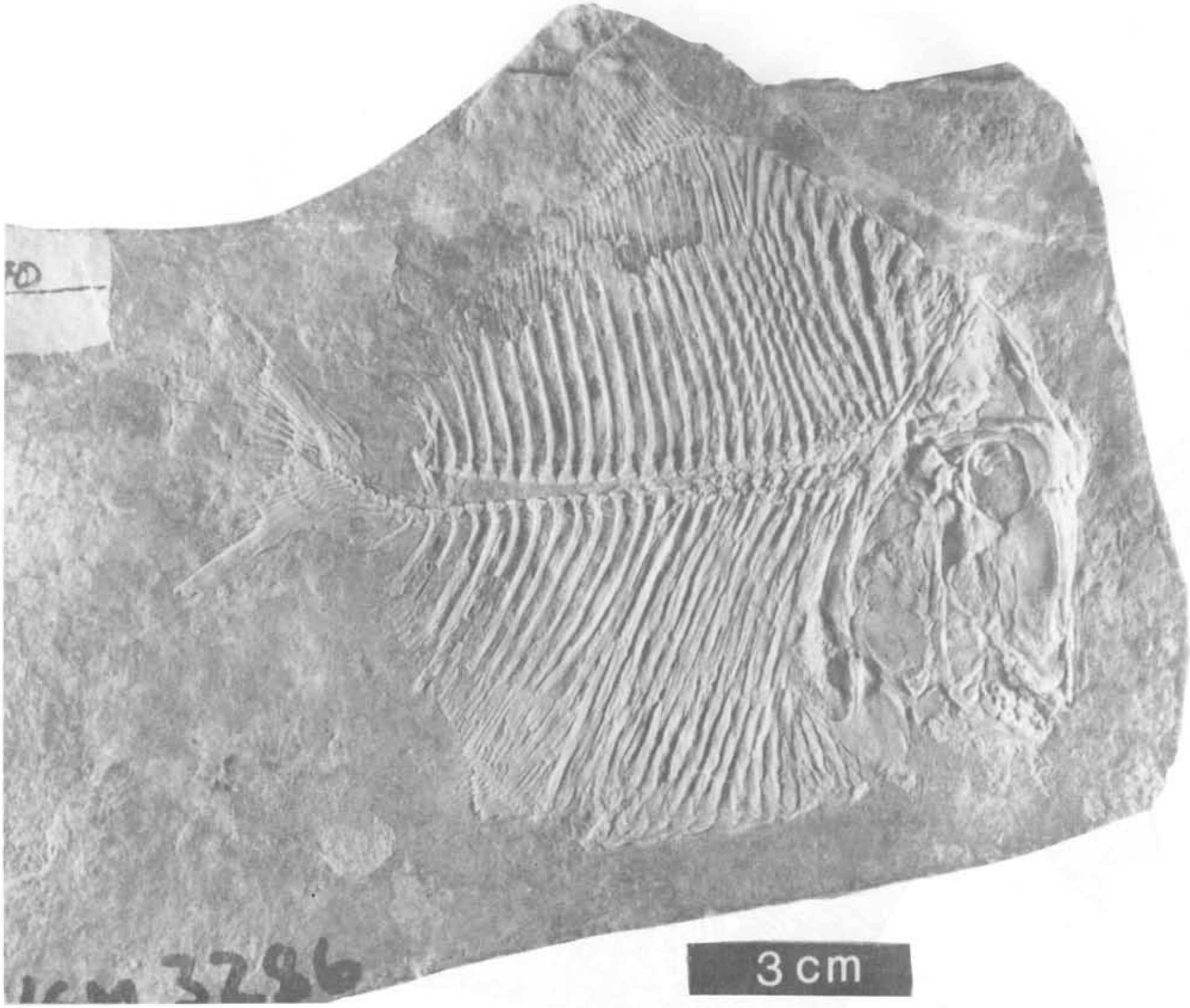

Figure 3.- Photograph showing the holotype of *Tepexichthys aranguthyorum*, IGM-3286.

spike-like radiating extensions. Below the temporal fossa, in the better preserved specimens, there is a distinctive supraorbital. The largest head plate is the preoperculum, which bears punctations that radiate out in rows, from its anterior upper portion. In front of the preopercular, the maxillary is large and oval, with a very characteristic deep and narrow anterior notch (Figures 8 and 9).

Teeth show a good deal of variation. In the upper jaw, there are six rows of vomerine teeth (Figure 10, A, B). All these are about the same size, but have various shapes. In the unworn state, the teeth have crenulated or scalloped edges and their centers show many hemispherical protuberances. The articulars on the lower jaw show three rows of teeth (Figure 10, C). The innermost are pill-shaped (Figure 10, C, 1); the intermediates are irregular, ranging from pill-shaped to circular (Figure 10, C, 2); and the teeth in the outermost row tend to be circular or irregular (Figure 10, C, 3).

ETYMOLOGY

Tepexichthys. "Tepexi" refers to the town of Tepexi de Rodríguez, Puebla, and "ichthys" is from the Greek *ichthyos*, meaning fish.

Tepexichthys aranguthyorum sp. nov.
(Figures 3-11)

DIAGNOSIS

As for genus.

DESCRIPTION

General shape and size—(Figures 3 and 4). In large—adult—undistorted specimens, the body tends to have a diamond shape. In the small specimens, presumably juveniles, the shape is more rounded. Nevertheless, the most common form of distortion—in large and small specimens—produces a more circular body shape. The caudal fin is forked and pointed, with a very shallow V-shaped posterior notch. The caudal peduncle is short and almost nonexistent. As with all known pycnodonts, in life this deep-bodied species must have been highly compressed laterally. Specimens range from 30 to 360 mm in total length.

Head plates—(Figures 8 and 9). The head plates may be described as follows: (a) The posteriormost median plate of the skull roof is the supraoccipital. In lateral view, only 1/2 of the plate can be seen. The posterior portion of this plate is fan-shaped with

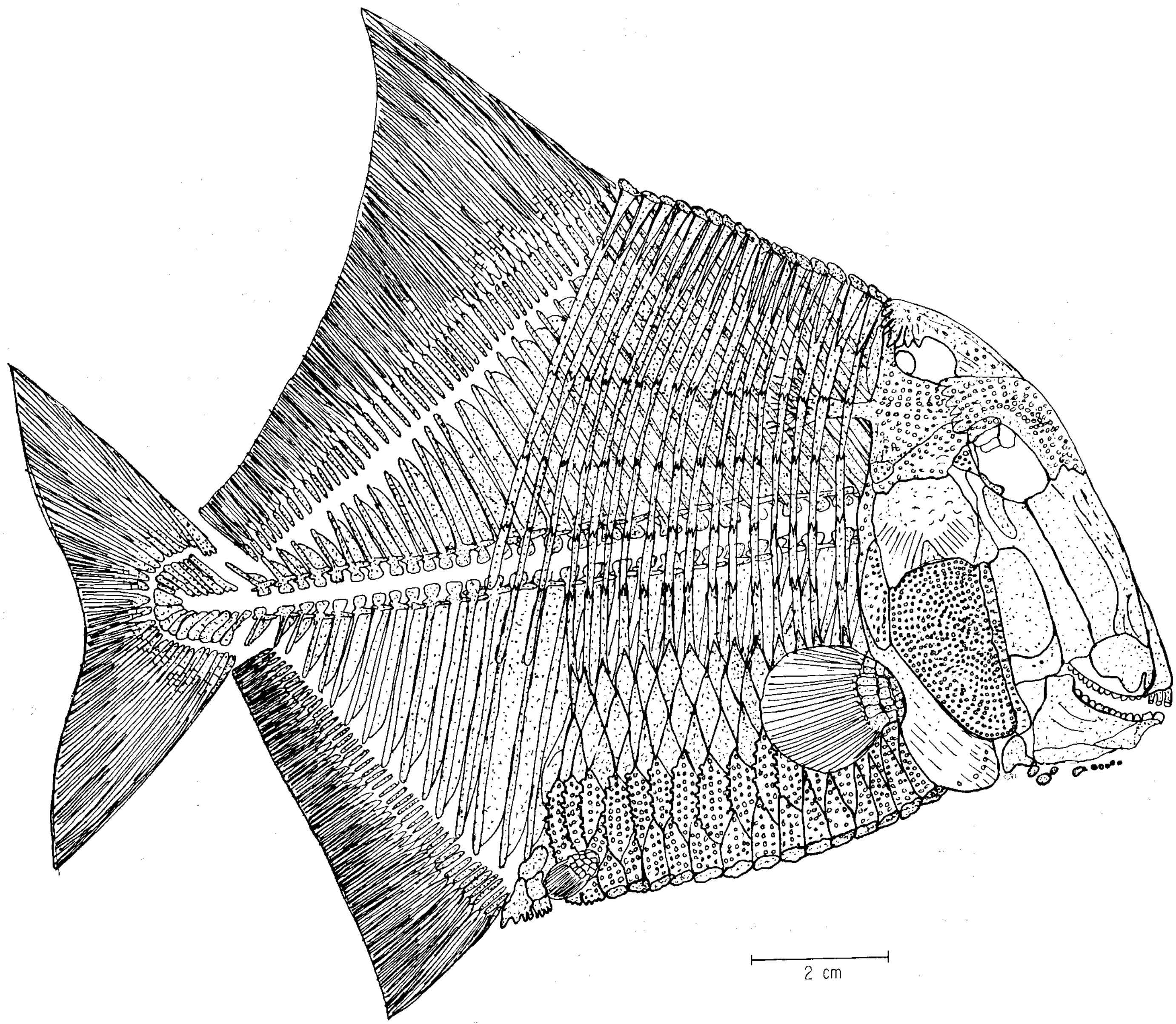

Figure 4.- Reconstruction of *Tepexichthys aranguthyorum*, based on the types used in this study.

about six points separated by conspicuous striations. The central portion of the plate is rectangular and the anterior part is triangular. The length of the plate is about three times greater than the width. In the central and posterior portions of this structure, there are a few rounded punctations. All the studied specimens showed the same condition described by Gardiner (1960) [Figure 5], in which no sensory canal occurs on the supraoccipital.

(b) Ventrally to the supraoccipital lies the temporal fossa, which is roughly rectangular. Anteriorly, the fossa is bordered by the posterior edge of the frontal. Posteriorly, it is bordered by the supraoccipital—the fan-like structure—and the parietal complex—upper limb—. On its upper edge, the fossa is bordered by the median portion of the supraoccipital, and below by the upper side of the parietal complex.

(c) Within the temporal fossa of the type—IGM 3286—a small rounded plate with punctations, similar to those of the parietal complex, was noted. This is interpreted as an abnormal fragmentation of the parietal plate.

(d) The parietal complex, equivalent to the parietal of Woodward (1939) and Lehman (1966), is here considered a compound element formed by the fusion of plates. Such a parietal occurs, for example, in *Macromesodon*, *Proscinetes* and *Coelodus*. Regarding this structure as a complex, Gardiner (1960) reached similar conclusions, but simply called the plate a parietal. In this complex, the anteriormost element is the parietal. Immediately behind this and attached to it is a part of the extrascapular series, which bears the sensory canal of the parietal complex. The canal runs ventrally to a free extrascapular (Figure 11). Behind the fused extrascapular part of the parietal complex, there is an extension, the digitate prominence of Gardiner (1960), also named the parietal peniculus by Nursall and Maisey (1991). This structure, whose origin and function are unknown, might be a highly modified scale bone or an ossified tendon. Most likely it is related to anchoring the skull to the body through muscle attachments. Gardiner (*op. cit.*) thought that this part of the parietal complex might represent a modified suprascapular; however, there is no evidence of sensory

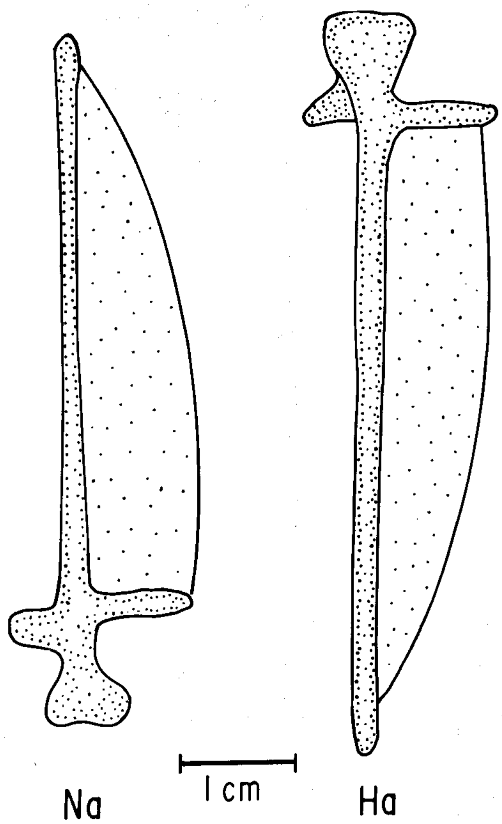

Figure 5.- Sketch of a neural arch (Na) and a haemal arch (Ha), from the central part of the body of *Tepexichthys aranguthyorum*, based on various specimens.

canals nor the normal plate-like bone that is associated with the suprascapular. The parietal complex is ornamented by rows of circular punctations that radiate from the median part of the complex, just in front of the sensory canal of the parietal complex. The punctations are missing in the extreme ventral portion.

(e) Posteriorly to the parietal complex and the supraoccipital, lies a plate that is club-shaped. Its exact nature is unclear. Here the plate is referred to as a postparietal, although it may represent a suprascapular or nuchal plate. The latter seems unlikely, as it is paired.

(f) An extrascapular lies below and laterally to the parietal complex. This is a small ovoid plate which receives a sensory canal from the parietal complex. Within the extrascapular, the same sensory canal—the extrascapular juncture—joins another canal (Figure 11). The latter posteriorly passes into the supracleithrum and anteriorly into the dermopterotic.

(g) The supracleithrum is a small, elongated oval plate behind the extrascapular. From the latter, it receives a sensory canal that posteriorly becomes the lateral line (Figure 11). Both the extrascapular and the supracleithrum are ornamented with punctations.

(h) Below and anteriorly to the extrascapular, lies the dermopterotic. As mentioned above, this plate receives a canal from the extrascapular. At its upper edge, the dermopterotic is bordered also by the parietal complex, the frontal, the supraorbital, the orbit, the dermosphenotic and the dermohyal. The dermopterotic is somewhat irregular, longer than deep, though deeper anteriorly than posteriorly.

(i) Anteriorly and ventrally to the dermopterotic, lies the dermosphenotic. This triangular-shaped plate receives a sensory canal from the dermopterotic (Figure 11), which in branching becomes the orbital canal. The anterior edge of the dermosphenotic borders the orbit and its posterior edge is adjacent to the hyomandibular or the dermohyal. The dermopterotic and the dermosphenotic bear rounded punctations, which on the dermopterotic may be arranged in rows.

(j) In front of the dermosphenotic, there is a portion of a membranous bone, here interpreted as an autosphenotic.

(k) Within the orbit, there are several fragments of smooth bone that were part of the sclerotic ring. The orbit is only slightly larger than the temporal fossa.

(l) In the upper part of the orbit, there is an elongated pill-shaped plate, the supraorbital. This plate can be identified by its sutures and by the small size of its punctations. There exists the possibility that this may be simply a fragmentation of the frontal, but since it has been noted in the type and at least two other specimens, it is here believed to be a separate plate.

(m) The frontal is a curved rectangular plate thickened in its medial part, in front of the orbit. This element shows a conspicuous ridge in its central part. On the ridge and in front of it, there are abundant punctations that radiate out from the center. In front of the orbit and behind the ridge, the frontal is smooth. The edge of this head plate is scalloped in its upper posterior portion. This is where it abuts the temporal fossa, the parietal complex and the dermopterotic.

(n) The mesethmoid consists of two parts: a dermal anterior portion and a posterior membranous element. Dorsally, the dermal portion forms a suture with the frontal and ventrally it abuts the premaxillary and maxillary. It is elongated and the lower part is bulbous. The membranous part of the mesethmoid is almost rectangular, and it is smooth and thin. This element, in its lowermost extremity, shows the remains of a sensory canal that comes from the anterior dermal portion of this plate (Figure 11).

(o) The parasphenoid can be seen running from the orbit to the posterior portion of the maxillary. This membranous bone is smooth, though generally covered by the surrounding plates.

(p) The infraorbital overlies the upper part of the parasphenoid and part of the hyomandibular. It lacks ornamentation and describes an elongated and anteriorly-curved shape.

(q) The hyomandibular is smooth and poorly exposed on all the specimens that were examined.

(r) The metapterygoid is large and oval in shape. It lies behind the posterior membranous portion of the mesethmoid and, in our specimens, it has been seen behind the parasphenoid.

(s) The endopterygoid lies directly below the metapterygoid. This plate is longer—in an anterior-posterior direction—than deep and curved to fit the rounded base of the metapterygoid.

(t) The quadrate is found ventrally to the endopterygoid. No symplectic was seen in the specimens studied.

(u) The dermohyal is the second or third largest dermal plate in the head. Its shape is approximately square and it is ventrally concave to fit the top of the preoperculum. The lower part of the dermohyal is ornamented by ridges that form a chevron pattern. The upper part of the plate is generally smooth.

(v) The preopercular is the largest dermal plate. It is ovate, being about twice as deep as long. In its anterior portion, there is a straight, raised bar, which bears three rows—or less—of punctations in its upper portion, and it is slightly striated in its lower portion. The rest of the preoperculum shows rows of punctations that radiate from the anterior upper part of the plate to the outer edge.

(w) The operculum is very elongated in a dorso-ventral direction, being five times deeper than long. It is rounded dorsally and more pointed ventrally. The center of ossification and ornamentation is at the anterior edge about 1/5 the distance below

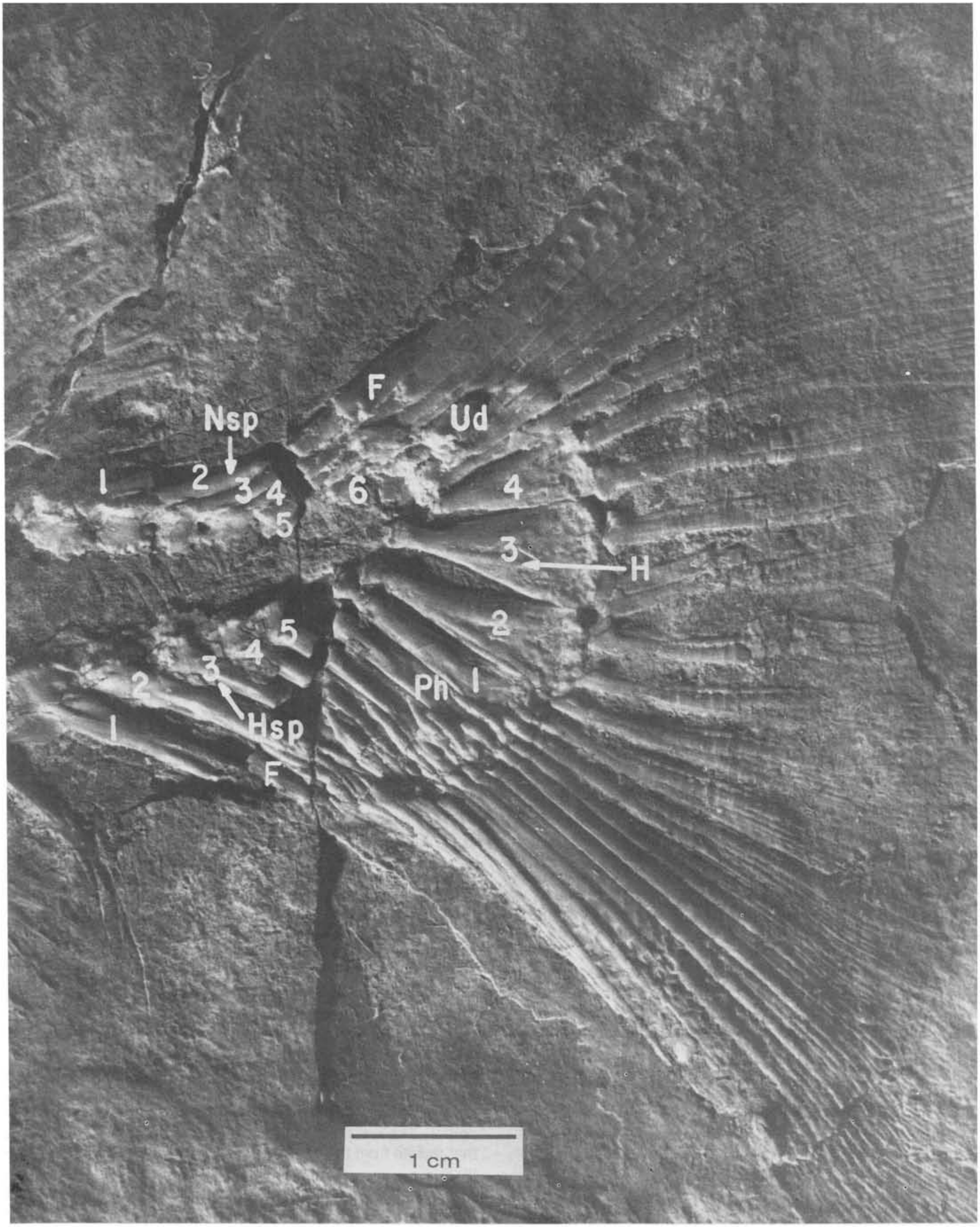

Figure 6.- Photograph showing the tail of referred specimen IGM-4111 of *Tepexichthys aranguthyorum*, locality IGM-1971.

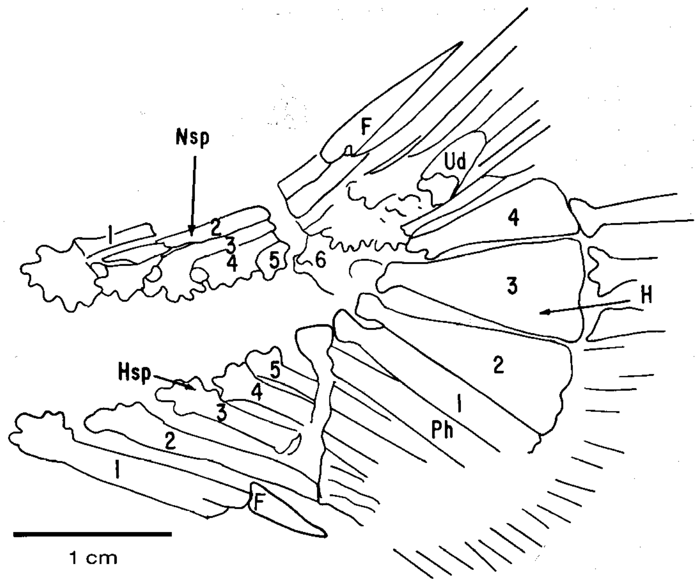

Figure 7.- Sketch of the tail, based on various specimens of *T. aranguthyorum*.

the top of the plate. As one proceeds from this point, the ornamentation goes from round punctations to oval and, in the lower part of the plate, elongated depressions.

(x) The cleithrum lies behind the lower part of the operculum and the preoperculum. Most of its upper portion is obscured by the operculum and in the specimens studied, only the dorsal posterior portion is shown. Below the operculum, there is an indentation of the cleithrum to accommodate the pectoral fin. Below the indentation, this plate expands, describing an ovoid shape, being rounded at its ventral edge. In its lower portion, the cleithrum is marked with fine punctations between the conspicuous striations.

(y) Under the preoperculum and in front of the lower part of the cleithrum, lies the ceratohyal, which is fan-shaped, with the handle pointing forward.

(z) In front of the ceratohyal, there are several plates or plate fragments, which must be part of the branchial apparatus.

Jaw elements—(Figures 8 and 9). (aa) The tooth-bearing element of the lower jaw is the prearticular, which possesses three rows of small teeth and has a strong, high coronoid process (Figures 9 and 10, C).

(bb) A strap-like articular lies along the ventro-posterior part of the prearticular.

(cc) An angular bone lies along the lateral surface of the posterior part of the prearticular, dorsally to the articular. The suture between the angular and the prearticular was not seen in any of the specimens that were studied.

(dd) The anteriormost plate in the lower jaw is the dentary, a triangular wedge, which bears three large, incisor-shaped teeth (Figures 9 and 10, E). These teeth are concave on the inner surface and convex on the outer, giving them a shovel-shape appearance, very similar to human incisors.

(ee) In the upper portion of the mouth, the vomer is the plate that bears the teeth. Its attachment to the hyomandibular is ill-defined.

(ff) The maxillary has a deep and narrow anterior notch and is oval in shape.

(gg) The premaxillary bears three small incisor-shaped teeth. It lies in front of the maxillary and the anterior dermal portion of the mesethmoid. It is elongated and triangular when seen from the side, about five times higher than long.

Teeth—(Figure 10). The upper jaw has teeth on the median vomer and the premaxillary. The vomerine teeth normally consist of five rows—but six can also be present—. The shape of the teeth in the medial row varies greatly from oval to rounded, with even some teeth being squared. Adjacent to the central row, there are two files of smaller teeth, generally aligned with the interspaces of the medial row. These lateral teeth are less than 1/2 the size of the adjacent central dental elements. The outermost rows of teeth tend to be more pill-shaped, with a longer antero-posterior axis. Their outer side is straight, and depending on the amount of wear, may or may not show crenulations. When seen from above, the unworn teeth show mound-like protuberances, which form an irregular, complex pattern that varies greatly in incidence, from 20 or more per tooth, to just five or six. These mounds are the first features to be worn away.

The premaxillary shows three small incisor-shaped teeth with rounded outer edges. Each lower jaw has teeth on the two plates, the prearticular and the dentary. The prearticulars are paired, each with three rows of teeth (Figure 10, C). These plates, including the dental elements, form a U-shaped trough, into which the vomer occludes. The teeth in the innermost and bottom rows are the largest—normally pill-shaped with the transverse axis being the longest—. They become larger and more elongated towards the rear of the mouth. The next higher outer row on the prearticulars has teeth considerably smaller than their inner neighbors. These elements vary from rounded to pill-shaped. The teeth in the upper or lateralmost row are about the same size as the ones in the second row, but in most of the specimens their shape is more circular.

There is a pair of dentary bones. Each side shows three teeth. These teeth have smooth sides and they are quite wide.

Scales and scutes—(Figures 3 and 4). There are 17 dorsal scutes that lack definite dorsal serrations or spines. The tops of these scutes show lenticular thickening, below which the scute is triangular and fits into the reduced strap-like scales. The scales are confined to the anterior half of the body. These first 14 rows run from the top of the body to the ventral scutes —ventral external armor—. There appear to be five scale files. The last three rows of scales do not reach the ventral part of the body, but stop just below the notochordal area, as described for the genus.

The upper three rows of the lower four ventral scutes are smooth. The lowest scutes of the ventral external armor bear three rows of punctations. Below this file, there are 16 rows of ventral scutes—the lowest—that have two or four vertical rows of minute punctations. The anterior 14 bottommost scutes show a slightly rounded edge, whereas the two under the pelvic fin show a serrated edge. The two behind the cloaca, besides being completely smooth, present finger-like projections, which are known in other groups of pycnodonts. The first scute behind the cloaca has two additional smooth scutes lying above it. In all, there are 18 ventral scutes.

Vertebral column—(Figures 3, 4 and 5). In the vertebral column, there are no centra. Excluding the tail, there are approximately 33 neural and haemal arches. The arches are similar in general shape and size. The neural arch bears a long dorsal spine, in front of which is attached a knife-like blade. Posteriorly, the spine has a short process that fits below an anterior projection of the base of the next posterior spine. At its base, the spinal blade is attached to the anterior process of the neural arch. No blade

Figure 8.- Photograph showing the head plates of the holotype IGM-3286, *Tepexichthys aranguthyorum*.

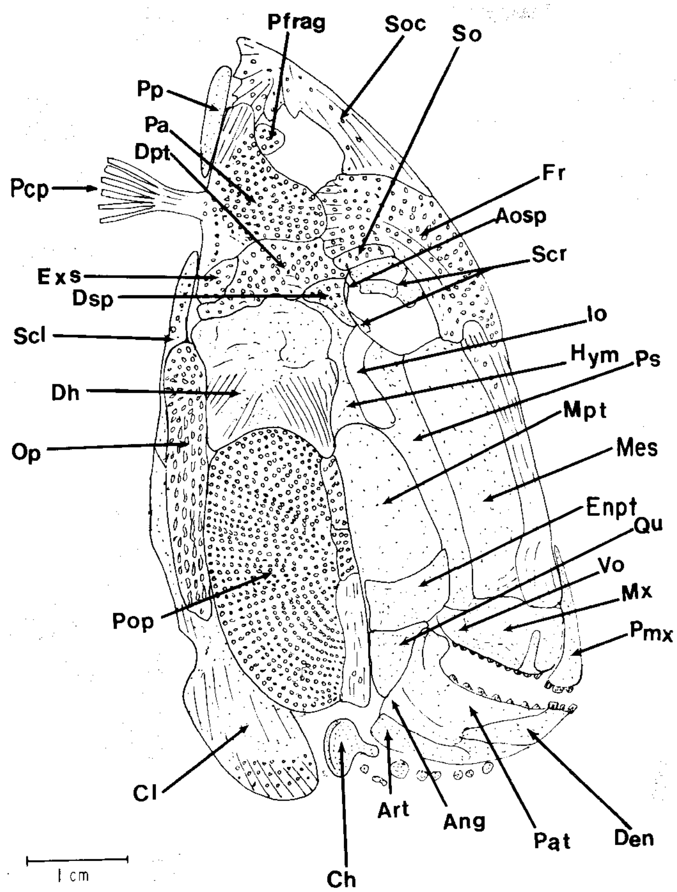

Figure 9-. The head plates of *Tepexichthys aranguthyorum*, based on various specimens.

reaches the very tip of its spine. The extreme base of the arches is knob-like and smooth, with rounded lower corners. The haemal arches tend to be identical in shape and sizes as the neural arches above them.

Fins—(Figures 3 and 4). The pectoral fin is rounded, with eight radials and about 24 lepidotrichia. The pelvic fin has six radials and about 11 lepidotrichia. The dorsal fin has 51 lepidotrichia supports and 51 lepidotrichia. The anal fin has 46 lepidotrichia supports and an equal number of lepidotrichia. Both the dorsal and the anal fins bear a single fulcrum. The caudal peduncle is short, and only a single vertebra with its neural and haemal spine lies between the posterior end of the dorsal and anal fins and the caudal fin supports. The caudal fin has about 28 fin lepidotrichia; the splitting of these lepidotrichia makes difficult this count.

Dorsally, there is a single enlarged fulcrum with three anterior processes at its base. Ventrally, there is a similar fulcrum, which has two anterior basal processes. The tail has a forked shape, with a shallow notch. In its lower portion, there are five haemal spines, a single parhypural and four hypurals. The third hypural is the largest. In the upper portion of the tail, there are six neural spines and, at least, two uroneurals and a dermal scale.

ETYMOLOGY

The species name *T. aranguthyorum*, refers to the Aranguthy family; that is, Don Miguel Aranguthy and his children. This is the family that owns and operates the Tlayúa quarries, where this new form of pycnodont was discovered.

MATERIAL

Holotype—IGM-3286, an almost complete fish from the Aranguthy quarry, locality 370.

Paratypes—IGM-3288, a complete specimen; IGM-3289(a), a complete small specimen; IGM-3289(b) a complete specimen; IGM-3291, a complete specimen; IGM-3292, a complete fish in three parts; IGM-3293, a complete specimen; IGM-3294, a fish with no tail; IGM-3295, a fish with no tail; IGM-3296, a fish with no tail; IGM-3297, a large fish, no tail, four parts; IGM-3298, a complete fish? covered; IGM-3299, a complete fish distorted; IGM-3300, a large complete fish, four parts; IGM-3455, a complete fish fragmented; IGM-3513, a fish with no tail; IGM-3587, a fish with no tail; IGM-3689, a fish in 12 parts; IGM-3690, a complete fish, five parts; IGM-4052, a complete fish, lacking the head; IGM-4053, a distorted fish lacking the bottom; IGM-4054, top of fish with head; IGM-4055, top of fish with head; IGM-4056, fish impression without head; IGM-4057, fish impression with gut contents; IGM-4058, head and part of the body; IGM-4059, head and part of the body; IGM-4060, head and part of the body; IGM-4061, body impression; IGM-4062, body impression; IGM-4063, top of the head; IGM-4064, a covered body; IGM-4065, tail and fragments; IGM-4066, fragmented fish; IGM-4067, head plates; IGM-4068, head; IGM-4069, back part of a fish; IGM-4070, body fragment; IGM-4071, several body fragments; IGM-4072, five body fragments; IGM-4073, several teeth and part of the body; IGM-4074, back part of a big fish; IGM-4075, one endocranium; IGM-4076, a tail fragment; IGM-4077, head with teeth; IGM-4078, vomer and two prearticulars; IGM-4079, vomer and prearticular; IGM-4080, vomer and prearticular; IGM-4081, two prearticulars; IGM-4082, two prearticulars?; IGM-4083, two prearticulars; IGM-4084, prearticular; IGM-4085, prearticular; IGM-4086, prearticular; IGM-4087, prearticular; IGM-4088, prearticular; IGM-4089, prearticular; IGM-4090, prearticular; IGM-4091, prearticular; IGM-4092, prearticular; IGM-4093, prearticular; IGM-4094, prearticular; IGM-4095, prearticular; IGM-4096, prearticular; IGM-4097, prearticular; IGM-4098, prearticular impression; IGM-4099, prearticular; IGM-4100, prearticular; IGM-4101, prearticular; IGM-4102, vomer; IGM-4103, vomer; all from locality IGM-370.

Referred specimens—IGM-4104, fish lacking dorsal fin; IGM-4105, body and teeth; IGM-4106, body and teeth in five parts; IGM-4107, top of head; IGM-4108, prearticular; IGM-4109, prearticular; IGM-4110, prearticular; all from locality IGM-1970; IGM-4111, complete specimen; IGM-4112, fish with no tail; IGM-4113, fish with no tail; IGM-4114, fish with no tail; IGM-4115, vomer in two parts; IGM-4116, prearticular; IGM-4117, prearticular; IGM-4118, prearticular; IGM-4119, vomer in two parts; IGM-4120, vomer in two parts; IGM-4121, vomer; IGM-4122, vomer; all from locality IGM-1971.

OCCURRENCE

Type locality—The Aranguthy portion of the Tlayúa quarry, IGM loc. 370. This is the original area of the quarry that was worked from 1959 to the present. The length of this quarry is approximately 70 m, the depth 5 m and the width from 3 to 20 m.

Other localities—The National Geographic quarry, Alacranes, IGM loc. 1970, lies approximately 45 m east of IGM loc. 370. The quarry consists of a 10 x 10 m cut on the northern side of the Tlayúa canyon. This area was gridded for each meter and the depth of excavation was 8 m. The National Science Foundation quarry, IGM loc. 1971 was a 5 x 20 m quarry, dug at

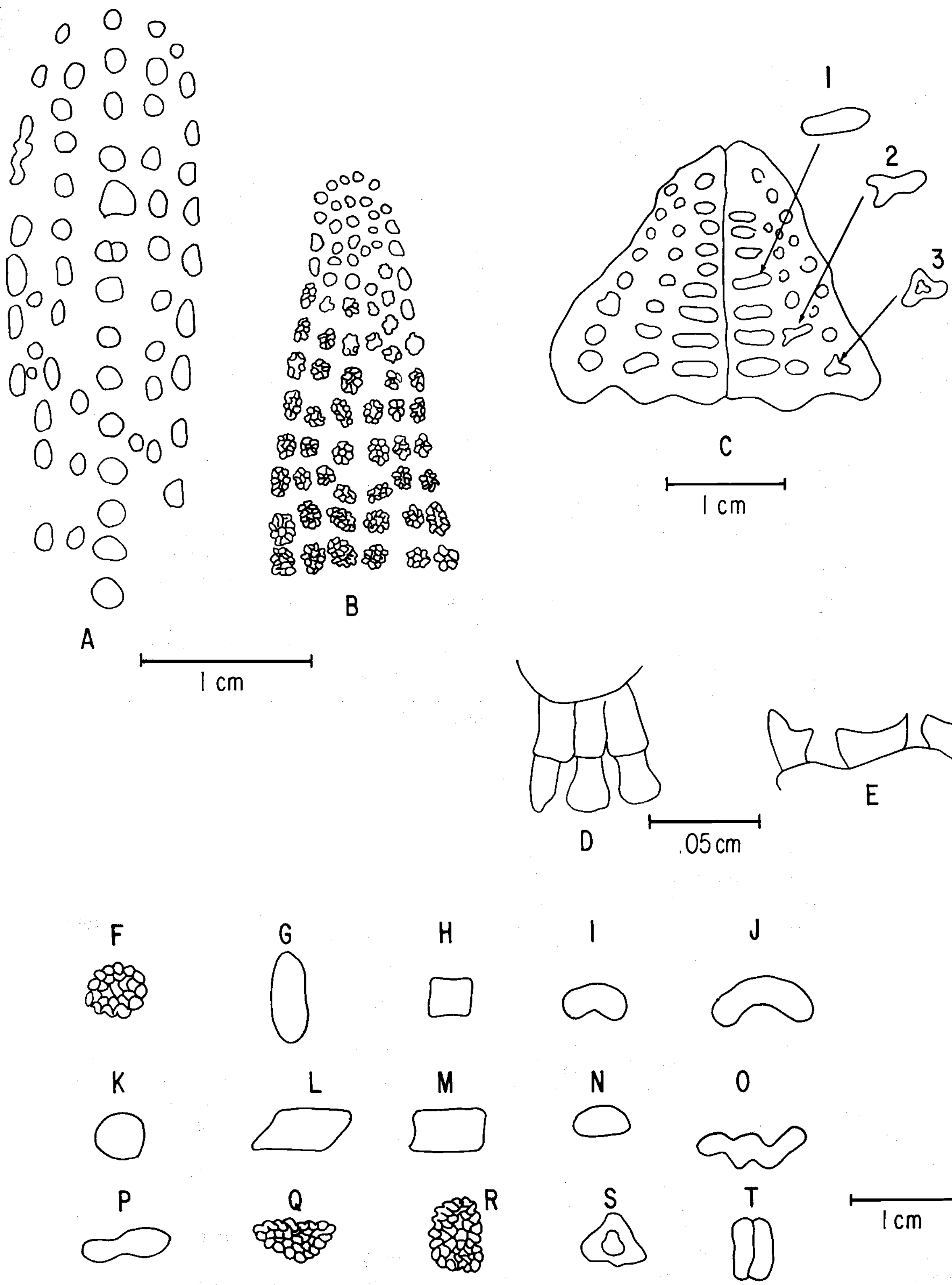

Figure 10.- A, vomerine teeth of paratype IGM-4103; B, vomerine teeth (arranged in six rows) of paratype IGM-4102; C, two prearticulars in place from paratype IGM-4083, number 1 represents an enlargement of an oblong tooth from the innermost row, number 2 is an irregular and elongated tooth from the second row and number 3 is a triangular and irregular tooth from the outermost row; D, represents the three prehensile incisiform teeth that occur on the premaxillary, paratype IGM-3289(b); E, shows the three teeth of the dentary (taken from various individuals and therefore there is no specimen number); F, is an example of an unworn circular tooth from referred specimen IGM-4120; G, a worn and oblong tooth from paratype IGM-4096; H, a square tooth from paratype IGM-4102; I, a bean-shaped tooth from paratype IGM-4077; J, a more elongated version of the previous, from paratype IGM-4079; K, a round worn tooth from paratype IGM-4079; L, a trapezoidal tooth (with rounded corners) from paratype IGM-4096; M, tooth with a rectangular shape, from paratype IGM-4083; N, tooth with a hemispherical outline, paratype IGM-4102; O, tooth with a highly irregular form, paratype IGM-4102; P, tooth with a slipper shape, from paratype IGM-4096; Q, unworn tooth with an elongated triangular shape, referred specimen IGM-4120; R, two fused and unworn teeth of unequal size, referred specimen IGM-4120; S, tooth with a triangular outline and deeply pitted, from paratype IGM-4083; and T, worn teeth that appear to have been split from a single element, drawn from paratype IGM-4102.

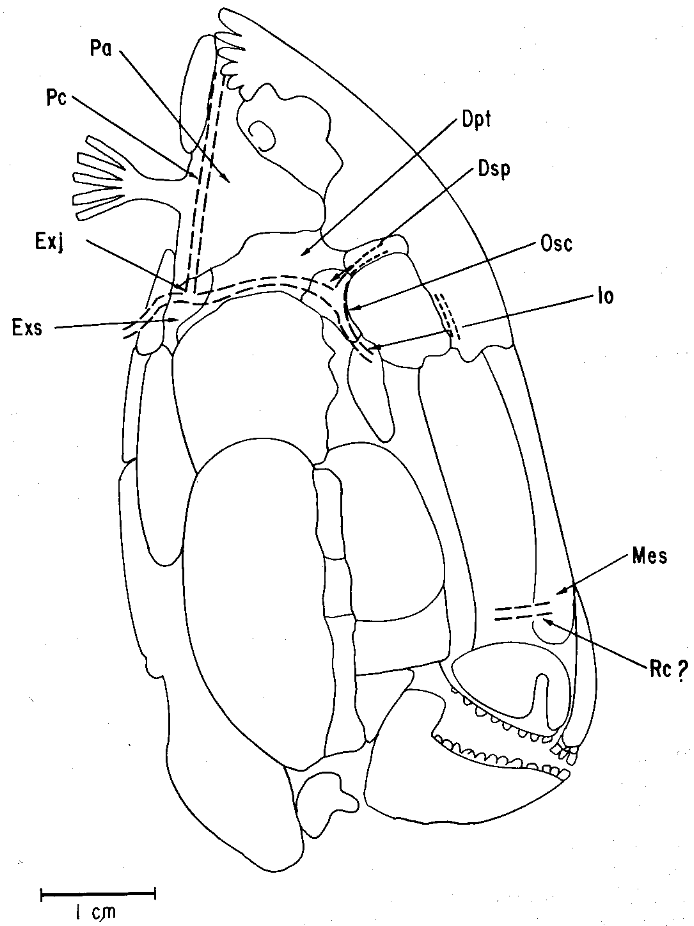

Figure 11.- Traces of the lateral lines of the cephalic region, discernible in the head plates of *Tepexichthys aranguthyorum*, based on various specimens.

the base of the eastern portion of IGM loc. 370, the depth of excavation was of 4 m.

Formation and Age—Tlayúa Formation (Pantoja-Alor, 1990; Pantoja-Alor *et al.*, 1989), middle and late Albian (Seibertz and Buitrón, 1987).

REPOSITORY

The studied material was deposited in the museum of the Department of Paleontology, Instituto de Geología, Universidad Nacional Autónoma de México. The abbreviation used for catalogue and/or locality number is: IGM, Instituto de Geología, Universidad Nacional Autónoma de México.

SYSTEMATIC CONSIDERATIONS

Regarding the phyletic placement of *T. aranguthyorum*, the first aspects to consider are its holostean affinities. *Tepexichthys* possesses a hemiheterocercal tail *sensu* Gardiner (1960). Also, within this fish, the scales are reduced to two layers and, most important, there is an unrestricted and uncalcified notochordal space, which is a primitive holostean character.

The pycnodont characters in *Tepexichthys* include: (1) the supraoccipital plate separating the parietal complex; (2) a reduction of the suborbitals or cheek plates; (3) a mouth with a small gape; (4) the mandibular suspensorium oriented in a forward direction; (5) the preopercular enlarged and the opercular reduced; (6) the branchiostegal rays greatly reduced in size and number; (7) the lepidotrichia are stout, well spaced and articulated; (8) prehensile teeth on the premaxillary and dentary; (9) teeth missing on the pterygoids and the maxillary; (10) teeth lacking vertical succession (Woodward, 1895); and, (11) no nasal plates present.

Within the pycnodonts, there are at least six distinctive groups. The first of these, considered the most primitive, includes the Triassic *Brembodus* and *Gibbodon*, described and discussed by Tintori (1981). These genera have bodies completely covered with rectangular scales. The unpaired fins bear fringe-like fulcra. In *Brembodus*, the neural spines are not fused to the neural arches anterior to the caudal region, and there is a strong dorsal spine formed by the anteriormost dorsal scutes. The hypurals diminish in size posteriorly. The dorsal fin is much larger than the anal in both genera. In *Gibbodon*, the parietal is small, triangular and it lies just aside of the supraoccipital. In *Brembodus*, the parietal is large and it lies behind the frontal and the supraoccipital. The Jurassic genus *Eomesodon* has a parietal also located to one side of the supraoccipital and frontal, but contrary to what happens in *Gibbodon* and *Brembodus*, this plate in *Eomesodon* belongs to the orbital border, a condition not shown in the Triassic pycnodonts. Nevertheless, *Eomesodon* can probably be placed in the *Brembodus-Gibbodon* group, with which it shares other important characters. In these three genera, neither a temporal fossa nor a parietal peniculus—or digital process—are present. Therefore, with the inclusion of *Eomesodon*, within this first primitive group of pycnodonts, these genera would have a range from the Late Triassic through part of the Jurassic.

The next most advanced pycnodonts include Jurassic forms, such as *Mesturus* and *Gyrodus*. In these genera, the parietal does not reach the back of the skull, but it is bordered posteriorly by a series of plates that could be extrascapulars, or the supratemporals of Woodward (1895), or the dermo-opistotique or dermoepiotique of Saint-Seine (1949). In this younger group, as in the previous discussed above, the trunk is covered with scales and there is neither a temporal fossa, nor a parietal peniculus or digital process present. The so-called *Palaeobalistum gutturosum* of Arambourg (1954) seems related to this group in that it lacks a brush-like protuberance or peniculus.

The third group in the succession includes *Proscinetes*—the *Microdon* of Woodward, 1915—*Macromesodon* and *Neoproscinetes*. In this group, as in the previous forms that have been reviewed, there is no temporal fossa; nevertheless, the parietal—or parietal complex—is in a posterior position and a peniculus is present. In these pycnodonts, the trunk shows strap-like scales that run from the dorsal scutes to the ventral body armor. In this last structure—the ventral body armor—there are one, two, or three rows of scutes that interlock with the strap-like scales.

The fourth group includes *Tepexichthys*, *Coelodus* and another genus that will be described from the Tlayúa complex. In these genera, a temporal fossa is present. The parietal complex is posterior, with a peniculus—or digital process—at its rear. In these three genera, in common with the third group—the *Proscinetes-Macromesodon* group—there are strap-like scales that interlock with the ventral body armor, and in both groups these structures lie in the anterior portion of the body.

Although *Tepexichthys*, *Coelodus* and the undescribed genus form an apparent natural group, the differences between *Tepexichthys* and *Coelodus* should be noted. In *Coelodus costae* Heckel, 1856, the dorsal and ventral scutes are strongly serrated; this is not so in *Tepexichthys*, which has scutes with smooth edges. Also, in *Coelodus* the head sculpture consists of fine radial lines, as opposed to randomly placed punctations in *Tepexichthys*. *Coelodus rostronii* Heckel (1856, plate V) shows squareshaped neural arch bases with finger-like projections, in contrast to the rounded bases of *Tepexichthys*. Also, in both of these species of *Coelodus*, the caudal fin shows a posterior central rounded lobe, which may be characteristic of the genus. This does not occur in *Tepexichthys*, where the tail is notched. Finally, there appears to be a definite caudal peduncle in *Coelodus*, with several neural arches lacking associated radials and several haemal arches without radials. In *Tepexichthys*, no caudal peduncle is evident and there are only a single neural arch and a single haemal arch that lacks a radial. From the above discussion, it is evident that, although belonging to the same family, *Tepexichthys* shows several valid differences from *Coelodus* that point out the fact that *Tepexichthys* warrants a separate generic entity from *Coelodus*.

The fifth group includes highly specialized forms of pycnodonts, represented by *Coccodus* and *Trewavasia*. In this advanced group, the trunk is highly elongated and the head is enlarged. Also, both genera show huge occipital spines.

The sixth group includes *Palaeobalistum*, *Pycnodus* and perhaps *Hadrodus*. In these three genera, the neural and haemal arches are fused basally and cross the notochordal space. When compared with the *Tepexichthys* group and others, in these pycnodonts the dorsal and ventral scutes are fewer and highly modified.

Although not all of the known genera and species of pycnodonts have been considered in this analysis, the proposed model, with six groupings, is only one tentative attempt to place *Tepexichthys* within the Order Pycnodontiformes. Nevertheless, until this group of interesting fishes is thoroughly revised, this exercise should be considered as one of several other possible classifications (*e. g.,* Woodward, 1939; Saint-Seine, 1949; Lehman, 1966).

ECOLOGICAL CONSIDERATIONS

The specimens examined in this study prove that *Tepexichthys* is one of the most common fishes present in the Tlayúa quarries, exceeded in number only by the small clupeids. *Tepexichthys* ranges from 30 to 360 mm in total length —considered from the tip of the snout to the tip of the tail—and from 22.5 to 250 mm in total depth—considered from the base of the dorsal to the ventral scutes—. The pycnodonts in this study show a widespread range between these extremes. It might be concluded that *Tepexichthys* was living in the immediate environment of deposition, or very close by, because all sizes above 30 mm in total length are present.

Although no hard corals have been discovered in the Tlayúa Formation, the presence of an abundant pycnodont fauna suggests that reefs were near by. This idea finds support in the fact that pycnodonts are deep-bodied fishes and although this particular body shape design may be found in other environments, it is very common in communities of coral reef fishes. Because of their narrow width, these fish are well adapted for hiding between heads of coral and in other vertical cavities that are so common in large reefal structures.

Regarding other anatomical elements related with the living conditions of these organisms, the teeth add to this interpretation. Many of the studied specimens of *Tepexichthys* show large amounts of tooth wear. Some of these fish of almost the same size, on one hand, have completely worn teeth; others, only slightly larger or smaller, show the crenulations and mounds of unworn teeth. Therefore, the great amount of rapid wear suggests that these fish were crushing hard material—*e. g.*, coral—. A recent analogy might be the brilliantly colored parrot fish that inhabits coral reefs today. This fish has well-formed incisors and crushing pharyngeal teeth. *Tepexichthys* has similar incisiform teeth. The prearticular and vomerine teeth would function similarly to the parrot fish pharyngeals. The claw-like pharyngeal teeth in *Tepexichthys* may have served to keep the coral debris out of the esophagus and/or away from the gills. A parrot fish grazes on living coral polyps and algae, biting into the coral and shearing off large fragments with its incisors, then crushing the coral fragments and the polyps. The crushed coral as granules falls through the gills. The polyps and pieces of coral are swallowed.

In paratype IGM-4057, there exist coprolitic masses composed of a white powdery substance; all of them are exposed in the body cavity in the form of a rope-like strand that must represent the gut contents. The white powder, when viewed under a microscope, consisted of pure white angular grains that could be dissolved completely in acetic acid. These fragments were assumed to be calcium carbonate and are thought to represent smashed coral that was passing through the gut.

THE TOOTH PROBLEM

Many genera of pycnodonts have been described on such characters as tooth form and row number. An interesting aspect of this study has been the remarkable amount of variation found in the teeth of *Tepexichthys aranguthyorum*. In this species, the most common number of rows of vomerine teeth is five. Nevertheless, in the two examples shown in Figure 10 (A and B), this number is exceeded. In specimen IGM-4103 (Figure 10, A), most of the teeth are arranged in five rows; however, some teeth occur out of place. In the same figure (Figure 10, B), specimen IGM-4102, there are six rows of teeth; the front rows are very worn and the back ones are unworn. If these jaws had been found isolated, they would have been placed not only in separate species, but perhaps even in distinct genera.

In Figure 10, C, two prearticulars in place are shown—specimen IGM-4083—the median two rows of teeth are elongated, oblong and large. The next lateral row varies from being oblong to rounded in shape and the outermost row has small and rounded teeth. As with the vomerine teeth, the prearticulars show a considerable amount of variation. In Figure 10, C, 1, a normally worn oblong tooth of the inner row is illustrated. In the second row (Figure 10, C, 2), there is an irregular and elongated normally worn tooth. In the outer row (Figure 10, C, 3), there is a highly irregular triangular tooth that is so deeply worn as to have a pitted center.

In the premaxillary, the shapes of the teeth seem to be constant and resemble human incisors, as shown in specimen IGM-3289-b (Figure 10, D). The three teeth of the dentary (Figure 10, E) are long and with concave upper surfaces, as it was seen in various specimens. There is very little indication that the dentary teeth, as well as those in the premaxillary, vary at all. In Figure 10, the letters F through T give examples of individual teeth that show a great deal of variation, both in the vomers and in the prearticulars. More details and explanations regarding the variation are given in the figure caption.

CONCLUSIONS

A new genus and species of pycnodont, *T. aranguthyorum*, has been described from the Tlayúa quarries near Tepexi de Rodríguez, Puebla. These fish occur in fossiliferous beds of middle or late Albian (Early Cretaceous) age. The fossils are embedded in red hematitic layers, which lie between beds of varying thickness of honey-colored, micritic limestone. The strata of the quarries and the surrounding area have been given the name of Tlayúa Formation.

In the present study, over 90 specimens of *Tepexichthys aranguthyorum* have been examined. As a result of this analysis, the uniqueness of this form is borne out by the following characters: (a) the arrangement and shape of the caudal supports; (b) the scale-scute relationships; (c) the position and shape of the head plates; and (d) the ornamentation, size and shape of the teeth—but only in the most general sense—.

For the moment, *Tepexichthys* is placed in the family Pycnodontidae; however, this is meant as a tentative arrangement, because this genus shows many characters that caused it to differ markedly from *Pycnodus*. On the other hand, the genus *Coelodus* lies close to *Tepexichthys* and therefore warrants an inclusion in a family that may be other than Pycnodontidae.

Tepexichthys represents a rather advanced pycnodont, in that it shows the reduction of scales, a temporal fossa and the presence of a peniculus—or digital process—in the posterior region of the parietal complex.

The dental apparatus and known gastric contents of *Tepexichthys* suggest the possibility that these fish fed on coral polyps and were intimately associated with the reefs themselves. Finally, the variation in the teeth of this species, as seen in this study, raises the question of the value of using dental plates alone to erect new genera and species.

ACKNOWLEDGMENTS

First of all, I would like to acknowledge the continuous aid of the whole Aranguthy family, for which this species is named. Don Miguel, the patron of the Tlayúa quarries, who has given permission to work in the area and to have the specimens in question. The actual collectors of these fossils are the five sons of Don Miguel Aranguthy: Félix, Ranulfo, Faustino, Sebastián and Benjamín Aranguthy-Contreras.

Luis Espinosa-Arrubarrena has given valuable advice and technical help at all levels of this work and has been paramount in the final editing and revising of this paper. Miguel Angel Cabral-Perdomo has not only worked in the quarries, packing and cataloguing the fossil material, but has done the ultimate curation of the specimens. Also, of special help, have been Dr. Ma. del Carmen Perrilliat and Katia González-Rodríguez in curating the material and assigning museum numbers.

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The photographs were taken by Gregorio Chávez-Cruz and Antonio Altamira-Gallardo and the inking of the illustrations was done by Arturo Osorio-Betancourt. Finally, I would like to thank Dr. R.J. Nursall and Dr. Ma. del Carmen Perrilliat for their critical but helpful review of this paper.

ABBREVIATIONS

Angular	Ang
Articular	Art
Autosphenotic	Aosp
Ceratohyal	Ch
Cleithrum	Cl
Dentary	Den
Dermohyal	Dh
Dermopterotic	Dpt
Dermosphenotic	Dsp
Endopterygoid	Enpt
Extrascapular	Exs
Extrascapular (juncture)	Exj
Frontal	Fr
Fulcra	F
Hyomandibular	Hym
Hypural (num. sequentially)	H
Haemal arch	Ha
Haemal spine	Hsp
Infraorbital	Io
Lateral line	Ll
Maxilla	Mx
Mesethmoid	Mes
Metapterygoid	Mpt
Neural arch	Na
Neural spine	Nsp
Orbital sensory canal	Osc
Opercular	Op
Parasphenoid	Ps
Parhypural	Ph
Parietal complex	Pa
P. complex (sen. canal)	Pc
P. complex peniculus	Pcp
P. fragment	Pfrag
Postparietal	Pp
Prearticular	Pat
Premaxillary	Pmx
Preopercular	Pop
Quadrate	Qu
Rostral canal?	Rc
Sclerotic plates	Scr
Supraorbital	So
Supracleithrum	Scl
Supraoccipital	Soc
Uroneural	Ud
Vomer	Vo

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