



GUIDE BOOK



FOR THE FIELD TRIP OF

PALEONTOLOGICAL HIGHLIGHTS OF THE MIXTECA POBLANA IN CENTRAL MEXICO

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FISH FAUNA OF THE TLAYÚA QUARRIES

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INTRODUCTION

Although in México there are reports of Cretaceous bony fish localities in Coahuila, Chihuahua, Durango, San Luis Potosí, Veracruz, Oaxaca, Chiapas and recently one found in Vallecillo, Nuevo León, another in Zimapán, Hidalgo, the discovery of the Tlayúa quarry represents the most important deposit regarding diversity and abundance of this group of vertebrates. To date we have over 5,420 fossils of invertebrates and vertebrates of which 4094 are fishes. Since the last overview made by Applegate (1996), the total number of specimens collected in the Tlayúa quarries has increased about 25% and more new taxa have been found, including one coelacanth, five berycoids and six ionoscopids. The rest of the ichthyofauna comprises the Halecostomi *incertae sedis* which are primitive neopterygian fishes, such as pycnodonts and macrosemiids, (the latter reported by the first time in the New World), both groups known previously as coral reefs dwellers. The Halecomorphy are represented by primitive and more advanced forms, including semionotids, ophiopsids and amiids; the latter represented today by *Amia calva*, one relict of this group restricted to the eastern North America fresh waters. The most abundant, diverse and advanced group in the Tlayúa beds is the Teleostei, containing, at least eleven families. This group includes fishes related to modern groups that actually live in the waters of the entire world.

Most of the fishes found in Tlayúa, considered as a Lagerstätte (Espinosa-Arrubarrena and Applegate, 1996), are exquisitely preserved. In most cases they are recovered nearly complete, although fragmentary specimens (e.g., teeth, isolated bones or body parts) are also common, and without exception, all have been found within the bedding planes, that show a characteristic red color due to hematite (Applegate, 1996).

The richness of teleosts (3412 specimens) and the low number of primitive taxa (686) in the deposit agrees with the teleost radiation that occurred just before the beginning of the Late Cretaceous. The primitive neopterygians such as the ones present in Tlayúa, were widespread in the warm Mesozoic waters. Their striking decline perhaps was due to the great competition for space and food with teleosts, so by the end of the Early Cretaceous most of them were extinct.

The importance of this fauna has been recently call to the attention of some fossil fish specialists, who are interested in visiting our country and studying this material because most of the fishes are new forms that could fill some of the gaps that still exist in the phylogeny of many fossil groups. It is important to notice that in variance with other renowned fish localities (Solnhofen, Santana, Green River, etc.), whose collections are scattered all over the world, in Tlayúa over 97% of the specimens are housed in the Paleontological Collection of the Instituto de Geología, UNAM.

PALEOECOLOGICAL ASPECTS OF THE FISH ASSEMBLAGES

According with the paleoecological model proposed by Applegate (1992) and Espinosa-Arrubarrena and Applegate (1996); there existed different environments nearby the deposit and the fishes could lived in most of them (including fresh and brackish waters). The environments include: a land mass with meandering rivers to the west of the Tlayúa lagoon (the area of fossilization) with stagnant waters and hypersaline or anoxic bottom; an adjacent bio-rich lagoon (densely populated, with high productivity and a bioturbated bottom) bordered to the east by a great barrier reef; and beyond that, eastward the open oceanic waters of the Tethys sea [see general discussion of the Tlayúa Quarry and the paper of Espinosa-Arrubarrena and Applegate (1996)].

It is possible that pycnodonts and macrosemiids lived in or near the coral reef perhaps because of their feeding habits and shape body, moreover, both groups have been extensively reported associated to this paleoenvironment. Fishes such as ophiopsids, clupeomorphs and ichthyodectids could have lived in the bio-rich lagoon or behind the live reef, all of these may have been washed into the Tlayúa lagoon during very high tides or large storms.

Some of the fishes must have lived in the upper waters of the Tlayúa lagoon as shown by the abundance of coprolites. Also there is a possibility that some of the fishes could come from fresh water or brackish environments related to the connections of the Tlayúa lagoon with the meandering rivers. Probably during storms or heavy rains the rivers carried into the deposit the hematite along with some fresh water organisms including fishes, as well as terrestrial forms that could be carried from the land by the rivers. It is also possible that some of the ichthyofauna came from deeper oceanic waters (e. g. ichthyodectids, clupeomorphs, elophomorphs, etc.).

FISH FAUNA

The study of the great diversity of fish fauna in Tlayúa began many years ago, but due to the lack of paleoichthyologists in general, just some groups so far have been investigated, including pycnodonts, macrosemiids, ichthyodectiforms and amiids. The fauna has been reviewed, but not in detail. In this paper we pretend to give an overview of some of these fishes, based on the previous work (Applegate, 1996), plus new discoveries. The best known groups in the quarries are listed below:

SARCOPTERYGII

Sarcopterygii comprises lobe finned fishes known as coelacanths, with only one living member *Latimeria chalumnae* that lives at great depths in the Southeast of Africa. For the first time in Mexico the presence of a coelacanth referable to the genus *Axelrodichthys* Maisey 1986, is reported probably belonging to the species *A. araripensis* Maisey 1986, from the Early Cretaceous Romualdo Member of the Santana Formation in Brazil (Espinosa-Arrubarrena *et al.*, 1996). The specimen was discovered by Dr. Lance Grande in the unidentified fish section of the Tlayúa collections. We expect to find more coelacanth specimens to improve (to a specific level) our taxonomic assessment and complete the study of this important group in México.

NEOPTERYGII

Neopterygii are ray-finned fishes that constitute the vast majority of primitive and modern bony fish groups, including the Halecostomi (in the past called “holosteans”); the Halecomorphi (primitive and advanced actinopterygians not included among teleosts) and advanced Teleostei (known as bony fishes).

HALECOSTOMI INCERTAE SEDIS

Semionotidae

The family Semionotidae is represented by eight specimens, belonging to the genus *Lepidotus*. The semionotids are characterized by a deep body covered with thick rhomboid scales and head bones strongly ornamented. Unfortunately semionotids represent a greatly diversified group including many species, mainly described by isolated scales. For this reason the study of the Tlayúa semionotids is complicated and it is necessary to make a wide revision of the group, to determinate the Mexican species.

Pycnodontidae

Among Halecostomi the family that is better represented in Tlayúa is the Pycnodontidae, with at least three genera and three species. Pycnodonts are deep bodied fishes that are considered to be coral reef inhabitants (Applegate, 1992). Their characteristic crushing dentition suggests that they could feed on corals present in the live reef, and their narrow body also suggests that they could hide within the cavities of the reef, just as their recent teleost analogous butterfly and angel fishes do today in this type of environment. Although most specimens in the deposit are complete, we have found teeth as well as other body elements isolated or in coprolites (Applegate, 1996). Recently Grande and Bemis (1998) discovered a vomer plate within the intestinal contents of a *Pachyamia mexicana* specimen, this suggests that at least, amiids that lived in the Tlayúa lagoon or nearby, were pycnodont predators. Today only one new pycnodont genus and species *Tepexichthys aranguthyorum* has been described by Applegate (1992), this genus is considered as an advanced form of the family (Figure 8), related to *Coelodus*.

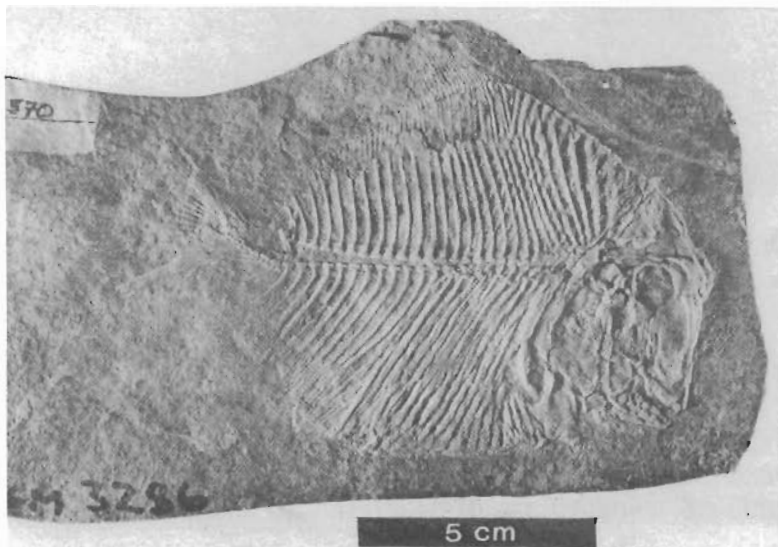


Figure 8. *Tepexichthys aranguthyorum*, Applegate, 1992; holotype IGM 3286.

Macrosemiidae

Macrosemiidae (Figure 9) is a group of fishes reported by the first time in the New World. They had been recovered from European localities such as Solnhofen, Germany; Cerin, France; Montsec and Las Hoyas, Spain and other places. At the moment three new forms have been studied from the Tlayúa beds, two represent new genera and the other a new species of *Notagogus* (González-Rodríguez, 1996). Macrosemiids are small fishes with long dorsal fins and thick ganoine scales that are associated to reef environments (Bartram, 1977), although *Notagogus* and *Propterus* have also been reported in fresh water deposits of Spain (Fregenal-Martínez and Meléndez, 1995; Poyato-Ariza and Wenz, 1995). There are more than 157 macrosemiids deposited in Museum of Paleontology of the Instituto de Geología, UNAM. These include at least six new taxa, some of them similar to *Notagogus*. Many features on the structure of teeth and alimentary canal of macrosemiids, suggest that they were invertebrate and small fish predators. Samples of the gut content have been processed by palynological technics and have revealed the presence of microscopic rests of crustaceans (copepods), algae and many unidentified palynomorphs (González-Rodríguez and Martínez-Hernández, 1998). The study of these new forms will help to elucidate the poorly known characters of the group and maybe the taxonomic position of the family within neopterygians, which at the moment is uncertain. Besides, the investigation of the alimentary canals, will help to determinate the diet of these fishes and maybe some aspects of the paleoenvironment.



Figure 9. A new undescribed genus and species of macrosemiid fish from the Aranguthy quarry. x 1.6

HALECOMORPHI

Halecomorph category is applied to primitive as well as highly advanced neopterygians not included among teleosts. This group is represented today by the only living species *Amia calva* and a score of closely related Jurassic and Cretaceous genera (Carroll, 1988).

Amiidae

A recent investigation on amiids made by Grande and Bemis (1998), revealed the presence of a new species of *Pachyamia* in Tlayúa, named *P. mexicana* (Figure 10), because of its occurrence in our country. Some years ago Applegate (1996) thought that at least two amiids existed in the Tlayúa quarries, due to the presence of small and big fishes that apparently seemed to have enough taxonomical differences. Nevertheless, the study on 13 specimens made by Grande and Bemis (1998) showed that adult amiids had a wide size range, varying from 400 mm to about 790 mm in standard length. It is interesting to notice that while many immature specimens of other groups of fishes have been found in Tlayúa, so far only adult amiids have been recovered.



Figure 10. Paratype of *Pachyamia mexicana* (IGM 7379) from the Tlayúa Quarry described by Grande and Bemis (1998).

Ophiopsidae

Teoichthys kallistos Applegate (1988) was the first fish to be formally described from the Tlayúa beds and was placed within the Ophiopsidae family (Figure 11). At the moment it is the best preserved fish in the quarries, that received the name of "God's most beautiful fish". Although 14 specimens of the family have been recovered, they all belong to the same species.

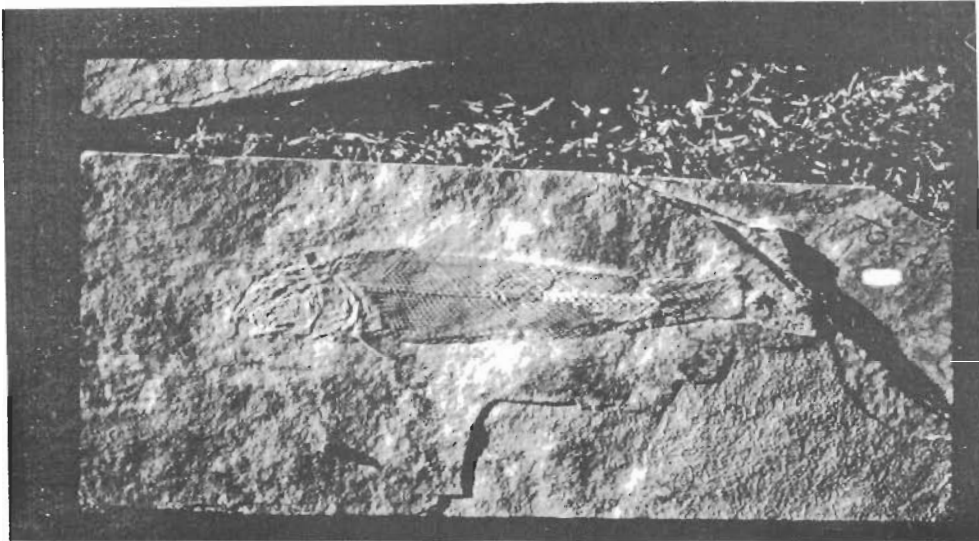


Figure 11. *Teoichthys kallistos*, holotype IGM 3460, one of the most beautiful fishes of Tlayúa Quarry. x 0.25.

TELEOSTEI

Among Teleostei the ichthyodectiforms are formally under investigation by Jesús Alvarado Ortega, and other teleost groups like the aspidorhynchiids and the clupeomorphs, have been partially reviewed.

Aspidorhynchidae

These fishes are represented by the genera *Vinctifer* and *Belonostomus*, although the most abundant is the second, which is frequently found in a circular or u-shape probably due to muscular contraction associated with hypersalinity (Applegate, 1996). They resemble gars in the retention of thick ganoid scales and in body form, that is related to fast swimming and predaceous feeding habitats, the lower jaws are moderately elongated and there is a toothless rostrum.

Ichthyodectiformes

Most ichthyodectiforms were large predaceous fishes with marginal dentition composed of long conical teeth such as *Ichthyodectes* and *Xiphactinus*. These genera were pelagic, inhabiting inland seas and even deep oceanic areas (Applegate, 1970). Nevertheless, the smaller Early Cretaceous ichthyodectids, like the ones of the Tlayúa quarries may have been more coastal, with the possibility of entering bays and lagoons (Applegate, 1996). The recent unpublished revision of this group made by Alvarado-Ortega (1998) revealed the presence of three new forms belonging to the Suborder Ichthyodectoidei, although in an uncertain position by the moment. The reason of this lack of taxonomic precision is because the systematics of the order is far from settled and there are a number of uncertainties in the establishment of the families. A further study of the order and of the Tlayúa specimens will help to determine the correct classification of this group.

Clupeomorpha

Clupeomorphs are the most abundant fishes in the quarries (1899 specimens). In general they are small fishes with cycloid scales and jaws that curve upwards. Their recent relatives are composed by herrings, anchovies and sardines. At least two kinds of clupeomorphs are represented in the beds: double armored herrings belonging to the Paraclupeidae and another clupeid which is the most numerous with an extensive size range, with almost every life stage present in the sample (Applegate, 1996). We believe that this undescribed species could have lived in the Tlayúa lagoon during its whole life cycle because of the great number of specimens found in the deposit, and even may have been tolerant to fresh, brackish and saline waters as occurs with their recent relatives.

The remainder Teleost fishes are mentioned in Table 1 with a change in some of the previous interpretations

LIST OF TAXA OF TLAYÚA FISHES

TAXA	NUMBER OF SPECIMENS
OSTEICHTHYES	
SARCOPTERYGII	1
Coelacanthidae	
1) <i>Axelrodichthys araripensis</i> Maisey, 1986	
NEOPTERYGII	
Halecostomi <i>incertae sedis</i>	
Order Semionotiformes	9
Semionotidae	
1) <i>Lepidotus</i> sp. A	
2) <i>Lepidotus</i> sp. B	
Order Pycnodontiformes	457
Pycnodontidae	
1) <i>Tepexichthys aranguthyrum</i> Applegate, 1992	
2) Undescribed genus and species A	
3) Undescribed genus and species B	
4) Undescribed genus and species C	
5) Undescribed genus and species D	
6) Undescribed genus and species E	
7) Undescribed genus and species F	
8) Undescribed genus and species G	
Order <i>incertae sedis</i>	
Macrosemiidae	163
1) <i>Notagogus</i> sp. A	
2) Undescribed genus and species B	
3) Undescribed genus and species C	
4) Undescribed genus and species D	
5) Undescribed genus and species E	
6) Undescribed genus and species F	
7) Undescribed genus and species G	

Unidentified macrosemiids

Halecomorphi	
Order Amiiformes	
Amiidae	35
1) <i>Pachyamia mexicana</i> Grande and Bemis, 1998	
Order <i>incertae sedis</i>	
Ophiopsidae	15
1) <i>Teoichthys kallistos</i> Applegate, 1988	
Ionocospidae	6
2) cf. <i>Oshunia</i> sp. A	
Total number of non-teleost fishes	686

TELEOSTEI

Order Aspidorhynchiformes	354
Aspidorhynchidae	
1) <i>Vinctifer</i> sp.	
2) <i>Belonostomus</i> sp.	
Order Pholidophoriformes	5
Pholidophoridae ?	
1) A new taxon of pholidophorid-like fish	
Order Ichthyodectiformes	240
Suborder Ichthyodectoidei	
Family <i>incertae sedis</i>	
1) Undescribed genus and species A	
2) Undescribed genus and species B	
3) Undescribed genus and species C	
Superorder Elophomorpha	173
A group of highly distinctive elopomorphs that at least represent 13 new taxa including a <i>Brannerion</i> -like form and a <i>Rhacolepis</i> -like species	
Superorder Clupeomorpha	67
Order Ellimmichthyiformes	
Paraclupeidae	
Undescribed genus and species	
Order <i>incertae sedis</i>	1812
1) Unidentified clupeomorph, which is the most abundant fish in the quarry	
Order Gonorhynchiformes	5
1) Undescribed genus and species	
Order Salmoniformes	
1) <i>Yabrudichthys</i> -like, sp. A	10
2) <i>Enchodontid</i> -like, sp. B	

Order Beryciformes	5
1) Undescribed genus and species	
Unidentified teleosts	741
Non-teleost fishes	686
?Teleostei	741
Teleostei	2671
Grand Total	4098

CONCLUSIONS

The richness of the ichthyofauna in the Tlayúa quarries represents the most important Cretaceous discovery made in México and one of the most unique localities of fossil fishes in the world. At the present more than 4,000 specimens are represented in the deposit, most of them belonging to Teleostei, due to the great radiation that occurred in this group during the Cretaceous. Nevertheless, we need more specialists within each fossil fish group to determine the materials and to understand the paleoenvironments where this ichthyofauna lived.