

## DESCRIPTION OF TWO EARLY MIDDLE EOCENE MARINE FISH FROM EASTERN CUBA DESCRIPCIÓN DE DOS PECES MARINOS DEL EOCENO MEDIO TEMPRANO DE CUBA ORIENTAL

 JOHANSET ORIHUELA<sup>1</sup>,  YASMANI CEBALLOS IZQUIERDO<sup>2,✉</sup>,  EDELIS FIGUEREDO GARCÉS<sup>3</sup>

1. Department of Earth and Environment (Geosciences), Florida International University, Miami, Florida 33199, USA,
2. Independent researcher. Calle 40, #2702 e/27 y 29, Madruga, Mayabeque, Cuba.
3. Museo de Historia Natural “Carlos de la Torre y Huerta”, Holguín, Cuba.

**ABSTRACT:** The ichthyofauna from the Cenozoic of the Caribbean is mostly known from fossil sharks and rays, and a reduced number of bony fishes. Most of these fossils were collected from Neogene deposits, whereas those of Paleogene age are rare. Here we report and describe two early Middle Eocene ray-finned fish (Teleostei) from vulcano-sedimentary deposits of the El Caney Formation of Eastern Cuba. The extraordinary preservation of the fossils, which includes the soft tissue outline of the specimens, allow for a unique opportunity to study, and approximate their classification. Morphological characteristics and preliminary taxonomic analysis suggest that one of these specimens belongs to the family Percopsidae while the other exhibits affinities to either the Lutjanidae or Cichlidae families. These two specimens are the oldest known members of their respective families in the Antillean region, and they add significantly to our understanding of the Eocene marine vertebrates and aquatic ecosystems of the Caribbean.

**KEYWORDS:** Cichlidae, Cuba, Eocene, Lutjanidae, Percopsidae.

**RESUMEN:** La ictiofauna del Cenozoico del Caribe es conocida principalmente por tiburones y rayas fósiles, y un número reducido de peces óseos. La mayoría de estos fósiles se han colectado en depósitos del Neógeno, mientras que aquellos de edad Paleógeno son raros. Aquí informamos y describimos dos peces del Eoceno Medio temprano de depósitos vulcano-sedimentarios de la Formación El Caney de Cuba oriental. La extraordinaria preservación de los fósiles, que incluye el contorno de tejido blando de los especímenes, ofrece una oportunidad única para estudiar y aproximar su clasificación. Las características morfológicas y el análisis taxonómico preliminar sugieren que uno de estos ejemplares pertenece a la familia Percopsidae, mientras que el otro muestra afinidades con las familias Lutjanidae o Cichlidae. Estos dos ejemplares son los miembros más antiguos conocidos de sus respectivas familias en la región antillana, y contribuyen significativamente a nuestra comprensión de los vertebrados marinos del Eoceno y los ecosistemas acuáticos del Caribe.

**PALABRAS CLAVE:** Cichlidae, Cuba, Eoceno, Lutjanidae, Percopsidae.

### INTRODUCTION

The Eocene epoch, a time interval spanning from approximately 56 to 33.9 million years ago, represents a pivotal period in Earth's history, characterized by significant transformative climatic changes and the consequent evolution of diverse vertebrate lineages (Cramwinckel *et al.*, 2018). As the world transitioned from the Paleocene, marked by the recovery from the

Cretaceous-Paleogene extinction event, the Eocene witnessed the rise of many modern mammalian orders, the diversification of birds, and fishes, and the evolution of the first large marine mammals. But even while the Eocene vertebrate fossil record has been extensively studied in regions such as North America, Europe, and Asia, the Caribbean, and particularly Cuba, remains enigmatic primarily because of its limited or scant marine vertebrate fossil record.

✉ Yasmani Ceballos Izquierdo  
[yasmaniceballos@gmail.com](mailto:yasmaniceballos@gmail.com)

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So far, the Cuban Eocene vertebrate material includes sharks (Iturralde-Vinent *et al.*, 1996) manta ray teeth (Viñola-López *et al.*, in press), and other unidentified specimens. In this context, the report of two complete fish specimens from Eocene strata of eastern Cuba represents a significant and rare addition to the island's paleontological record.

The two specimens were collected from a quarry located in the foothills of the Sierra Maestra, near Loma Pimienta, approximately 24 km from the coast 18 km from Campechuela (Granma province), and about 500 feet above sea level. They were discovered by quarry workers who informally named them “biajaca” (Cuban cichlid) and “robalo” (snook). On February 17, 1961, researchers Eduardo Solano Osorio and Milton Pino donated the specimens to the former Museo Guamá, and at the end of the '60s, the specimens became part of the new Museo de Historia Natural Carlos de la Torre y Huerta (Holguín province, eastern Cuba). However, the fossil material remained neglected for decades, until geologist and paleontologist Manuel Iturralde-Vinent and geologist Carl Bowin visited the museum collection and photographed the material. Consequently, Iturralde-Vinent (2004, 2009) illustrated these specimens highlighting their importance for future research.

This paper aims to describe these two fish specimens and evaluate their biogeographic implications while emphasizing the challenges and opportunities presented by the scant Eocene fossil record of the island. These specimens not only provide insight into the aquatic ecosystems of the Eocene of Cuba but also represent new records of marine vertebrate fossils in the region. The identification and description of these two previously unidentified fish specimens contribute to our knowledge of circum-Caribbean marine paleoecosystems, as well as the evolution and biogeography of these organisms.

## MATERIALS AND METHODS

The specimens studied here are housed in the collections of the Museo de Historia Natural Carlos de la Torre y Huerta (MHNCT) under the number MHNCT 12-23. Since they are regarded as a lot, the two specimens are under the same catalog number, but originally, they had different numbers: the larger specimen was labeled MHNCT 14-81, and the smaller, MHNCT 14-82. We propose that the labeling be changed after this publication and differentiate the specimens by placing letters A and B in the inventory number at the end.

Detailed morphological studies were conducted on the specimens, focusing on their size, shape, and distinctive features. The specimens were also

compared with contemporaneous faunas from other regions to ascertain their evolutionary and ecological significance.

## GEOLOGICAL SETTING

In 1961, workers discovered specimens from a 45-meter-high wall outcrop at the “El Aji” quarry, situated near Campechuela, Granma province, eastern Cuba. This location exposes the early Middle Eocene El Caney Formation (Fm), and the specimens seem to originate from it (refer to Figure 1).

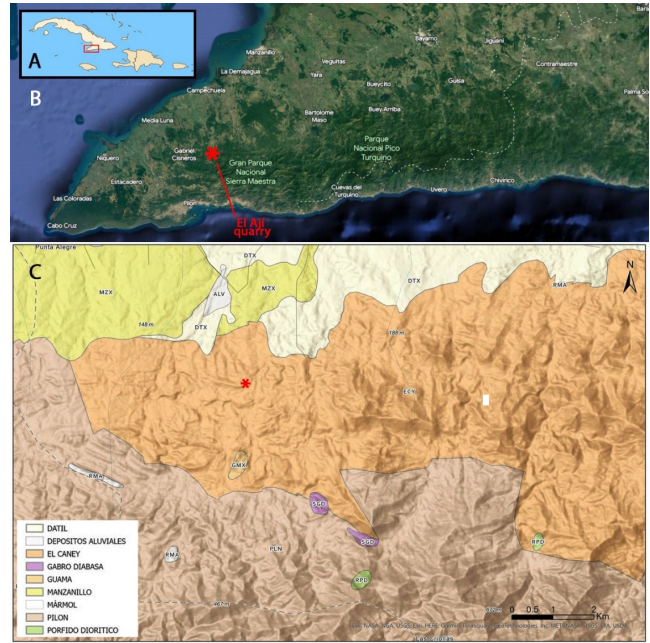


FIGURE 1. A: Map of Cuba, B: Satellite map of part of eastern Cuba showing the location of El Aji quarry (red star) - a locality near Campechuela (Granma Province) where the fossil fish specimens discussed in this report originated, C) Geology of the studied area (Map courtesy of Rafael Coutin-Lambert).

FIGURA 1. A: Mapa de Cuba, B: Mapa satelital de una parte de Cuba oriental mostrando la ubicación de la cantera El Aji (estrella roja) - una localidad cerca de Campechuela (Provincia de Granma) de donde provienen los peces fósiles discutidos en esta contribución, C) Geología del área estudiada (Mapa cortesía de Rafael Coutin-Lambert).

The El Caney Formation belongs to the upper part of El Cobre Group and crops out on the northwestern and northeastern slopes of the Sierra Maestra (Granma and Santiago de Cuba provinces). It is characterized by pyroclastic and sedimentary rocks, conglomerates, and lava flows (García-Delgado and Torres-Silva, 1997; Iturralde-Vinent, 1996, 2021; Sokolova, 1966). It lies concordantly over the Lower Eocene Pilon Formation and below the Middle

Eocene Puerto Boniato Formation. The foraminifera assemblage includes the following index taxa: *Morozovella aequa*, *M. aragonensis*, *Acarinina brodermanni*, *Discocyclusa barkeri*, *Pseudophragmina (Pseudophragmina) cedarkeyensis*, *Amphistegina cubensis*, *Eoconuloides wellsi*, *Helicolepidina spiralis* (Iturralde-Vinent, 2021). The El Caney Fm was deposited in an open marine basin, in the final stage of the Paleogene volcanic arc, mostly during the early Middle Eocene, with abundant contribution of tuffogenic and terrigenous material.

## RESULTS

### SYSTEMATIC PALEONTOLOGY

Order PERCOPSIFORMES Berg, 1940  
 Suborder PARACANTHOPTERYGII  
 Family PERCOPSIDAE Agassiz, 1850  
*Fishia incertae sedis*: gen. sp. indet.

### MATERIAL

MHNCT 12-23-A, a complete articulated fish skeleton with traces of soft tissues and scales on matrix (preserved in halves) - [Figures 2-7](#).

### LOCALITY AND AGE

The specimen was collected from “El Aji” quarry, near Campechuela, Granma, in matrix of the early Middle Eocene El Caney Formation.

### DESCRIPTION

Elongated specimen with a large head and well-developed pelvic and dorsal fin. The specimen seems to have been preserved in an oblique or slanted position, and the head is thus preserved perpendicularly (on dorsal view). The skull is widest posteriorly, with a narrow supraoccipital, but rounded cranium. A sagittal suture is slightly visible running midway through the cranium. There is no evident raised crest. There are no apparent, additional sutures. The orbit is not visible, but the upper maxillary and dentary do not seem to extend closely to the front of the eyes. The opercular bones are large and ovoid, scattered posteriorly, and openly. The ceratohyal is elongated and arched ([Figures 2-4](#)). Several possible accessory fin rays and spines can be observed towards the dorsum-neck area. The anterior portion of the skull (nasal frontal) tapers gradually into a thin point towards what could be the maxilla, premaxilla, or palatine. Traces of possible stub-like teeth are hardly detectable on this specimen (X-ray imaging has not been possible).



FIGURE 2. MHNCT 12-23-A from El Aji quarry, near Campechuela (Granma Province), Early-Middle Eocene, El Caney Formation (set in tuffaceous matrix).

FIGURA 2. MHNCT 12-23-A de la cantera El Aji, cerca de Campechuela (Provincia de Granma), Eoceno Medio temprano, Formación El Caney (incrustado en matriz tufácea).

Traces of the basipterygia can be inferred in the ventral nape, behind the opercular or supraopercular bones. The cephalic canal is not evident in this specimen. The hypohyal and anterior ceratohyal elements are not well preserved in this specimen, but there are large flat-bone impressions that could represent this element ([Figure 4](#)). The dorsal spine does not originate at the occiput.

The specimen contains ~30 vertebrae, of which seven are precaudal, located in the anterior portion of the dorsal nape. The thoracic contains hemal and hemapophyses on the ventral side of the vertebral body, originating dorsally, and zygapophyses also on the dorsal, with traces of intermuscular bones, and what could be remains of rays. The ribs and spines are generally attached to the centrum of the vertebrae, except towards the caudal fin. Some of the vertebral processes seem fused. The neural spines are usually attached to the vertebral centrum and arched posteriorly. The vertebral intercentrum is well-defined, with accentuated pleurocentrae. Prezygapophyses are more accentuated than postzygapophyses in the cephalad vertebrae, whereas the opposite is true in the caudal, tapering towards the hypurals ([Figures 3, 5, and 6](#)).

The specimen has well-preserved and developed dorsal and anal fins, of which the first is the largest. The anal fin is sub-squared, and its posterior margin is near straight. The dorsal fin is curved and tapers at the tip. The dorsal fin lies midway between the pelvic (anterior-most) and anal fins (posterior-most). The pelvic fin is poorly preserved, but it is represented by five thick spines. Small traces of accessory thin rays

or fragments of a pectoral fin lie immediately posterior to it.

Articulated to the pelvic fin is a series of ribs, intermuscular bones, and hemal spines. These fins have both spinous and soft rays. The anal fin has ~ eight hard spines and ~ eight soft bifurcating rays towards the tips. The dorsal fin has nine hard spines in the same mode as the dorsal fin (Figure 7). These spines tend to bifurcate towards the distal ends, whereas they are thicker toward their origins. There seem to be a few floating ribs at the distal spinous ray fins in the anal and pelvic fins. There are no vestiges of an adipose fin on this specimen. However, evidence of a possible tissue bulge ('?' in Figure 3) between the dorsal fin and caudal peduncle. This area does not contain superficial evidence of spines or rays, and thus cannot be identified as a small fin.

The tail is incomplete, containing hard, grooved spines and bifurcation fin rays towards the tips of the fin. The caudal fin is truncated and does not seem forked or notched. There are at least six, well-defined caudal vertebrae with preural centrum (Figure 7). The most posterior attachment of neural-hemal spines occurs at the third caudal vertebrae from the

hypural. The parahypural are slanted, covered in soft fine rays. The hypural seems more solid and fussed. From both structures, at least 15-16 hard spines arise. Six accessory or rudimentary fin rays lie over them on the vertices of the tail.

Thanks to the exceptional preservation of this specimen, a soft tissue silhouette is evident. It shows a round, bulging head with an elongated nape and caudal peduncle. Remnants of scales and fragments of skin are also observable towards the head and trunk. The scales have a crosshatching cycloid pattern of laterally compressed ganoid (rhomboid) scales (Figure 5). The openings or lateral line canals are thin. Since the specimen is slightly rotated, what seem to be parts of the second pelvic fin can be observed behind the head, and in front of the dorsal fin. The full ossification suggests the specimen was likely an adult (although perichondral elements have not been preserved in this specimen).

### COMPARISONS

Percopsidae is a family of five genera of small, elongated fish that are endemic to North America,

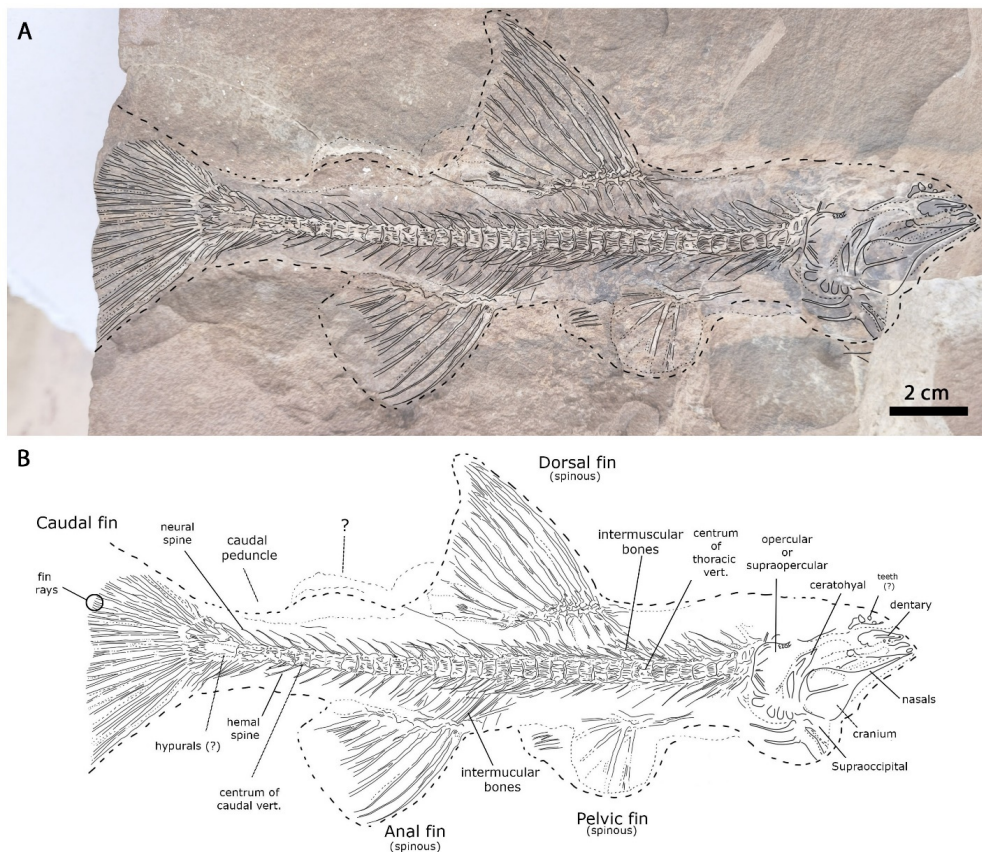


FIGURE 3. Superposition and line drawing (B) for specimen MHNCT 12-23-A (A) demonstrating general tentative osteology. Drawing by JO.

FIGURA 3. Superposición y dibujo lineal (B) del ejemplar MHNCT 12-23-A (A) mostrando una osteología tentativa general. Dibujo por JO.

where they are known from both marine and freshwater environments. Only one genus remains extant, *Percopsis*, whereas four are extinct: *Amphiplaga*, *Erismatopterus*, *Lateopisciculus*, and *Libotonius*, known from Paleocene-Eocene (~66-41 Ma) freshwater-lake deposits (Wilson, 1979; Grande, 1984; Murray and Wilson, 1996). Their earliest fossils are known from the Paleocene, but their origins could extend to the Cretaceous (Cavender, 1986). Percopsids have a diet of insects and small crustaceans.

Specimen MHNCT 12-23-A display the following diagnostic discrete characters of the percopsid family: The premaxilla contains a single row of teeth; the opercular bones are serrated on the posterior margin; the posttemporal has a narrow and elongate process, with a lunate-shaped supraoccipital (Agassiz, 1849, 1850; Murray, 1996; Polly, 2004).

Our specimen differs from *Amphiplaga brachyptera* and *Erismatopterus levatus* in several important diagnostic features. The head of *A. brachyptera* and *E. levatus* is not as elongated, and the nape is pronounced. The frontal-nasal and occipital areas of the cranium are also shorter and thicker in *Amphiplaga* and *E. levatus*. The main difference lies in the morphology of the dorsal and pelvic fins. In *Amphiplaga* and *Erismatopterus*, these are near the same size (the dorsal slightly larger). The pelvis is much larger and flipper-like than in both genera. Our specimen lacks a pectoral fin (which could be due to preservation and not morphology), present in *Amphiplaga* and *Erismatopterus*. The vertebrae seem much smaller in *Amphiplaga* and *Erismatopterus* than in MHNCT 12-23-A, and the thoracic ribs and spines are of unequal size (same size in *Amphiplaga* and *Erismatopterus*).

They are similar, however, in having at least eight hard spines, with fine bifurcating rays towards the tips. They both have similar accessory fin rays on the vertices of the tail. The scale pattern crosshatching is also congruent.

In caudal fin osteology, specimens differ considerably from several extant and fossil percopsids mentioned above, particularly in the arrangement and morphology of the parhypural and hypurals. These elements in the extant polymixiiform *Plumixia nobilis*, the Cretaceous *Sphenocephalus brachypterygius*, in addition to the percopsids and lobotoniids *Percopsis omiscomaycus*, *Amphiplaga brachyptera* and *Erismatopterus levatus* (after Borden et al., 2013; Rosen and Patterson, 1969) are elongated and palate-like; much broader in direction of the tail-tip. In MHNCT 12-23-A, these osseous elements are much more reduced and grouped. Although they are tapered caudally and wider caudally (much smaller palette-like form) their articulation

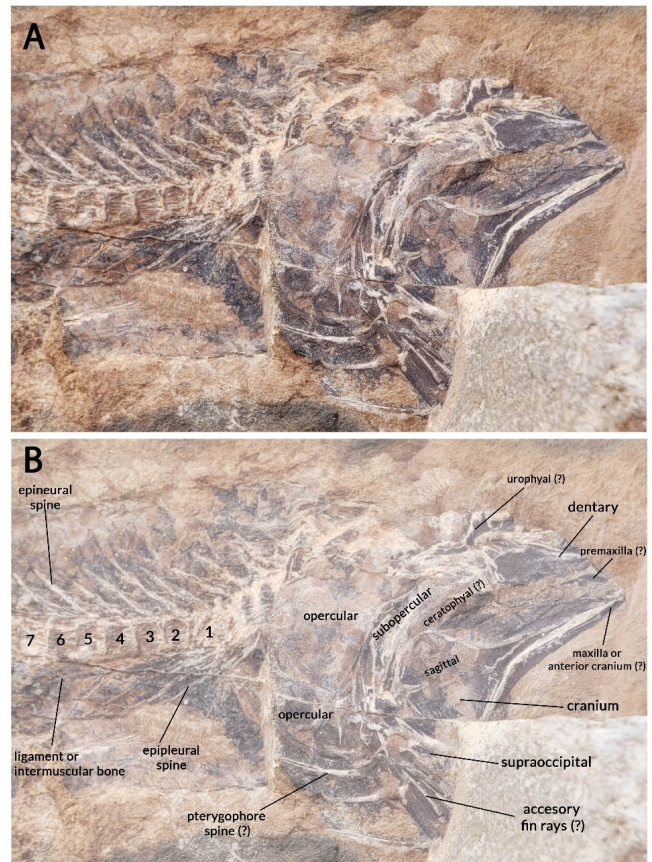


FIGURE 4. Skull osteology (A) and indicated (B), tentative, terminology of specimen MHNCT 12-23-A.

FIGURA 4. Osteología del cráneo (A) e indicación (B), tentativa, de la terminología del ejemplar MHNCT 12-23-A.



FIGURE 5. Example of scale and soft tissue preservation on specimen MHNCT 12-23-A.

FIGURA 5. Ejemplo de conservación de escamas y tejido blando en el ejemplar MHNCT 12-23-A.

to the first pleural and ural centrum is not superimposed, but straight and direct. In this sense, it resembles the percopsiform *Massamorichthys wilsoni* and basal *Mcconichthys* sp. (Grande, 1988; Murray, 1996) in addition to the esocid *Esox kronneri* illustrated in Grande (1999: 280). These are sister taxa to extant trout

perches, mostly recovered from shallow lake deposits (freshwater) (op. cit.).

Tentatively identified as a “robalo” or snook (*Centropomus undecimalis*) originally by the fossil’s discoverers, this specimen does not seem to represent a specimen of the Centropomidae.

#### REMARKS

This specimen may represent a percopsid new genus and species, that existed in the paleo-Caribbean during the Eocene. However, more detailed comparisons and analyses are required to properly diagnose and name this specimen.

Order PERCIFORMES Bleeker, 1859  
Suborder LABROIDEA, Bleeker, 1859  
Family LUTJANIDAE or CICHLIDAE  
*Fishia incertae sedis: gen. sp. indet.*

#### MATERIAL

MHNCT 12-23-B, near complete articulated fish skeleton with soft tissue silhouette in matrix. [Figures 8-9](#).

#### LOCALITY AND AGE

The specimen was collected from the "El Ají" quarry, near Campechuela (Granma Province), in sediments of the early Middle Eocene El Caney Formation.

#### DESCRIPTION

Well-preserved, near complete, and fully articulated fossil fish skeleton with soft tissue



FIGURE 6. Fossilized counterpart of specimen MHNCT 12-23-A. Note the vertebral body and abdominal spine arrangement.

FIGURA 6. Contraparte fosilizada del ejemplar MHNCT 12-23-A. Observe el cuerpo vertebral y la disposición de las espinas abdominales.

silhouette. The specimen is generally small and short, about ~ 12 cm in length. The head is large with a large, ovoid open orbit, preserved in lateral view ([Figures 8-9](#)). The cranium is short but thick in the frontals and nasals. Two probable sphenotic bones are visible posterior to the orbit. The orbit is smaller than the snout length. The dorsal spine does not originate above the occiput. The premaxilla is regular. The remains of the maxilla are evident below. This element is nearly straight pallet-like, tapering caudally. Small, stubby teeth are preserved in the dentary and distal premaxilla. The dentary is wedge-shaped, and thicker caudally. The dentary articulation lies under or at the anterior margin of the orbit. The premaxilla seems to contain a sinus or fenestra (opening). The supraoccipital is wide and rounded, immediately posterior to and not fully fused to the frontal bone. The opercular bones are large, ovoid, flattened, and moderately wide and striated, covering most of the lateral aspect of the

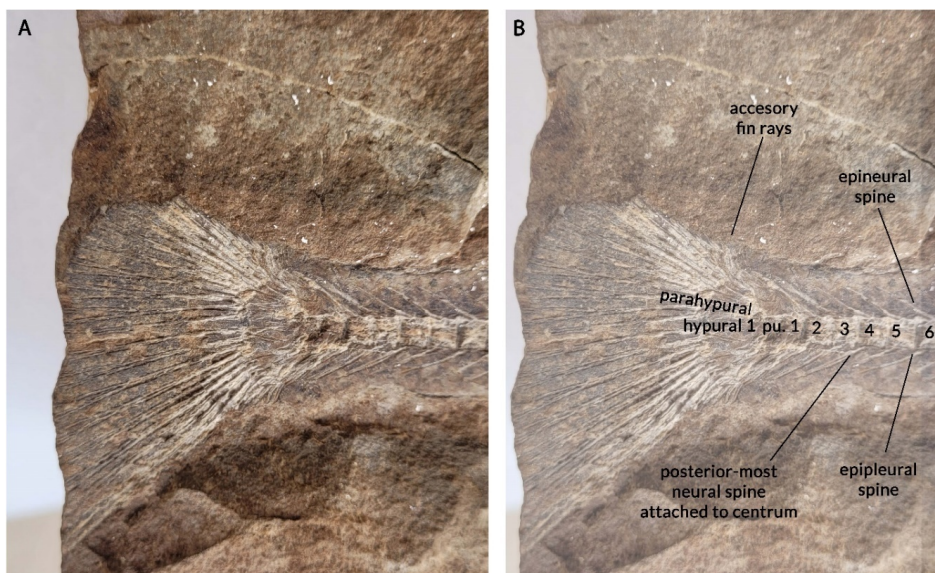


FIGURE 7. Caudal fin osteology (A, B) with indicated (tentative) terminology of specimen MHNCT 12-23-A.

FIGURA 7. Osteología de la aleta caudal (A, B) con terminología indicada (tentativa) del ejemplar MHNCT 12-23-A.

head. A large, flat bone lies (interneural?) just behind the supraoccipital. The remains of a pectoral arch seem to be preserved ventrally at the gills.

The body extends nearly three times the size of the head and it includes three well-preserved spinous fins. The dorsal fin is the largest, extending from the nape, nearly behind the head, to a short caudal peduncle - thus covering most of the dorsal length. There is a small soft tissue gap between the head and the remains of a pterygophore that extends nearly most of the dorsal fin. The remains of scales are evident in that region. The dorsal fin is supported by 13-14 spinous rays attached to dorsal ribs (and intermuscular bones?). The pelvic or pectoral fin is poorly preserved, but it seems to have been small, with ~ 5 spinous rays, supported by thoracic, and ventral ribs (Figures 8- 9). The anal fin is larger than the pelvic or pectoral fin, and more squared in shape. This fin has ~ 10-11 hard rays. Remains of soft rays can be seen distally, within the ghost of soft tissues.

The tail is small, nearly the size of the head, and slightly forked or emarginated. Remains of scales can also be noted in that region. The backbone terminates abruptly, proximally, the caudal fin origin. These are ctenoid (elasmoid?) or cycloid. The urohyal and hypurials are not well preserved, thus inhibiting a better assessment of the caudal fin osteology. There are approximately 16-17 caudal fin rays, with the soft rays appearing progressively thinner towards the tip. There seems to be a gap or missing section between the first caudal vertebra and the caudal fin osseous elements. The last hemal spine attached to the centrum is at the second caudal vertebra. The neural and hemal spines are of similar size and thickness. The larges lie in the thoracic region. Accessory fin rays are present on the vertices of the tail.

There are a total of ~ 20 vertebrae, of which at least five are caudal. The hemal and neural spines arise from the centrum of the vertebral body in the thoracic-abdominal, anteriorly in the nape and caudal. The vertebral bodies are slim and generally fused, particularly in the cervical and caudal. The hemal or chevron arches lie in the centrum of the body but lean towards the anterior-most. At least well-developed parapophyses are present throughout the abdominothoracic region. This region has a slight kyphosis which marks the division between thoracic-abdominal vertebrae (Figure 9).

#### COMPARISONS

Upon first inspection, the specimen resembles a member of the Lutjanidae, Sparidae, or Cichlidae

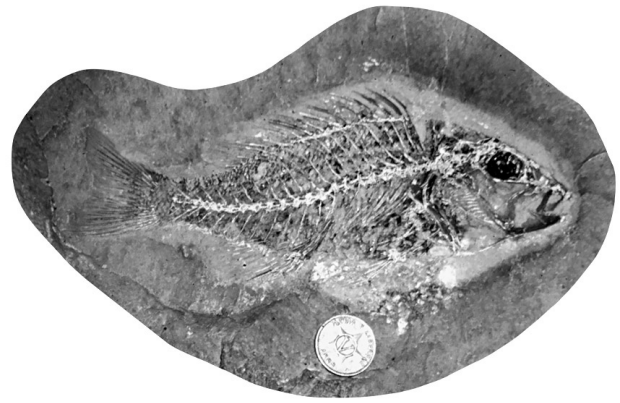


FIGURE 8. Articulated skeleton and soft tissue silhouette of specimen MHNCT 12-23-B from El Ají quarry, near Campechuela (Granma Province) set in fine grain tuffaceous slab of the early Middle Eocene El Caney Formation.

FIGURA 8. Esqueleto articulado y silueta de tejido blando del ejemplar MHNCT 12-23-B de la cantera El Ají, cerca de Campechuela (Provincia de Granma) incrustado en una losa tufácea de grano fino de la Formación El Caney del Eoceno Medio temprano.

families. These three are teleost percomorph fishes with varied and diverse adaptations and speciosity (Kullander, 1998). Cichlids are particularly diverse, inhabiting mostly freshwater environments, and with a meager fossil record (Bannikov and Zorzin, 2020).

MHNCT 12-23-B resembles the extinct cichlids *Gymnogeophagus eocenicus*, *Proterocara argentina*, and other spp. from the Eocene of Argentina (Malabarba et al., 2006) and *Nandopsis* spp (= *Cichlostoma*), known from the Caribbean Miocene (Chakrabarty, 2006).

*Proterocara* and MHNCT 12-23-B share the following morphologies: the overall body-tail shape is similar; the lachrymal bone lies right underneath the orbit and slightly posterior to the maxilla-premaxilla; the anal fin base is posterodistally inclined; the origin of the anal fin at the posterior half of the dorsal fin. They are most dissimilar in that MHNCT 12-23-B has a more elongated head, with a more dorsally positioned eye (bulkier, more erect, with lower orbit in *Proterocara*); ~ 20 vertebra in total, much less than the diagnostic nine abdominal and 19 caudal reported for *Proterocara* spp., a wide below, serrated, and elongated dorsally pre-opercle (erect, slender, and straight dorsally, wider and ached ventrally in *Proterocara* spp.). The caudal skeleton includes palette-like, wide hypurals, with thin and small uroneurals (elements not visible in specimen 00); thicker caudal peduncle in *Proterocara* spp. (elongated and thinner in MHNCT 12-23-B). Compared to *Gymnogeophagus eocenicus*, specimen

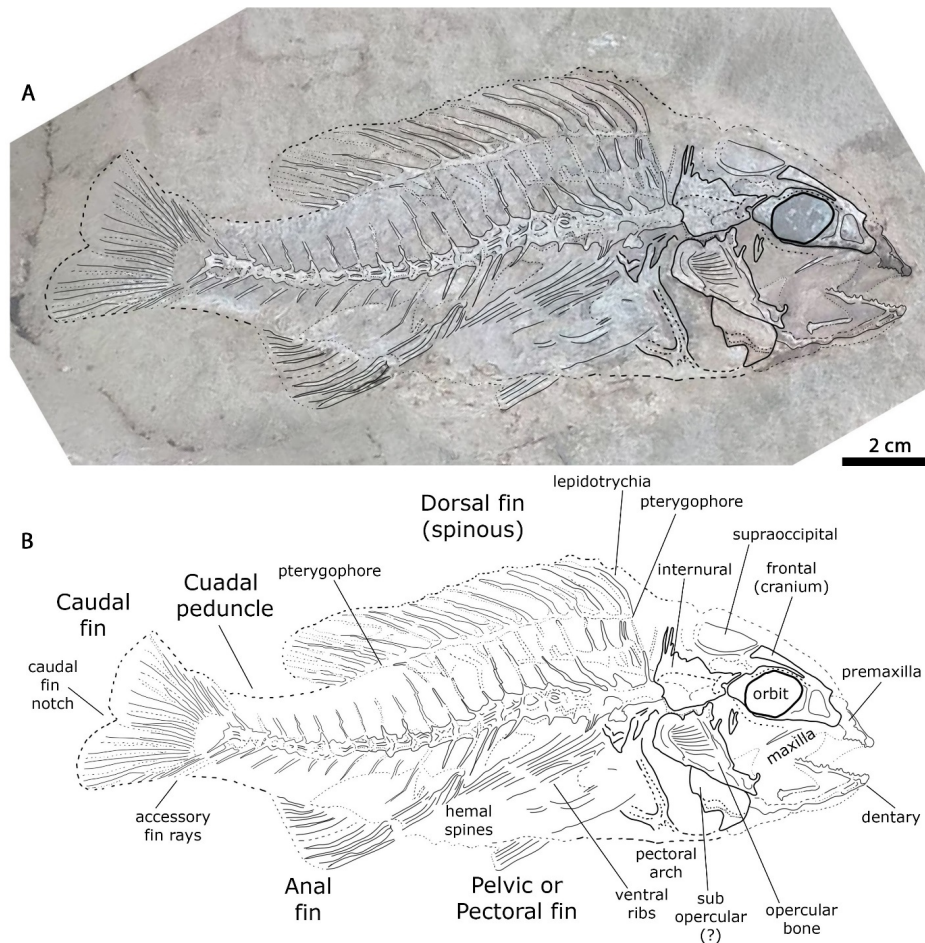


FIGURE 9. Superposition (A) and line drawing (B) for specimen MHNCT 12-23-B demonstrating general tentative osteology. Drawing by JO.

FIGURA 9. Superposición (A) y dibujo lineal (B) del ejemplar MHNCT 12-23-B mostrando una osteología tentativa general. Dibujo por JO.

MHNCT 12-23-B is slender, with a more elongated head; the orbit lies higher in the skull and is more ovoid (rounder and lower, with thicker frontals in *Gymnogeophagus eocenicus*). MHNCT 12-23-B lacks the diagnostic forward-directed spine on the first dorsal pterygophore and loss of supraneurals (Kullander, 1998; Reis and Malabarba, 1988).

MHNCT 12-23-B differs from the Caribbean *Nandopsis* spp., (Chakrabarty, 2006) in the latter has a more erect head, with a lower eye and nuchal hump (more elongated, with a higher and more posterior orbit, and lacks a nuchal hump in specimen MHNCT 12-23-B); the caudal fin is rounded in *Nandopsis*, as in other Central American cichlids (op. cit.), but slightly forked in MHNCT 12-23-B. The caudal peduncle in *Nandopsis* is usually short and thick, with the dorsal fin extending to its recess (absent in MHNCT 12-23-B); the dorsal fins are erect and curved posteriorly in MHNCT 12-23-B, but flat and recumbent in *Nandopsis woodringi*. There are

12 abdominal vertebrae reported for the Hispaniola fossil *N. woodringi* like MHNCT 12-23-B. They are also similar in average dorsal spines and ray frequency. Their scales are also highly similar, ctenoid in decreasing series, but seem more quadrate in *Nandopsis*. However, the anal ray count is much higher in specimen MHNCT 12-23-B (~16) than in *N. woodringi* (Cockerell, 1924; Nelson, 1994; corrected in Chakrabarty, 2006).

MHNCT 12-23-B shares several morphologies with the Lutjanidae and Sparidae families. These include a forked tail, a single dorsal fin, and a small mouth, an ovate to elongate body shape, the presence of small conical teeth, a serrated operculum, a continuous dorsal fin that does not extend to the caudal peduncle space, a snout that extends to below the eye, with a complete lateral line (Gill, 1861, 1864 and 1893; Van Der Laan *et al.*, 2014). The presence of a subterminal mouth, pelvic fin originating posterior or at the level of the



pectoral fin, and slightly forked tail suggest it belongs to the Lutjanidae family (Gill, 1861), resembling genera such as *Apsilus*, *Rhomboplites* and *Lutjanus* spp.

Particularly, MHNCT 12-23-B resembles the genera *Lutjanus*, *Ottaviana*, *Goujetia*, and *Veranichthys* spp. for having an elongated, but thick body, small, thick heads that gradually slant dorsally, and large orbits, plus a single, wide-based dorsal fin, and smaller anal and pectoral fins. Their caudal fins are hypocentral-like and slightly forked. *Ottaviana leptacanthus* (Bannikov, 2006), from the Middle Eocene of northern Italy, holds great similarity but has a wider base, bimodal dorsal fin (same throughout in specimen MHNCT 12-23-B), more elongated skull, with a lower orbit and thicker dentary. It also resembles *Goujetia crassispina* (op. cit.) in having a similarly stocky body and large head. However, in *Goujetia crassispina* the head is less slanted dorsally, with more abrupt frontals and post occipitals, and the vertebral bodies seem thicker. The orbit in MHNCT 12-23-B sits closer to the frontal. The dorsal and anal fins are similar. *Veranichthys ventralis* is similar, but it has more pronounced maxillary and dentary teeth, but a thicker and slanted frontal. The scale pattern seems similar to MHNCT 12-23-B (compared to Fig. 10 in Bannikov, 2006).

#### REMARKS

Lutjanid or cichlid, likely a new genus + species combination.

#### DISCUSSION

The presence of true spinous rays in the dorsal and anal fins allocate both specimens (MHNCT 12-23-A, MHNCT 12-23-B) in the superorder Acanthopterygii (Greenwood *et al.*, 1966; Rosen and Patterson, 1969; Weitzman and Myers, 1966) or Percomorpha of Nelson (2006). MHNCT 12-23-A contains ~ 20 vertebrae, which agrees with the basal number of vertebrae in Perciformes (24-25; Gosline, 1971). However, likely, more vertebrae are not visible or present due to preservation. More interestingly, these specimens preserve traces of coloration or original pigmentation, which further analyses (under X-ray, UV light, and chemical) could provide further enlightening data.

The presence of both fossil percopsid and lutjanid/cichlid fish in the Antillean fossil record has significant biogeographical implications. For instance, the presence of a percopsid in the Cuban fossil record suggest of a North American component in the Eocene fish fauna in the Caribbean basin and suggests that the circum-Caribbean seas

were once home to a more diverse of fish species during Eocene than expected.

Lutjanids are a family of marine fish that are typically found in tropical and subtropical waters, including the modern Caribbean and Atlantic waters. Most are active carnivores and commonly inhabit shallow, coral reef environments. The presence of an Eocene lutjanid fossil in the Antillean fossil record could represent some of the earliest representatives of the family and indicate the presence of warm, tropical marine-reef environments.

On the other hand, several biogeographic problems arise with these data if specimen MHNCT 12-23-B is indeed an Eocene cichlid. Molecular studies suggested a separation of Greater Antillean cichlids from Central American sister groups around the early Eocene (~50 Ma), whereas the node of Cuban cichlids seems to have evolved in the Late Oligocene (~25 Ma) (Chakrabarty, 2006; Chakrabarty and Albert, 2011; Smith *et al.*, 2008).

More recent molecular clock-dates and biogeographical analyses, as well as the paleogeographic scenario for the Caribbean Eocene (Iturralde-Vinent, 2006; Iturralde-Vinent and MacPhee, 2023), strongly support two cichlid colonization events: one of the Greater Antilles and another of Middle America from South America in the Oligocene (Řičan *et al.*, 2013). If MHNCT 12-23-B is indeed an Eocene cichlid, it would not agree with the molecular divergence data, suggesting instead that the Cuban cichlids may have arrived in Cuba earlier than the molecular data suggests, or that they may have originated in Cuba and then migrated to continental America later, and thus it may represent another colonization event altogether.

It is also possible that any early Middle Eocene fossil cichlids from Cuba are not closely related to the modern Cuban cichlids. As the fossil record is often incomplete, an alternative hypothesis could be postulated in which the Middle Eocene cichlids may represent a now-extinct lineage of cichlids that is not closely related to the modern Cuban cichlids, suggesting several waves of cichlid colonization to the Greater Antilles. However, further research is needed to better understand the origin and diversification of Cuban cichlids. More fossil discoveries from Cuba and the rest of the Greater Antilles, as well as more molecular and phylogenetic studies, could help to resolve any discrepancy between the fossil record and the molecular data.

If these specimens represent new species, they may offer crucial evidence for understanding the evolutionary history and biogeographic patterns of fishes in the Eocene Caribbean region. Comparisons with known fish species from other geological localities could shed light on dispersal routes, connectivity, and potential barriers to gene flow

during this period. Also, the study of their biogeographic distributions and extinction patterns could provide insights into the responses of fish species to the Eocene Thermal Maximum (ETM), as discussed in works like [Arcila and Tyler \(2017\)](#). Further morphological analysis of these specimens can also contribute to the refinement of fish taxonomy within the region. Moreover, their unique features, and taxonomy, may challenge existing taxonomic classifications or suggest the presence of previously unknown lineages.

#### DEPOSITIONAL ENVIRONMENT AND PRESERVATION

Based on the preservation and articulation of the specimens, several hypotheses can be made for a paleoenvironmental reconstruction.

Fish decay experiments have demonstrated that temperature, high hydrostatic pressure, and salinity are crucial taphonomic factors in underwater preservation ([Gäb \*et al.\*, 2020](#); [Whitmore, 2003](#)). Hydrostatic pressure in the water column prevents fish carcasses from floating, allowing for rapidly sinking to bottom sediments, whereas high salinity and pH suppress bacterial putrefaction ([Elder and Smith, 1988](#); [Gäb \*et al.\*, 2020](#); [Whitmore, 2003](#)).

Temperature or oxygen-deficient or anaerobic conditions of the deposition environment cannot be ruled out in our samples, given that detailed geochemical analyses are yet to be done, but they are not considered major significant factors to preservation ([Gäb \*et al.\*, 2020](#)). Instead, the presence (preservation) of soft tissue silhouette, scales, and pigmentation suggests that these fish carcasses came to rest in enclosing sediments in a deep marine setting with high salinity, pH, and hydrostatic pressure (*op. cit.*). These conditions must have persisted long enough to arrest advanced decomposition, scavenging, and bioturbation (or bioerosion). The near complete articulation, and lack of direct evidence for predation, in their skeletons, are congruent with low-energy, deep-water environments.

Articulation is also revealing of preservation with little or no flotation or decomposition bloating (*op. cit.*). Since fish carcasses tend to disarticulate more frequently, in shallow water, and higher energy environments, it can be assumed that these specimens are deposited in deep, marine environments ([Whitmore, 2003](#)). This hypothesis is congruent with the open marine setting established for the El Caney Fm ([García-Delgado, 2013](#)). However, the influence of volcanism - such as quick burial due to ash deposition -, salinity, pH, and organic matter preservation on the enclosing sediments and marine environment

where these fish came to rest cannot be evaluated at this time.

At the same time, the specimens (MHNCT 12-23-A, MHNCT 12-23-B) are significant for their preservation. Such completely well-preserved fossil fish specimens are rare in Cuban collections. Only a few other specimens with comparable completeness have been discovered from older Cuban geological formations. These include a few Oxfordian (Upper Jurassic) specimens, a Tithonian (Upper Jurassic) specimen, and a Neocomian (Early Cretaceous, encompassing the Berriasian, Valanginian, and Hauterivian periods) specimen. The existence of these other, though older, fossil material presents a potential to gain valuable insights into the ancient aquatic ecosystems during those ages.

#### CONCLUSIONS

The discovery of these two well-preserved and articulated fossil fish specimens adds the record of two extant families - Percopsidae and Lutjanidae or Cichlidae - to the Cenozoic fossil record of the paleo-Caribbean region. These specimens likely represent new genera and species combinations, but we have refrained from naming them here until better material and sufficient analyses of the fossil remains could be made. Nonetheless, these two specimens could be considered valuable components of any comprehensive study on the evolution and affinities of fishes in America.

These specimens are a rare and valuable addition to the island's paleontological record. Along with already published material ([Iturralde-Vinent \*et al.\*, 1996](#)), they provide valuable insights into the aquatic diversity in Cuba during the Eocene. When juxtaposed with similar faunas from regions like North America, Europe, and Asia, the Cuban specimens offer a unique perspective on the Eocene vertebrate diversity of the Caribbean. For instance, the percoid specimen shares a close affinity with the Paleocene-Eocene extinct percoid fauna of midwestern North America. So far, this is the first report of the family in the paleo-Caribbean basin, implying that percoid fish distribution (at least in marine environments) had a much wider extent during the Eocene.

The limited availability of vertebrate fossils from the Eocene epoch in Cuba presents both challenges and opportunities. While the scarcity makes each discovery invaluable, it also underscores the need for more extensive exploration and research to bridge the existing knowledge gap. Further analyses can better assess the systematics of both specimens. Nonetheless, these two new fish specimens provide a significant contribution to circum-Caribbean marine vertebrate paleontology and biogeography; and thus,

a glimpse into the rich biodiversity that inhabited the waters of ancient Cuba during the Paleogene.

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