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OLDEST †ELLIMMICHTHYIFORM FISHES FROM PERU AND THE EARLY RADIATION OF CLUPEI

BY

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Abstract — Two small, double-armored clupeomorphs assigned to †Ellimmichthyiformes are described. †*Ancashichthys peruensis,* a new genus and species of a small (ca. 60 mm standard length), fusiform clupeomorph, is characterized by the presence of a predorsal and abdominal series of scutes, the dorsal-fin insertion positioned anterior to the pelvic fin, and the anal-fin insertion at the level of the third to fifth caudal vertebrae. †*Aijaichthys brevis,* a new genus and species of a small (ca. 50 mm standard length), is deep bodied, half-moon shaped, and double-armored clupeomorph, is characterized by a complete series of predorsal and abdominal scutes and the dorsal fin positioned slightly anterior to the pelvic fin. Both taxa are assigned to the new family †Ancashichthyidae, which is characterized by a unique combination of characters of the predorsal series of scutes and supraneurals. These fishes were collected from uppermost Jurassic (Tithonian) deposits in the Department of Ancash, northern Peru. They represent the first and oldest members of the crown Teleostei (Clupeomorpha) on the Pacific slope of South America, and they are interpreted herein as the oldest known members worldwide, displacing the †ellimmichthyiforms from the Atlantic slope of South America, whose oldest representative is Barremian, middle Lower Cretaceous. Having the oldest clupeomorphs being discovered in Peru supports the hypothesis of South America as a center of origin and radiation of otomorphs, a large, economically important clade, which is sister to Euteleostei.

Resumen — Se describen dos especies de peces clupeomorfos de tamaño pequeño que presentan una armadura doble. †*Ancashichthys peruensis* n. gen. et sp., nuevo género y especie de clupeomorfo (aproximadamente de 60 mm de longitud estándar), presenta un cuerpo fusiforme caracterizado por una serie de escudos predorsales y otra de escudos abdominales (carácter diagnóstico único de clupeomorfos), una aleta dorsal ubicada anterior a las aletas pélvicas y una aleta anal que comienza a la altura de la tercera a quinta vértebra caudal. †*Aijaichthys brevis* n. gen. et sp., nuevo género y especie de aproximadamente 50 mm de longitud estándar se caracteriza por un cuerpo alto, en forma de semiluna, con series completas de escudos predorsales y abdominales, y una aleta dorsal ubicada ligeramente anterior al origen de las aletas pélvicas. Ambos taxones son asignados a una nueva familia, †Ancashichthyidae, que se caracteriza por una combinación única de caracteres tanto en la serie de escudos predorsales como en los supraneurales. Estos peces fueron recolectados

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en los depósitos más superiores del Jurásico Superior (Titoniano) en el departamento de Áncash, en el norte del Perú. Constituyen los primeros y más antiguos representantes de Clupeomorpha (Teleostei) en la vertiente Pacífica de América del Sur. Ellos se interpretan como los clupeomorfos más antiguos conocidos, desplazando de esta posición a los ellimmichthyiformes de la vertiente Atlántica de América del Sur, cuyos registros más antiguos provienen del Barremiano, Cretácico Inferior medio. Los taxones aquí descritos apoyan la hipótesis de que América del Sur fue el centro de origen y radiación de Otomorfa, uno de los principales clados de Teleostei, de gran importancia económica y ecosistémica, y grupo hermano de Euteleostei.

INTRODUCTION

Today, clupeomorph or Clupei (*sensu* Betancur-R. et al., 2017) teleostean fishes—commonly known as anchovies, sardines, herrings and shads—include two extant, large groups, Denticipitoidei and Clupeoidei, and a fossil one, †Ellimmichthyoidei (Nelson et al., 2016; Kevrekidis et al., 2024; Fricke at al., 2025). Extant Clupei are represented by ca. 400 species, with about half living in the Indo-West Pacific and one quarter in the Western Atlantic. They typically inhabit marine waters, but about 80 species are freshwater (Arratia, 2018). Many clupeomorph species are economically important worldwide (Whitehead, 1985; Whitehead et al., 1988; Lavoué et al., 2014; Kevrekidis et al., 2024). For example, the southern Pacific Ocean is inhabited by species of major economic significance, such as *Sardinops sagax*, *Spratus bentincki*, *Spratus fuegensis,* and *Engraulis ringens* (Canales-Aguirre et al., 2021), with the last being a major representative in Peruvian fisheries (Vildoso et al., 1999; Castillo et al., 2023). Although currently rich in extant clupeiforms, fossil members of the order are almost unknown from the southern Pacific Ocean, except for a few reports by Ordóñez et al. (2013, 2015) and Ordóñez (2017, 2022) of the fossil material that is formally described herein. In contrast, Early Cretaceous so-called clupeomorphs have been known for a long time from the Atlantic side of South America, and more recently, from Mexico, for example, †*Pseudoellimma gallae* (de Figueiredo, 2009a), †*Cynoclupea nelsoni* (Malabarba and Di Dario, 2017) and †*Nolfia riachielensis* (de Figueiredo, 2009b) from the Barremian of Alagoas, Brazil; †*Santanaclupea silvasantosi* (Maisey, 1993) from the Albian of Chapada do Araripe, Brazil; and from Mexico, †*Ranulfoichthys* (Albian; Alvarado-Ortega, 2014), †*Triplomystus applegatei* (Aptian and/or Albian; Alvarado-Ortega and Ovalles-Damian, 2008), and †*Armigatus felixis* (Albian; Than-Marchese and Alvarado-Ortega, 2022).

The main goals of this contribution are to describe the Peruvian fossil clupeomorphs, which were recovered from Upper Jurassic (Tithonian)-Lower Cretaceous (Berresian) strata of northern Peru, provide a taxonomic assignment, and discuss their significance in the understanding of the double-armored herrings (†Ellimmichthyiformes).

Geological Setting

The fossil teleosts examined in this study were found in the districts of Aija and La Merced, belonging to the Province of Aija, Department of Ancash, northern Peru. This area lies in the western sector of the Cordillera Negra, part of the Western Andean Cordillera (Fig. 1).

The first collections were done in 2009 and 2010 during the revision of the geological mapping of the Huaraz sheet (Navarro et al., 2010, 2011) in the framework of Project GR4: *Geology of the volcanic rocks of the Cordillera Occidental of northern Peru*. Also, in 2014 a generalized survey and sampling of the study area was carried out. Subsequently, in 2017 additional material was collected in the framework of Project GR29: *Paleontological Studies*. All these works were carried out under the leadership of the Regional Directorate of Geology of the Geological, Mining and Metallurgical Institute of Peru (INGEMMET). On a recent field trip in 2024, additional specimens of clupeomorphs and invertebrates were recovered.

The outcrops exposed between the towns of Aija and La Merced correspond to Mesozoic rocks of the Simbal, Punta Moreno, and Tinajones Formations (Chicama Group), and in the upper parts of La Merced, there is also the Chimú Formation (Goyllarisquizga Group), which is strongly folded by episodes of deformation and uplift associated with the development of the Andean Range (Mégard, 1984; Palacios et al., 1995). On top of the Mesozoic rocks are Cenozoic volcanic deposits belonging to the Calipuy Group (Cobbing et al., 1996; Navarro, 2014; Ordóñez et al., 2014; Chávez, 2016). Locally outcropping intrusive bodies cut Mesozoic and Cenozoic rocks (Fig. 2; Tumialán, 1975; Noble et al., 2004). The fossiliferous localities of the study area are sedimentary and volcanoclastic rocks of the Tinajones Formation of the Chicama Group, whose outcrops extend to the north, east, and south, along ca. 500 km from 7º–10º South, following the alignment of the Western Andes Range.

At the base of the studied sequence (Fig. 3), the Upper Jurassic Simbal Formation, consisting of sequences of marly sandstones with intercalations of shales and sandstones, represents prodelta deposits (Jacay, 1992). The succeeding Punta Moreno Formation in Aija and La Merced Districts consists mainly of sandstones with sparse shale layers and represents submarine fan deposits. Above this formation is the Upper Jurassic Tinajones Formation, which contains the fossiliferous localities of interest. Its basal part is layers of shales with intercalations of sandstones, representing deltaic deposits (Jacay, 1992). In the middle, the Tinajones Formation is mainly shales with parallel lamination intercalated with limestones and some sandstone layers. The upper portion is shale layers with intercalations of sandstones and were interpreted as

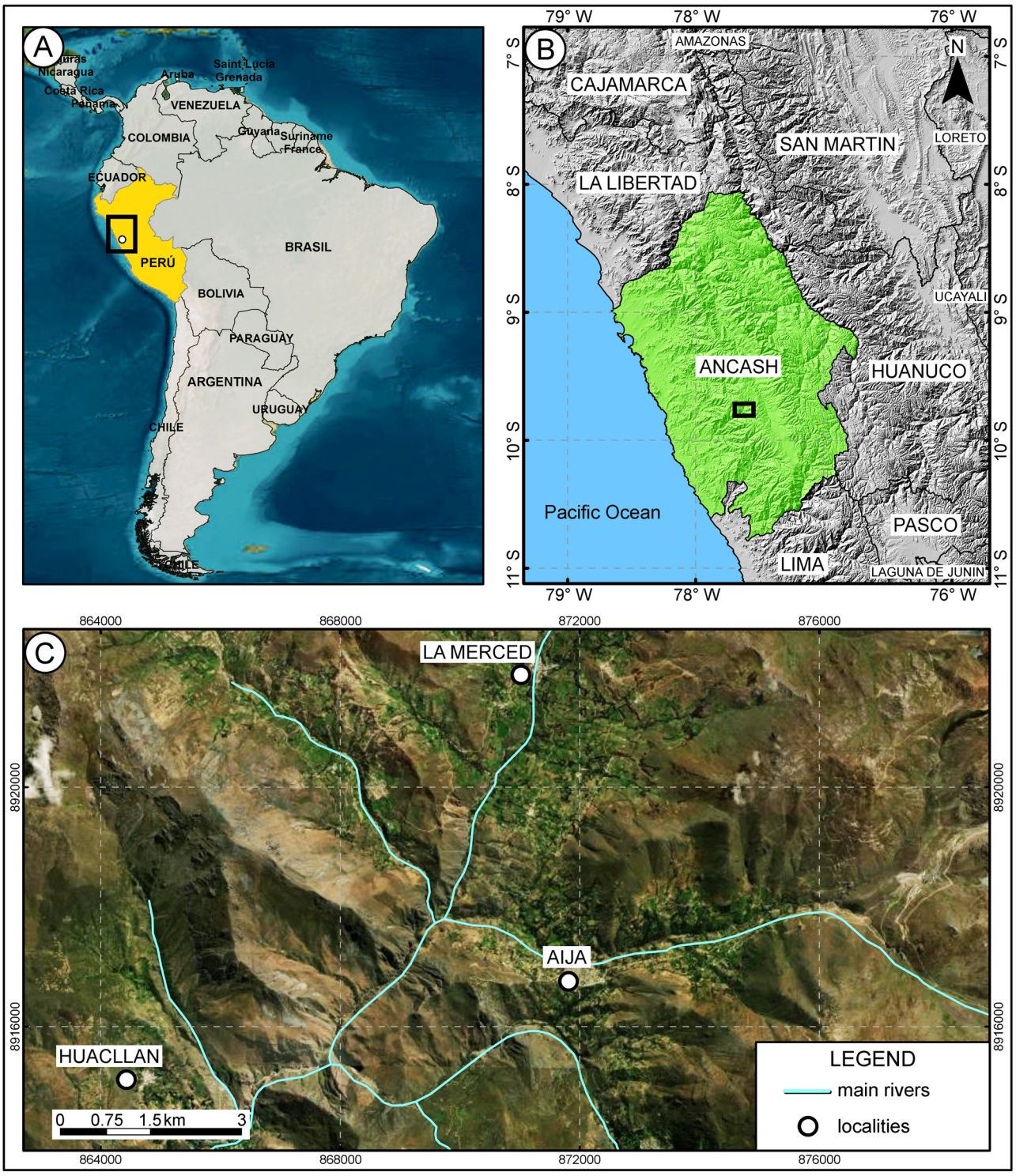


FIGURE 1 — Location of the study area. **A**, Northern Peru, northwestern South America. **B**, at the regional level, in the Department of Ancash. **C,** districts of Aija and La Merced, Province of Aija, where the fossil fishes described here were recovered.

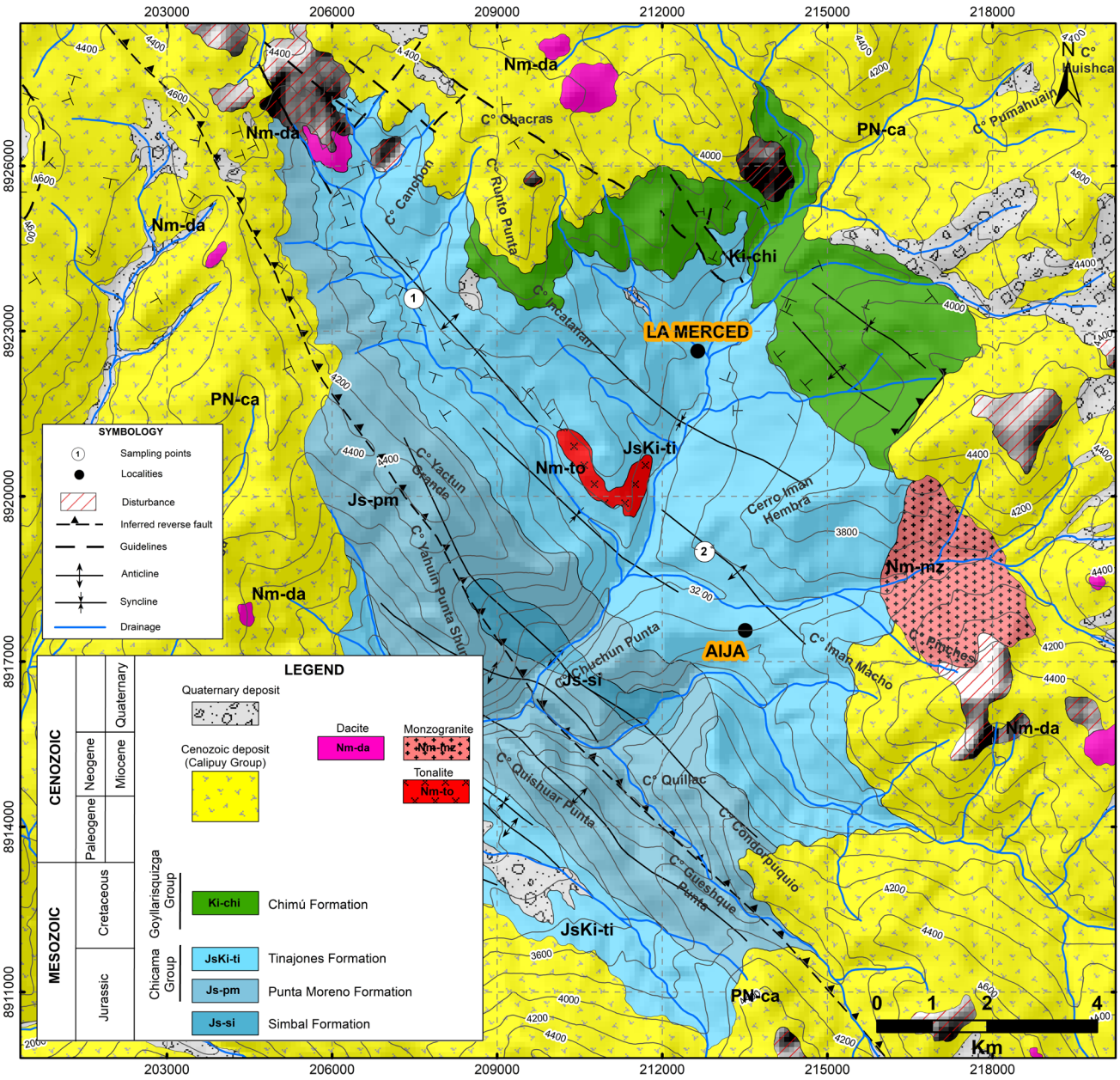


FIGURE 2 — Geology of the Aija and La Merced areas (after Navarro et al., 2010, 2011), illustrating sampling points in the sedimentary rocks of the Tinajones Formation.

deltaic, shallow platform, and transitional environments, including palustrine (Jacay, 1992). Overlying these Upper Jurassic sediments are the Lower Cretaceous sandstone beds of the Chimú Formation, which Jacay (1992) interpreted as fluvio-delta deposits. During the Upper Jurassic (Tithonian) and Lower Cretaceous (Berrasian), major paleoenvironmental changes occurred, marked by rising sea levels of the Paleo Pacific Ocean, which led to invasions of continental zones.

The material examined in this study comes exclusively from the Tinajones Formation, which is composed of dark gray, parallel-laminated shale, with intercalations of siltstones, sandstones, and grayish, wackestone limestones (Figs. 2–3; Navarro et al., 2010, 2011). In the shale layers, clupeomorph fishes were recovered (Ordóñez et al., 2013, 2015; Ordóñez, 2022), which are associated with Lamniformes (Suárez-Arana et al., 2019), Spinicaudata (Ordóñez et al., 2018), gastropods,

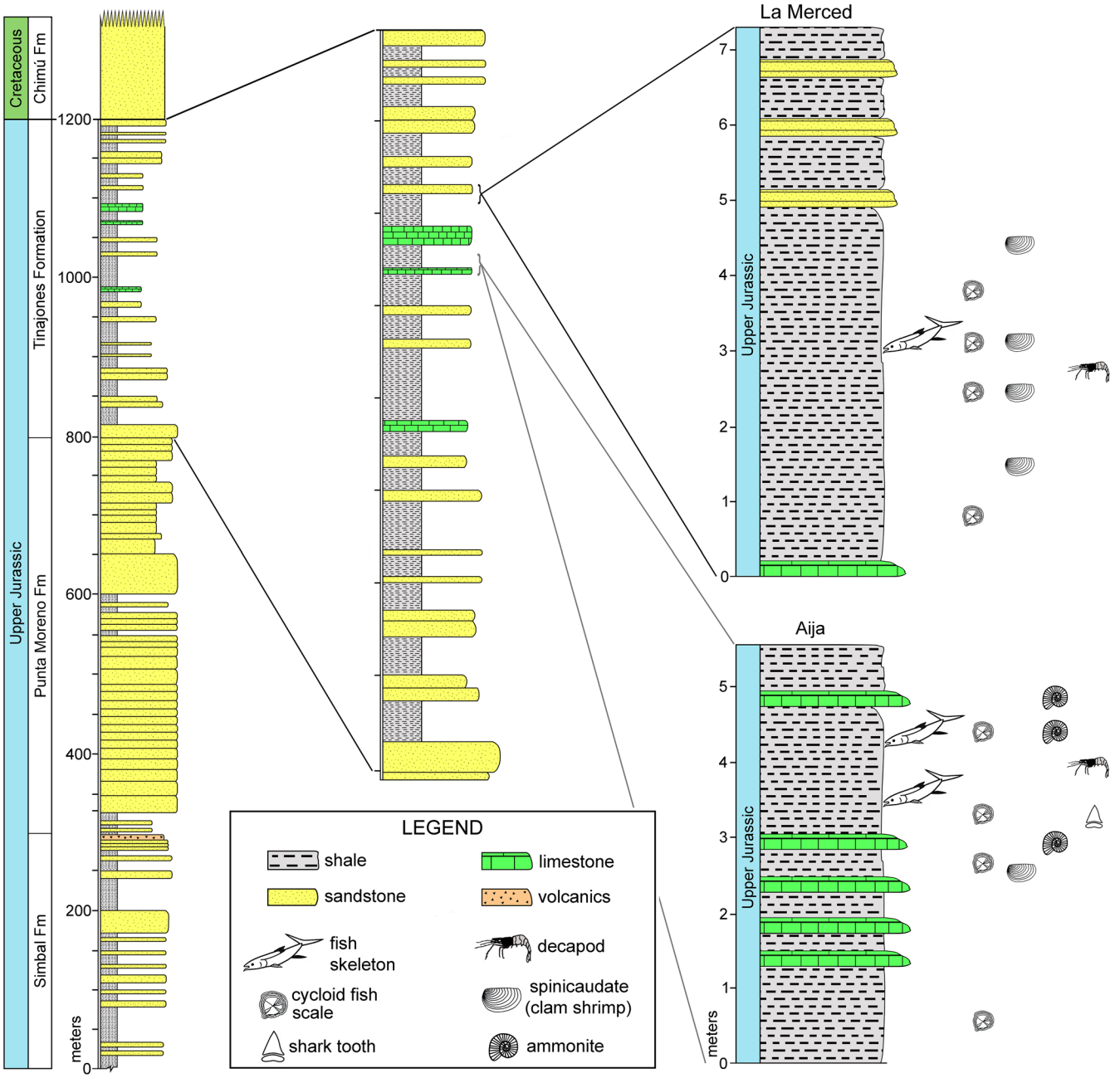


FIGURE 3 — Stratigraphic correlation of lithostratigraphic units and distribution of sampling points of fish and associated fossils in the localities of La Merced and Aija. (Modified by EO from figure 6 from the Paleontology Report, 2014 – Project GR29 "Paleontological studies", INGEMMET.)

and bivalves (under study). In the limestone layers, ammonites, such as *Berriasella chillonensis* and *Substeueroceras permulticostatum*, were recovered and reported (Jacay, 1992; Enay et al., 1996).

The two localities are in the towns of Aija and La Merced (Figs. 1 and 2). In 2015, as part of the work to collect information associated with the fossil samples, a regional stratigraphic column was prepared (Fig. 3). In addition, a more detailed column of approximately seven meters thick in La Merced was made, mainly represented by layers of grayish, parallel-laminated shale with a limestone layer at the base and a few sandstone layers towards the top. In the locality of Aija, a column a little over five meters corresponds to laminated, whitish to grayish shale with several, interspersed limestone layers. In the shales of these localities, the fish skeletons were associated with cycloid scales, spinicaudate shells (clam shrimp), other

decapods, and *Berriasella* type ammonites (Fig. 3). *Berriasella* type ammonites were also found in limestone bases, and the limestone layers also have *Substeuroceras* type ammonites.

Based on the ammonites collected in the Aija area, two biozones were distinguished. The *Berriasella jacobi* biozone, as evidenced by *Berriasella chillonensis* Rivera ammonites in the shale levels, ranges from uppermost Jurassic–lowermost Cretaceous (Tithonian–Berriasian), according to Salazar (2012), Gradstein et al. (2012), and Ogg et al. (2016). Ammonites from the *Substeueroceras koeneni* biozone (Rivera, 1951; Jacay, 1992; Enay et al., 1996; Salazar, 2012) correspond to *Substeueroceras permulticostatum* Steuer. According to Salazar (2015), this biozone is upper Tithonian for the section in Peru, and for the area in Argentina and Chile, it is also upper Tithonian, or in some cases, uppermost Tithonian. Therefore, based on the age of the ammonites *Berriasella chillonensis* Rivera and *Substeueroceras permulticostatum* Steuer recorded in the Tinajones Formation, it is concluded that the fish records are found in rocks of the Tithonian (Upper Jurassic).

MATERIAL AND METHODS

The fossil fishes studied herein were collected in 2009 and 2010, during field work of the project GR4 (*Geology of the volcanic rocks of the Occidental Cordillera of northern Peru*) under the guidance of the Ing. Pedro Navarro C. and the collaboration of EO and LT among others. The fishes were collected with associated invertebrates (see Geological Setting) that were used to study and determine the age of the fossiliferous sites. In a later expedition (2014) a few more fossil clupeomorphs were collected by L. Ayala, LT and EO, and more recently (2025), by EO. The studied specimens are deposited in the paleontological collections of the Instituto Geológico, Minero y Metalúrgico (INGEMMET) of Peru. A dagger (†) is used to identify fossil taxa.

Seventeen specimens identified as clupeomorphs were selected for this study because of their more informative preservation. Due to the type of preservation, they were mechanically prepared with the aid of sharpened metallic needles and brushes; those covered with FeO (iron oxide) and/or FeH_2O_2 (iron hydroxide) were not submitted to further preparation to avoid the destruction of fossilized structures.

Anatomical and Taxonomic Terminologies

The terminology of the skull roof bones is based on homology and ontogeny (Schultze, 2008; Teng et al., 2019). To avoid confusion, the first time that the parietal and postparietal bones are cited in the text, the traditional terminology is shown in square brackets, e.g., parietal bone [= frontal]; pa [= fr]. The use of "basipterygoid" process (instead of basipterygoid process) follows Arratia and Schultze (1990) and Marramà and Carnevale (2023) to indicate the uncertainties of the homology of this process. The terminology for vertebral column and associated elements follows Arratia et al. (2001), and for fins rays, follows Arratia (2008).

Illustrations

Illustrations are based directly on the specimens. Drawings were prepared by EO (with exception of two figures) with help of a camera lucida attached on a WILD stereomicroscope M5A and a Zeiss 47 50 52 stereomicroscope. Photographs were taken by LT with a Nikon Z5, equipped with a lens Nikkor MC 50mm f/2.8 and by EO with a Canon EOS 4000D, equipped with a lens Canon EF 100mm f/2.8 Macro USM. Certain structures (e.g., surface of scales and scutes) were studied and photographed by EO using the SEM at the Department of Paleontology, Universidad Complutense, Madrid, Spain. GA designed and executed the final layouts of Figures 4 to 15 and of the manuscript.

INSTITUTIONAL ABBREVIATION

CPI — Instituto Geológico, Minero y Metalúrgico, Peru.

SYSTEMATIC PALEONTOLOGY

TELEOSTEI Müller, 1845 *sensu* Arratia, 1999
CLUPEOCEPHALA Patterson and Rosen, 1977 *sensu* Arratia, 2010
OTOMORPHA *sensu* Arratia, 2018
CLUPEOMORPHA sensu Greenwood et al., 1966
†ELLIMMICHTHYIFORMES Grande, 1985 *sensu* Marramà and Carnevale, 2023

†Ancashichthyidae Arratia and Ordóñez new family
Zoobank Registration Number: 01301E01-A70B-409C-8C2E-D7F841FA69A7

Diagnosis.— (based on a unique combination of characters): Double armored clupeomorphs of small size, about 6 cm of standard length, with a complete series of predorsal scutes that are subrectangular or slightly oval-shaped, extending between the supraoccipital region and the dorsal fin. A series of eight to 10 supraneurals; the first supraneural is triangular-shaped and the broadest of the series; the second supraneural is the longest and inclined anteroventrally; and the third to last eight to tenth supraneurals are elongated and inclined anteroventrally. A complete series of prepelvic scutes extends from the pelvic fin insertion to below the pectoral girdle (coracoid).

Etymology.— The family name honors the region in Peru (Ancash) where the fossil clupeomorphs were collected, with "ichthyidae' for fish family.

†***Ancashichthys*** n. gen.

Diagnosis.— (based on a unique combination of characters): Fusiform-shaped and double-armored clupeomorph of small size, about 60 mm standard length (SL), with a large head of about 25% of SL. Supramaxilla 2 with very long and narrow dorsoanterior process extending over supramaxilla 1.

Large number of branchiostegal rays, more than 12. Dorsal fin originating at about 46% of SL, slightly anterior to the origin of the pelvic fin that lies just posterior to (or at the level of) the last dorsal pterygiophore. Anal-fin insertion behind last dorsal-fin radials. With ca. 28 precaudal or abdominal vertebrae, counting four covered laterally by the opercle; about 15 caudal vertebrae, with first three to five caudal vertebrae with elongate haemal spines, bearing ribs and preceding the first anal pterygiophore. Neural spines of abdominal vertebrae unfused medially. About 20 pairs of ribs. Ribs long and well-ossified, reaching the ventral body margin where they are associated with prepelvic scutes. One long, blade-like postcleithrum present. Triangular-shaped basipterygium supporting 10 or 11 pelvic rays. With a complete series of subrectangular-based and slightly ovoid-shaped predorsal scutes. A series of ca. 24 abdominal scutes placed posterior to the cleithrum, including ca. 17 prepelvic scutes, plus other three extending below the pectoral girdle, and ca. seven postpelvic scutes without a prominent ventral spine or keel.

Etymology.— The genus name honors the Department of Ancash, northern Peru, the region where the fossil clupeomorphs were recovered, with the Greek *ichthys* for fish.

†***Ancashichthys peruensis*** Ordóñez and Arratia n. gen. and sp.

(Figs. 4–11)

Zoobank Registration Number: 186E3B36-9B6E-4B22-9288-29972BED558F

2013 Clupeomorph fishes – Ordóñez et al.; mention, fig. 5.
2015 Clupeomorph fishes – Ordóñez et al.; mention, figs. 4–6.
2017 Clupeomorph fishes – Ordóñez; mention, figs. 12, 13, 18–20, 22–26.
2022 Clupeomorpha *incertae sedis* – Ordóñez; mention, figs. 5.1–5.15.

Holotype.— CPI 6348, preserved as part of an incomplete specimen with part of head and most of the trunk (41 mm long) and approximately 55–60 mm of standard length in a complete individual; La Merced District.

Paratypes.— CPI 6346 and 6346-1, part and counterpart of head and body up to the beginning of caudal vertebral region; dorsal parts of head and of body are not preserved; Aija District.

CPI 6348-1, incomplete fish missing body anterior to pelvic and dorsal fins, preserving the caudal region, including a poorly preserved caudal endoskeleton and fin; La Merced District. CPI 6348-2 and 6348-3, part and counterpart of head and anterior part of body; La Merced District. CP1 6348-4, scale; La Merced District. CPI 8052, partially preserved specimen missing caudal peduncle and tail; Aija District. CPI 8052-1, partially preserved specimen missing dorsal part of head and body and caudal region; Aija District. CPI 8178, complete specimen, slightly twisted, not well preserved; La Merced District. CPI 8311, partially preserved specimen missing dorsal part of head and trunk; trunk missing tail, well preserved; La Merced District. CPI 8311-1, specimen missing anterior part of body and head; posterior part of body well preserved, with caudal endoskeleton partially out of place; La Merced District. CPI 8311-2, ventral part of body trunk, with well-preserved ribs and abdominal scutes; La Merced District.

Localities and Horizon.— La Merced and Aija, Department of Ancash, Province of Aija, northern Peru (Figs. 1 and 2). Tinajones Formation, Tithonian (Upper Jurassic; Fig. 3).

Etymology.— The specific name honors the country, Peru, where the fossil material was collected.

Diagnosis.— Same as genus.

General Description

This is a small, double-armored clupeomorph whose identification is fundamentally based on the presence of predorsal scutes and a series of prepelvic and postpelvic scutes ventrally (Figs. 4 and 5).

The small fish of about 60 mm SL (e.g., CPI 6348; Fig. 4A) has a relatively large head, ca. 25% of SL, a moderately large orbit, with a diameter of 22% of head length, and with the deepest part of the body in the predorsal region, which is about 30% of SL. The fish has a short lower jaw with its articulatory region with the quadrate positioned below the anterior half of the orbit (Fig. 4).

Cranial Bones

As noted above, the cranium is incompletely preserved (Figs. 4–6) and represented by remains of the anterior part of the skull roof, such as the mesethmoid and pieces of the parietal [= frontal], postparietal [= pa] and lateral ethmoid, as well as sections of the parasphenoid. Their poor preservation does not permit a description. Dentition has not been observed in the preserved pieces of the parasphenoid or near it. Nothing can be added about a "basypterygoid" process. Additionally, information is not available concerning an otophysic connection, the pro-otic and pterotic bullae, the prepiotic fossa, recessus lateralis, supratemporal commissure, and other cephalic sensory canals.

Orbital Bones

The circumorbital bones are not preserved, except for an incomplete small bone, which because of its position, is interpreted here as part of infraorbital 3 (Fig. 6).

Upper Jaw

It is represented by the displaced supramaxillae; the maxilla is not preserved. Supramaxilla 1 or anterior supramaxilla is oval-shaped and elongate, and supramaxilla 2 or posterior supramaxilla (Fig. 6) is an oval-shaped, short bone with a long and styliform anterodorsal process extending over supramaxilla 1. Lacks ornamentation on the supramaxillae. No teeth are preserved in the available material.

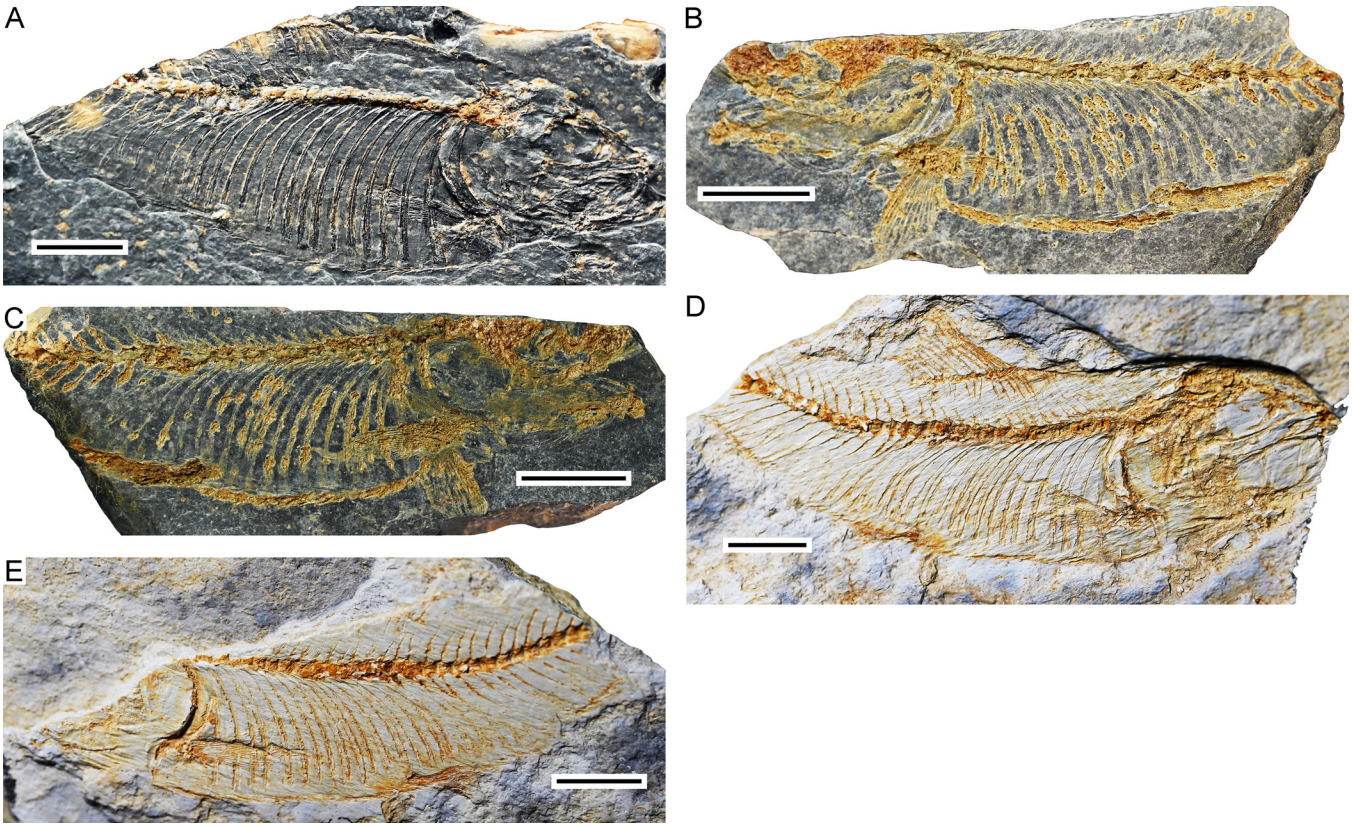


FIGURE 4 — †*Ancashichthys peruensis* n. gen. and sp. in lateral view. **A**, CPI 6348 (holotype), from La Merced; **B**, CPI 6346-1, from La Merced; **C**, CPI 6346, from La Merced; **D**, CPI 8052, from Aija; **E**, CPI 8052-1, from Aija. Scale bars = 5 mm.

Lower Jaw

It is poorly and incomplete preserved in the available material (Figs. 5, 6). While specimen CPI 6348 has poorly preserved parts of the dentary and anguloarticular, specimen CPI 6348-2 has a well-preserved portion of the posterior part of the jaw, exposing the external view of a well-developed anguloarticular, and ventrally, the posterior part of the dentalosplenial. According to the available information, the coronoid process would be formed mainly by the dentalosplenial. The articular surface of the jaw for the quadrate is followed by a short and well-defined postarticular process placed posteroventrally. Posterodorsally, the jaw is articulated with the quadrate, and ventrally it is very close to the preopercle, and both bones were likely connected by a ligament as in other teleosts. No teeth are preserved in the available material.

Palatoquadrate, Suspensorium, Hyoid Arch, and Urohyal

The triangular-shaped quadrate (Fig. 6) seems to be a large bone, but its limits are unclear because of the condition of preservation; it is preserved in position, articulating with the lower jaw. A curved, boomerang-shaped ectopterygoid (Fig. 6) articulates with the anterior margin of the quadrate. Remains of the entopterygoid are preserved ventrolateral to the parasphenoid. Other bones, such as the metapterygoid, hyomandibula and symplectic are destroyed or poorly preserved. Teeth, or their sockets, associated to the ecto- and entopterygoid were not observed, possibly an artifact of preservation.

The hyoid arch is displaced in specimen CPI 6346, and although poorly preserved, it is possible to observe that the anterior ceratohyal (Fig. 7) has a rectangular shape with the ventral margin slightly concave, with its anterior and posterior ends being slightly broader and the dorsal region missing. The so-called beryciform foramen is interpreted to be present because the preserved part of the anterior ceratohyal shows an incomplete almost rounded foramen (Fig. 7). The posterior ceratohyal is poorly preserved but seems to be larger than the anterior ceratohyal. A broad ventral hypohyal is placed anteriorly to the anterior ceratohyal in the counterpart of CPI 6346.

A urohyal is observed in the paratype CPI 6348-2 (Fig. 6), displaced below and posterior to the anterior ceratohyal and branchiostegal rays. The bone is narrower anteriorly, and its median dorsal blade expands posteriorly, ending in a dorsal projection; below, the bone has a smaller median

ventral blade or keel with a slightly oval margin projecting ventrally.

Opercular and Branchiostegal Series

Opercular bones (Figs. 4 and 6) are preserved in specimen CPI 6348-2. Their surface is smooth, and no crests or other ornaments are observed. The preopercle has both arms of almost similar length that form an angle of slightly over 90 degrees; the preopercular sensory canal is not preserved. The opercle is missing its dorsal border, but it is a moderately large bone, about double the size of the subopercle. Its posterior margin is slightly oblique. Opercle and subopercle are joined by an oblique suture; the anterodorsal margin of the subopercle is destroyed. An interopercle is not preserved.

The branchiostegal series is incomplete, but at least 12 rays are counted in specimen CPI 6346-1a (Fig. 7B). The anteriormost rays are small and narrow, while the posterior ones are larger and longer.

Vertebral Column

The column is incomplete, because the posterior part of the body is usually not preserved, but there are ca. 28 precaudal or abdominal vertebrae, plus ca. 15 caudal vertebrae, with the first three to five vertebrae with an elongate haemal spine preceding the first anal pterygiophore (Figs. 4 and 5). All vertebrae are formed by well-ossified autocentra bearing narrow neural arches. Most precaudal centra bear neural arches with unfused halves of the arches. The last precaudal centra are slightly rectangular, with their neural arches placed almost in the antero-middle region of the centrum. Both halves of each arch are fused medially, forming one neural spine; the spines are slightly inclined posteriorly, especially those that are placed ventral to the dorsal pterygiophores. The anteriormost caudal centra are slightly longer than the precaudal ones, with their neural and haemal arches narrow and placed about the middle of each centrum.

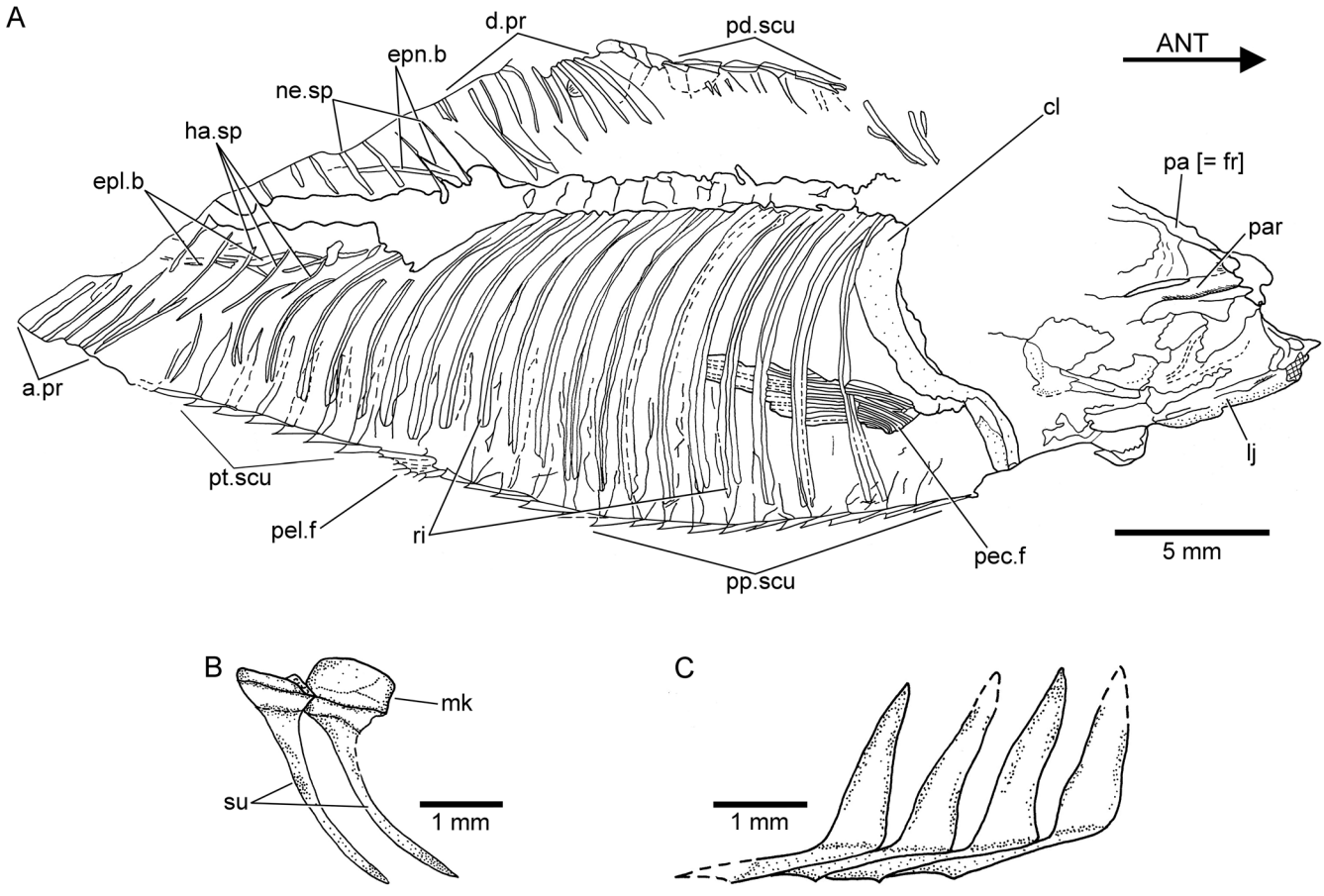


FIGURE 5 — Diagrammatic drawings of †*Ancashichthys peruensis* n. gen. and sp. in lateral view (CPI 6348). **A**, lateral view; **B**, detail of predorsal scutes. The median keel is destroyed in the second predorsal scute; **C**, detail of abdominal scutes. Abbreviations: *a.pr*, anal proximal radials; *cl*, cleithrum; *d.or*, dorsal proximal radials; *epl.b,* broken epipleural bones; *epn.b*, broken epineural bones; *ha.sp,* haemal spines; *lj*, broken lower jaw; *mk*, median keel; *ne.sp,* neural spines; *pa [= fr]*, parietal bone [= frontal]; *par,* broken parasphenoid; *pec.f*, pelvic fin; *pel.f*, remains of pelvic fin rays; *pd.scu*, predorsal scutes; *pp.scu*, prepelvic scutes; *pt.scu,* postpelvic scutes; *ri,* ribs; *su*, supraneural.

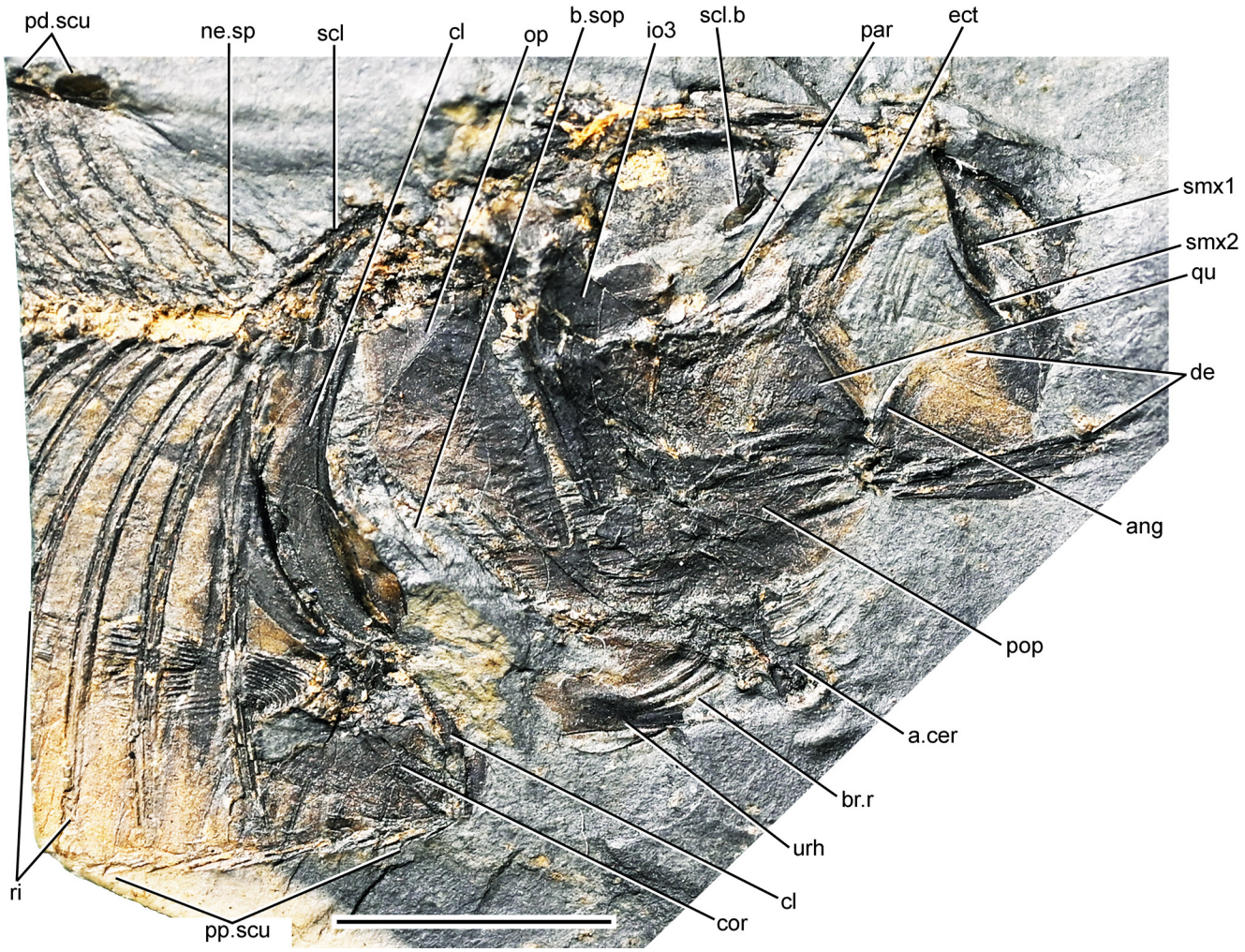


FIGURE 6 — †*Ancashichthys peruensis* n. gen. and sp. (CPI 6348-2). Head and anterior part of trunk in lateral view. Scale bar = 5 mm. Abbreviations: *a.cer*, anterior ceratohyal; *ang*, angulo-articular; *br.r*, branchiostegal rays; *b.sop*, broken supracleithrum; *cl*, cleithrum; *cor*, coracoid; *de*, dentary; *ect,* ectopterygoid; *io3*, infraorbital bone 3; *ne.sp*, neural spine; *op*, opercle; *par*, parasphenoid; *pop*, preopercle; *pd.scu*, predorsal scutes; *pp.scu*, prepelvic scutes; *qu*, quadrate; *ri*, ribs*; scl.b*, sclerotic bone; *smx1–2*, supramaxillae 1 and 2; *scl*, supracleithrum; *urh*, urohyal.

There are 19 preserved pairs of ribs that have a characteristic curvature close to the vertebral centrum and then extend ventrally in a straight manner. A well-developed groove is positioned along the length of each rib. There is no information available about the articulation between centrum and rib, but because of the position of the ribs, it is likely that the anterior ones would articulate in a fossa close to the lateroventral region of each centrum. The last ribs seem to articulate with elongate, anterolateral processes of the centra.

Most epineurals are lost because the predorsal region of the vertebral column is commonly destroyed. A few remains of epineural bones are lying along the dorsolateral surface of the neural arches. A few pieces are lying on the centra, and it is unclear whether these are epicentrals or broken epineurals; a few epipleurals are ventral to the centra of the first caudal vertebrae. There are not continuous series of epineurals and/or epipleurals associated with the neural and haemal spines in the caudal region. Elongate and narrow intermuscular bones are irregularly preserved in the epaxial region of the posterior part of the vertebral column; those of the hypaxial region, posterior to the anal fin, are V-shaped, with a short dorsal ramus and a ventral longer one. (For supraneural bones, see below the section Scutes.)

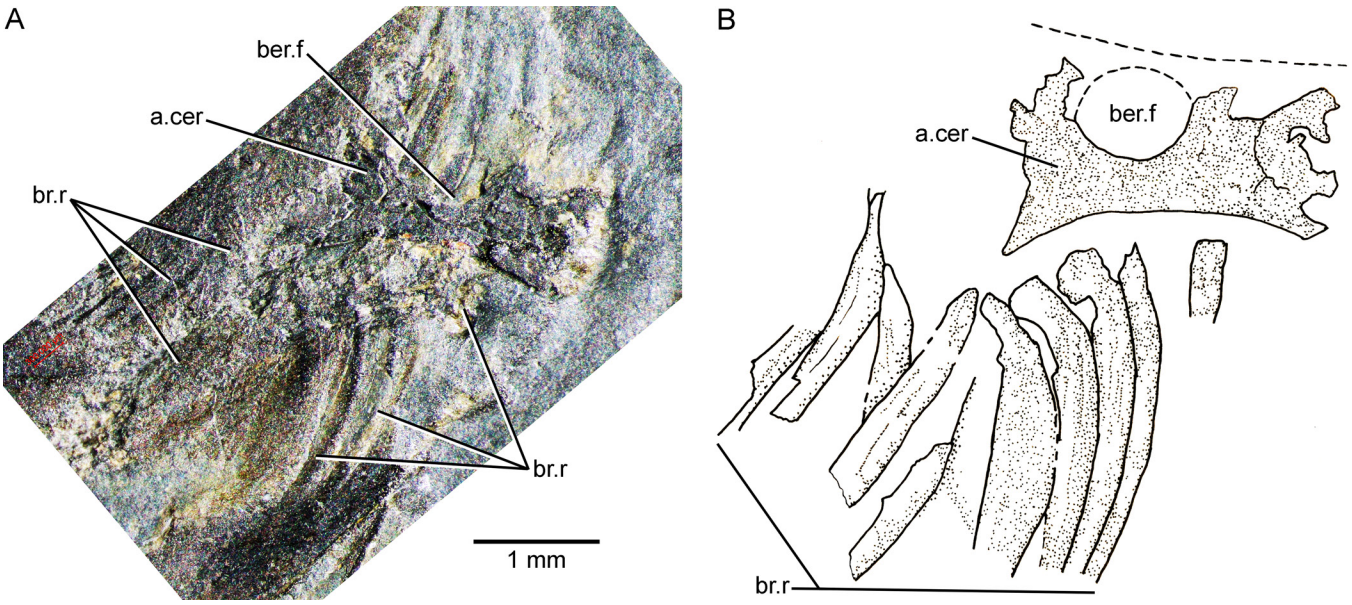


FIGURE 7 — †*Ancashichthys peruensis* n. gen. and sp. (CPI 6348-2). **A**, hyoid arch and branchiostegal rays in lateral view; **B**, diagrammatic drawing. Abbreviations: *a.cer*, anterior ceratohyal; *ber.f*, beryciform foramen; *br.r*, branchiostegal rays.

Paired Fins

From the pectoral girdle (Figs 4, 5, and 8), a supracleithrum, a heavily ossified, elongate, sigmoidal (or S-shaped) cleithrum, and remains of the scapula and coracoid are preserved. The trajectory of the lateral line, either associated with the supracleithrum or not, is unknown. The cleithrum is broader and heavily ossified dorsally and does show a small curvature ventrally, being almost straight along most of its length. One elongate, blade-like postcleithrum is preserved in CPI 6348-2 (Fig. 8). In specimen CPI 6348-2, the postcleithrum is preserved as a long styliform bone that extends posteroventrally, separating from the posterior margin of the cleithrum. The chondral elements of the girdle are poorly preserved; however, it is possible to observe a large coracoid below the curved ventral region of the cleithrum. Fifteen to 17 pectoral rays are counted, and their position suggests that the fin was placed closed to the ventral margin of the body than to the midflank. The rays have long, thin bases, and they are branched distally.

A small pelvic fin attached to an elongate, triangular basipterygium is present (Fig. 9). No processes or notches are observed in the anterior part of the basipterygia, and the ischial process is not observed because of preservation. A thin crest runs close to the lateral margin of each basipterygium. Ten or 11 pelvic rays are counted in specimen CPI 6348-1 (Fig. 9). The rays have thin, long bases and only branch distally. The basipterygium and fin are closer to the anal fin than to the pectoral fin, and the insertion of the dorsal is slightly in front of the pelvic fin (CPI 6348-3).

Unpaired Fins

Commonly, the dorsal fin is only represented by its series of proximal radials because the dorsal border of the body is destroyed. An almost complete dorsal fin is preserved in specimens CP 8052 (Fig. 4D) and CPI 8311-1 (Fig. 10);

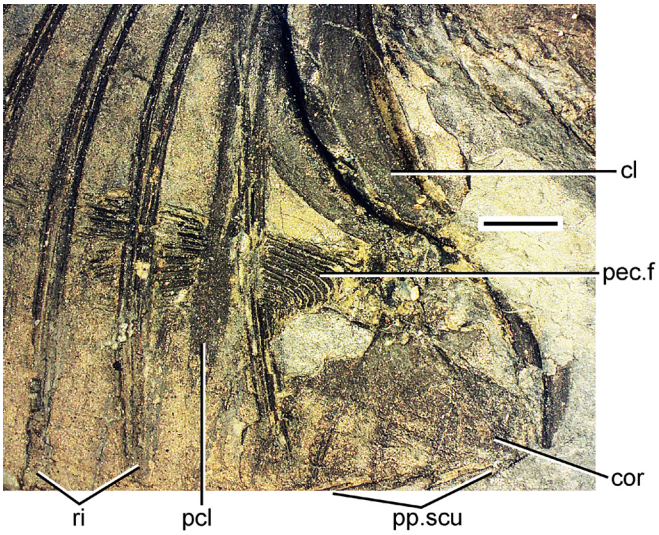


FIGURE 8 — †*Ancashichthys peruensis* n. gen. and sp. in lateral view (CPI 6348-2). Detail of the lower part of the pectoral girdle and fin and of the anterior prepelvic scutes with no association to the ribs. Scale = 1 mm. Abbreviations: *cl*, lower section of cleithrum; *cor*, coracoid; *pcl*, postcleithrum; *pec.f*, pectoral fin; *pp.scu*, anteriormost abdominal prepelvic scutes.

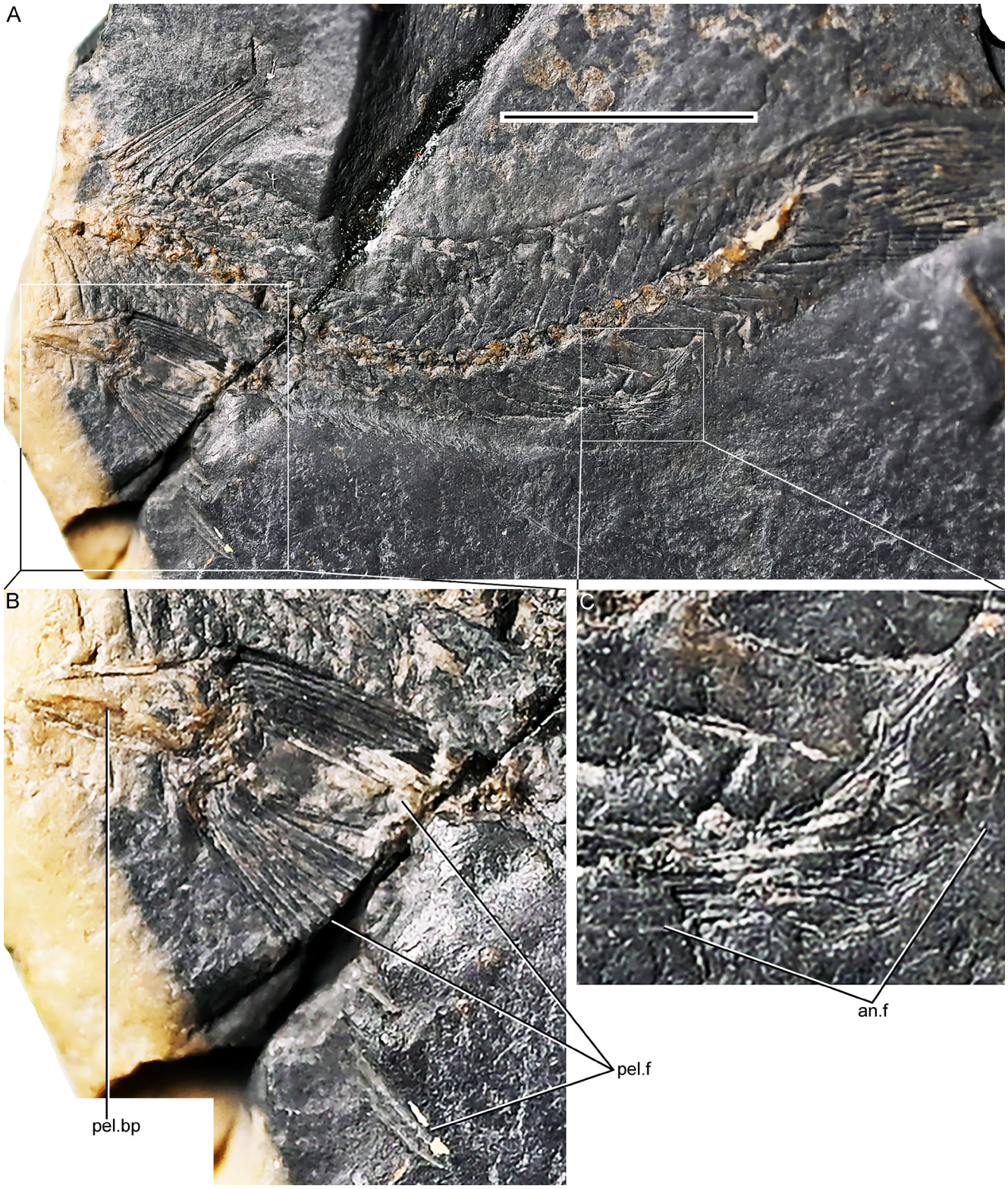


FIGURE 9 — †*Ancashichthys peruensis* n. gen. and sp. **A**, posterior part of trunk in lateral view (CPI 6348-1); **B**, detail of pelvic basipterygium and fins. Note the length of the lateral rays; **C**, poorly preserved anal rays. Note the series of elements placed on the dorsal margin of body that resemble postdorsal scutes. Scale bar = 5 mm. Abbreviations: *an.f*, anal fin; *pel.bp*, pelvic basipterygia; *pel.f*, pelvic fin.

the fin has at least 13 principal rays, but the anteriormost procurrent or simple rays are missing or damaged. The first three to five principal dorsal rays are longer than the following rays, giving the fin a slightly curved posterodorsal margin; the posteriormost rays are short. The dorsal rays are thin, with long bases and branch only distally. Thirteen elongate proximal radials are preserved in CPI 6348 and 14 in CPI 8052 (Fig. 4D), with the first one being the largest and longest of the series and bearing two or three branches (Fig. 5A); the following proximal radials decrease in length posteriorly and look weak. Each proximal radial looks like a thin bar, with an expanded, almost triangular distal portion that articulates with a short, slightly rectangular middle radial. A distal and well-ossified radial is seen at the base of the most anterior principal dorsal rays (CPI 8311-1; Fig. 10). According to the position of the first dorsal pterygiophore, the origin of the dorsal fin is anterior to the origin of the pelvic fins, which are closer to the anal fin.

The anal fin is not completely preserved, missing a few rays (Fig. 9) in most specimens; it is represented by its anterior five to eight pterygiophores (Figs. 4 and 5), which are also elongate and thin, as in the dorsal radials. Specimen CPI 8311-1 has eight pterygiophores preserved in position and another three that are displaced; there are two short, thin procurrent rays that are followed by the four longest anal rays, which are followed by four shorter rays. The total number of rays is unknown, but if we consider the number of preserved pterygiophores and rays, the total number would be less than 15 rays.

Caudal Fin

The caudal fin is preserved in specimens CPI 6348-1 and CPI 8311-1; however, a description of its endoskeleton, as well as of the fin rays, is not possible due to the poor preservation of this region. It is not possible to evaluate the number of epurals and hypurals, and whether hypural 2 is fused to its centrum 2. However, it is possible to observe the long preural neural and haemal spines reaching the margins of the body and are strongly inclined posteriorly, as well as the fine and delicate bases of caudal fin rays, especially those of the midcaudal principal rays that seem to be narrow in contrast with the broad-based, mid-caudal rays of recent clupeomorphs. Specimen CPI 8178, which is a poorly preserved specimen, shows an elongate caudal fin, with its posterior margin moderately notched, and with a series of 10+9 principal rays, whereas ca. 9+9 rays are counted in CPO 8311-1. The principal rays have long and thin bases and are weakly branched distally, except for the first and last marginal rays, which are simple. A few (ca. five) thin, short dorsal and ventral procurrent rays are preserved in CPI 8311-1; no signs of dorsal and ventral caudal scutes are observed preceding the procurrent rays, but this absence could be a result of incomplete preservation.

Scales, Scutes and Associated Supraneurals

Information on the scales is scarce, but specimens CPI 6348-4 and CPI-8311-1 have round and oval cycloid scales (Figs. 10 and 11) with circulii at the anterior margin, but without radii.

The fish has preserved at least three series of scutes: predorsal, prepelvic or abdominal and postpelvic. (Figs. 4–6, 8). The predorsal series is preserved mainly at its middle-posterior region, preceding the first dorsal proximal radial in specimen CPI 6348 (Fig. 5). At least eight scutes are preserved in this specimen; only the first scutes just posterior to cranium would be missing because this region is partially destroyed in this specimen. Each predorsal scute consists of a subrectangular base, from which a dorsomedian rounded or rectangular keel projects (Fig. 5B); this keel has been observed only in some scutes; ventrally; some of the predorsal scutes are tightly associated with a supraneural so that the supraneural looks like a process of a scute that is slightly curved anterodorsally, extending into the median body septum. The predorsal series is better preserved and more informative in CPI 8052 (Fig. 12A, B). In this specimen a few broken scutes close the space between the posterior part of the cranium and first supraneural, and the series of oval or subrectagular-shaped scutes ends in front of the dorsal fin. The first supradorsal, triangular-shaped, is the broadest of the series and expanded distally. The second supraneural is slightly bent proximally; it is elongate and narrow, and its proximal end almost touches the first supraneural. The third and following supraneurals are all narrow and of similar shape and parallell to each other.

Specimen CPI 6348-1 presents a series of incompletely preserved structures that resemble postdorsal scutes (see Fig. 9A); but this could be an artifact of preservation because these structures were not observed in other specimens.

The abdominal series of scutes consists of prepelvic and postpelvic scutes that are similar in shape and size (Figs. 4–6). These scutes are formed by an elongate, subrectangular base that has at its anterior margin an anterodorsally oriented process, which is sharp, as in the predorsal scutes. The series of abdominal scutes extends along the whole preanal body margin, but it is divided into two series, the pre- and postpelvic ones. The series of abdominal scutes placed posterior to the cleithrum includes a long series of ca. 17 prepelvic scutes and a short series of ca. seven postpelvic scutes. Three or four scutes are not associated with ribs and are positioned anterior to the ventral region of the cleithrum up to the isthmus.

†ELLIMMICHTHYIFORMES Grande, 1985 sensu Marramà and Carnevale, 2023

†Ancashichthyidae Arratia and Ordóñez new family

Aijaichthys n. gen.

Zoobank Registration Number: 1ECB4DB7-E321-4975-99FE-215E888509C2.

Diagnosis.— (based on a unique combination of characters): Half-moon shaped and double-armored clupeomorph of small size, about 40–50 mm standard length (SL), and with a maximum body depth of about 50% of SL.

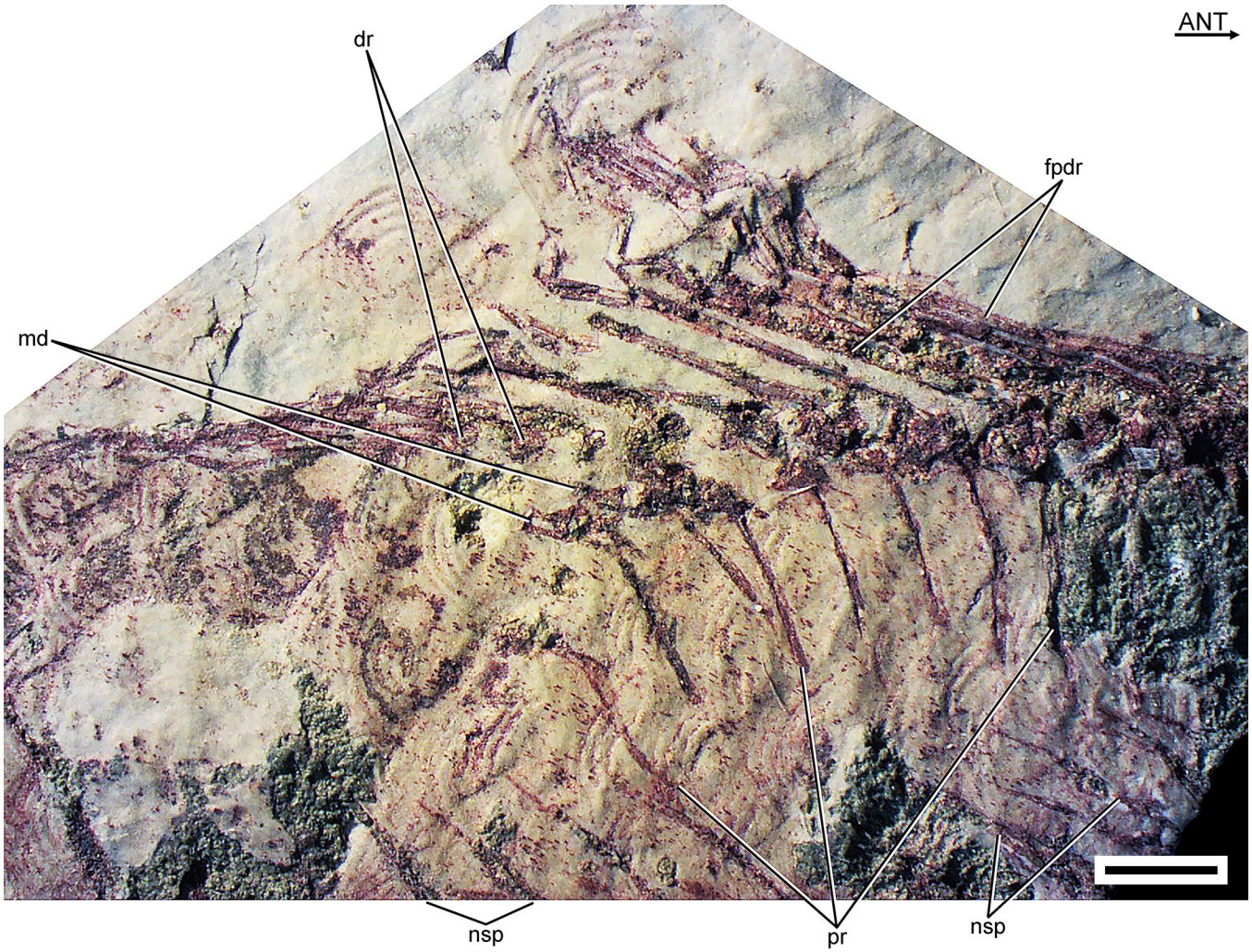


FIGURE 10 — †*Ancashichthys peruensis* n. gen. and sp. (CPI 8311-1). Dorsal fin and its series of radials and scales in situ. Scale bar = 1 mm. Abbreviations*: ANT,* points anteriorly; *dr,* distal radials; *fpdr*, anterior dorsal fin rays; *md*, middle radials of dorsal fin; *nsp*, neural spine; *pr*, proximal radials.

Head as deep as long. Dorsal fin originating slightly anterior to the origin of the pelvic fin that lies at the level of the middle dorsal pterygiophores. Quadrate characteristically shaped (scalene triangle). Ectopterygoid with expanded dorsoanterior process and bearing numerous tiny conic teeth medially. Anal-fin insertion behind last dorsal-fin radials. With ca. 22 or 23 precaudal or abdominal vertebrae (counting four covered laterally by the opercle); short caudal region including ca. 11 or 12 caudal vertebrae. Neural spines of most abdominal vertebrae unfused medially. Ribs long and well-ossified, reaching the ventral body margin; ventrally, ribs are associated with prepelvic scutes. With a complete series of ca. 10 oval or slightly subrectangular predorsal scutes. With a series of abdominal scutes extending from below the pectoral girdle to the first anal pterygiophore; and ca. 10 postpelvic scutes without a prominent ventral spine or keel.

Etymology.—The genus name honors the District of Aija, Department of Ancash, northern Peru, the region where the fossil clupeomorphs were recovered, with the Greek *ichthys* for fish.

Aijaichthys brevis Ordóñez and Arratia n. gen. and sp.
(Figs. 12–15)

Zoobank Registration Number: B4E985F2-E84A-4B6B-87DE-8B1EF20B53AA.

Holotype.—CPI 8309 (counterpart) and CPI 8309-3 preserved as part of an incomplete specimen, having the head and anterior part of the trunk (ca. 40 mm long); Aija District.

Paratypes.—CPI 8309-1 part of head and body missing fins. CPI 8309-2, part of body trunk, poorly preserved. CPI

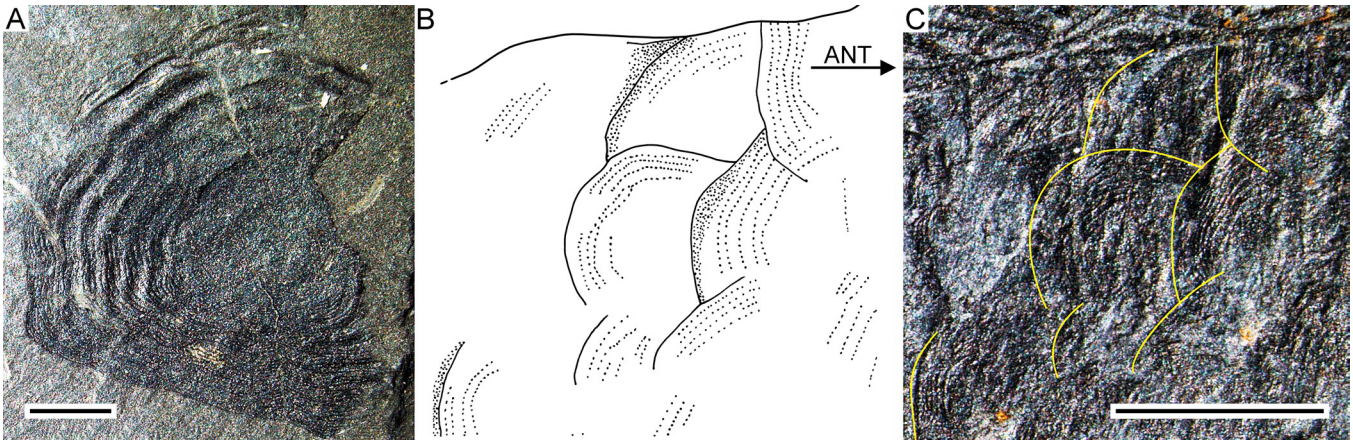


FIGURE 11 — †*Ancashichthys peruensis* n. gen. and sp. scales (CPI 6348-4). **A**, cycloid scale showing surface detail; **B, C**, section of skin. Scale bar = 1 mm. *ANT*, points to anterior.

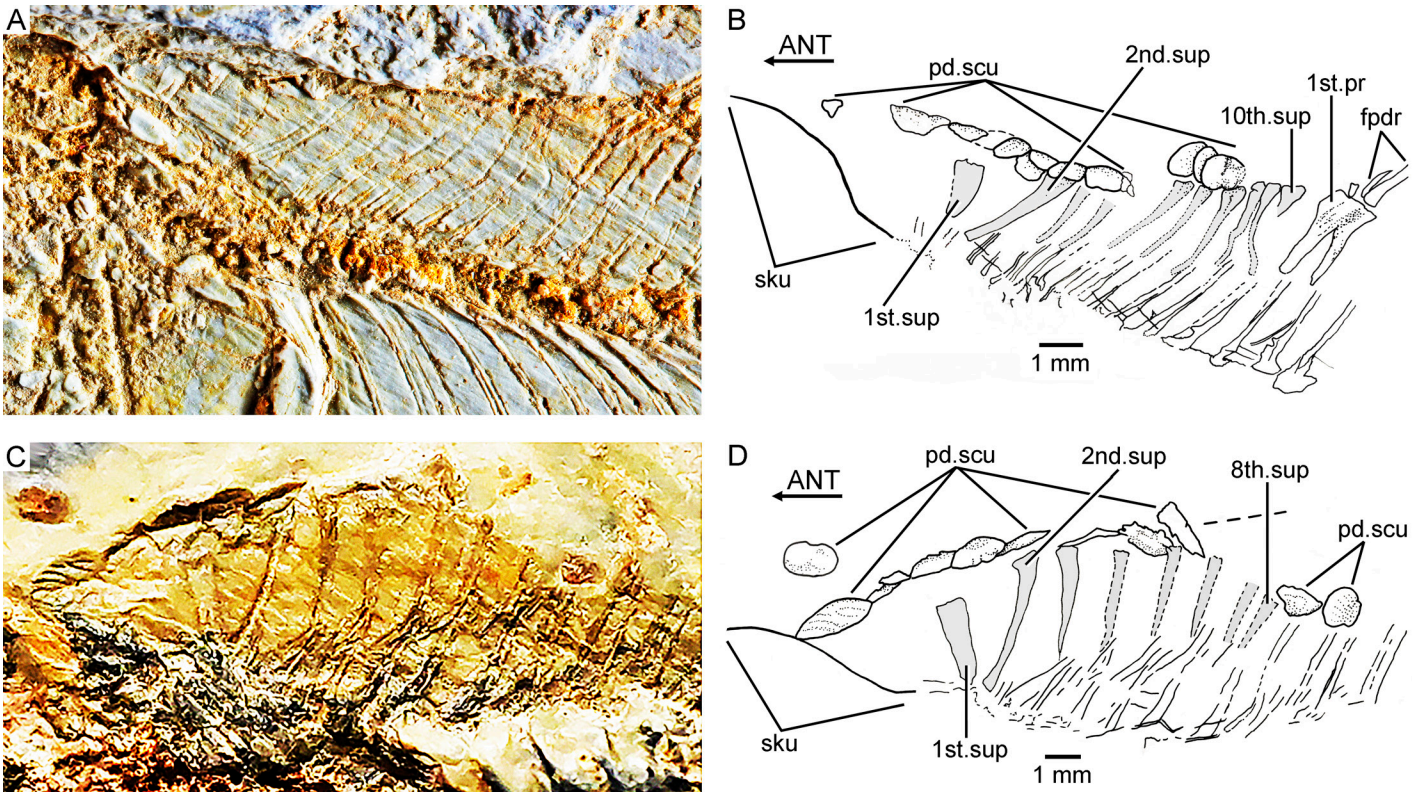


FIGURE 12 — **A**, †*Ancashichthys peruensis* n. gen. and sp. Predorsal series of scutes and supraneurals (CPI 8052) and **B**, diagrammatic drawing; **C**, †*Aijaichthys brevis* n. gen. and sp. Predorsal series of scutes and supraneurals (CPI 8309) and **D**, diagrammatic drawing. Abbreviations: *ANT,* points anteriorly; *fpdr*, first dorsal fin rays; *pd.scu*, predorsal series of scutes; *sku*, line following contour of the posterior cranial border; *1st.pr*, first proximal radial of forsal fin; *1st.sup*, first supraneural; *2nd.sup*, second supraneural; *10th.sup*, tenth supraneural.

83-9-4, well-preserved body, missing head and tail; Aija District.

Locality and Horizon.—Aija, Department of Ancash, Province of Aija, northern Peru (Figs. 1 and 2). Tinajones Formation, Tithonian, Upper Jurassic (Fig. 3).

Etymology.—The specific name *brevis* (Latin) denotes the small size of the fishes.

Diagnosis.—Same as genus.

General Description

This is a double-armored clupeomorph bearing a complete series of predorsal scutes and a series of abdominal scutes, including prepelvic and postpelvic ones (Fig. 13A–C); the fish is characterized by a semi-round dorsal profile and a deep ventral part of the body, half-moon-like. The deepest body point is at the level of the dorsal-pelvic fins, with the maximum body depth about 50% of SL.

†*Aijaichthys brevis* n. gen. and sp. is a small fish of about 40 to 50 mm SL with a head having a slightly triangular profile that is as deep as long, with a moderately large orbit, whose diameter is ca. 31% of head length. The fish has a short, slightly triangular lower jaw, whose articulatory region with the quadrate is placed below the middle of the orbit (Figs. 13B, 14).

Cranial Bones

The cranium, known in one specimen, is incompletely preserved (Figs. 13B, 14) and represented by remains of certain bones of the anterior part of the skull roof, such as the mesethmoid, parietal [= frontal], pterotic and posterior wall of the supraoccipital region. Additionally, information is not available concerning an otophysic connection, the prootic and pterotic bullae, the prepiotic fossa, recessus lateralis, supratemporal commissure, and other cephalic sensory canals. A section of the parasphenoid (Figs. 14, 15) is preserved; the bone bears a small lateroventrally directed "basipterygoid" process. A few, small conical teeth are observed in the ventral region of the parashenoid.

Orbital Bones

The circumorbital series (Figs. 13B and 14) is only represented by a poorly preserved infraorbital 1, which is a large, fan-like bone that seems to form most of the anterior margin of the orbit.

Upper Jaw

The upper jaw is represented by the premaxilla and maxilla (Figs. 13B–15). The premaxilla is small, slightly

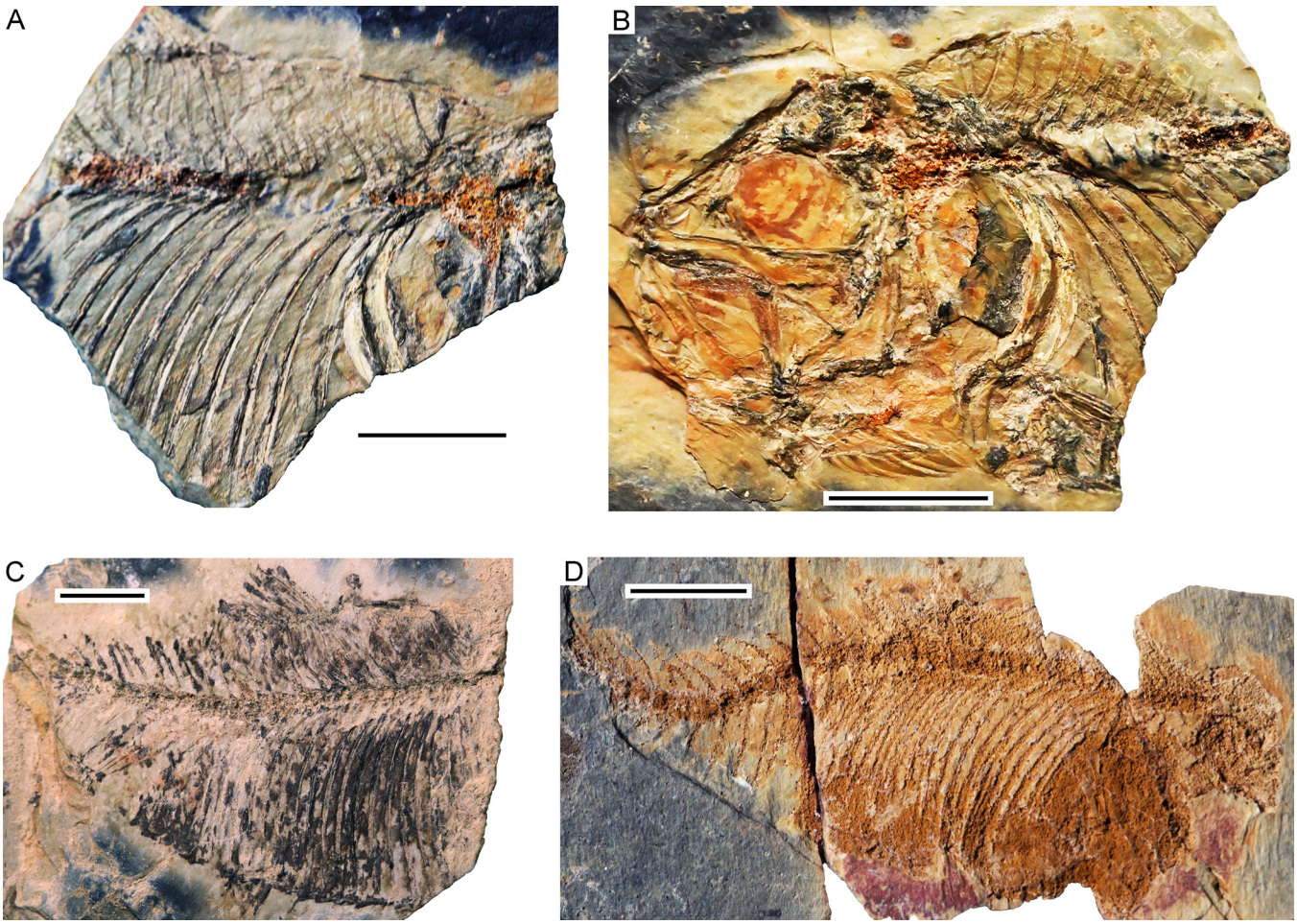


FIGURE 13 — †*Aijaichthys brevis* n. gen. and sp. in lateral view. **A**, CPI 8309 (holotype). **B**, CPI 8309-3 (holotype). **C**, CPI83-9-4. **D**, 8309-1.

squared-shaped and bears at least two small, conical teeth. The well-ossified maxilla is slightly curved and extends up to half of the orbit. It has a short anterior articular process, and its blade is narrow anteriorly, expanding slightly at its posterior third; its ventral margin is slightly curved and bears minuscule conical teeth that gives the impression of being distributed in more than one row. Teeth are missing at the posterior expansion of the blade.

Lower Jaw

The lower jaw is poorly and incompletely preserved in the available material (Figs. 13B and 14). It is tall, with a narrow symphysis, and from there, it expands dorsally; the limits between the dentalosplenial and the angular are not observed, but the dentalosplenial seems to form a large part of the jaw. A few, small, conical teeth are observed in the oral margin, which is partially destroyed. The posterior part of the jaw is not well-preserved, but the articular surface for the quadrate is narrow and is followed by a short postarticular process.

Palatoquadrate, Suspensorium, Hyoid Arch, and Urohyal

The tall, triangular-shaped quadrate (Figs. 13B–15) is a large bone, with its anterior margin longer than the posterior one, giving the bone a scalene triangular shape. The thick, well-ossified posterodorsal process of the quadrate seems to be as tall as the quadrate body. The quadrate is preserved in position, articulating with the lower jaw. A large, curved, boomerang-shaped ectopterygoid (Figs. 14, 15) articulates with the anterior margin of the quadrate; its anterodorsal region is expanded. Numerous, minuscule conical teeth are preserved in the inner side of the bone. The entopterygoid is an elongate bone exposed posterior to the maxilla and articulating laterally with the ectopterygoid and quadrate. Due to preservation, the medial margin of the ectopterygoid is partially displaced so that it is possible to observe small conical teeth displaced on the lateral side of the entopterygoid and posterior to the posterior margin of the maxilla. Part of the metapterygoid is preserved articulated with the posterior part of the entopterygoid and dorsal margin of the quadrate. Other bones, such as the hyomandibula and symplectic, are not preserved.

The hyoid arch is represented by an imprint of the posterior ceratohyal; below this imprint, but slightly displaced, is a series of seven well-preserved branchiostegal rays. Other branchiostegal rays are displaced on the lateral side of the lower jaw. A urohyal is not preserved.

Opercular Series

The opercle (Fig. 13B, 14) is poorly preserved in the holotype CPI 8309. The surface of the bone is partially smooth with some thin, inconspicuous crests radiating from the mid region of the bone downward. The suture between the opercle and subopercle is unclear so that the size of the bones cannot be determined. The triangular preopercle has both arms forming an angle of slightly over 90 degrees; the ventral arm of the preopercle is mostly destroyed, and the preopercular sensory canal and its tubules are not preserved. The dorsal arm of the preopercle is missing its upper part. An interopercle is not preserved.

Vertebral Column

The vertebral column (Fig. 13) is incomplete, because the posterior part of the body is partially preserved in the available specimens. There are 22 or 23 precaudal or abdominal vertebrae (including the inference of four being covered laterally by the opercle) and 11 or 12 caudal vertebrae. The neural spines of most abdominal vertebrae are unfused medially, and they are very thin and fragile. All vertebrae are formed by well-ossified autocentra bearing narrow neural arches.

Precaudal or abdominal vertebrae are square-shaped in contrast to the caudal ones, which are slightly elongated and rectangular-shaped, with their neural arches placed in the posterior region of the centrum. Both halves of each arch of the caudal vertebrae are fused medially, forming one neural spine, which is gently inclined posteriorly. The haemal spines of the first caudal vertebrae are elongated, following the pronounced ventral profile of the body.

The ribs are poorly preserved in general so that a precise number cannot be provided, except to say that there are ca. 19 long pairs, which have a characteristic curvature close to the vertebral centrum and then extend ventrally. A well-developed groove is positioned along the length of each rib, which slightly expand distally. There is no information available about the articulation between centrum and rib, except the first abdominal ones give the impression that they articulate in a cavity on the ventrolateral region of the centrum and the posterior ribs articulate with a lateroventral elongate process.

Epineurals are preserved as thin bones, and apparently, they are processes of the neural arches of the abdominal vertebrae. It is unclear whether epicentrals were present or not. A few poorly preserved epipleurals are ventral to the centra of the first caudal vertebrae. No intermuscular bones are associated to the neural and haemal spines of the mid-posterior caudal region.

Paired Fins

From the pectoral girdle (Fig. 13A, B), a heavily ossified, elongate, sigmoidal cleithrum is preserved and looks similar to that illustrated in Figure 6 for †*Ancashichthys peruensis* n. gen. and sp. The cleithrum does show a small curvature ventrally, being almost straight along most of its length. The structure and number of postcleithra is unclear. The pectoral fins are not preserved in any specimen. Poorly preserved pelvic rays are observed in CPI 83-9-4 (Fig. 13C).

Unpaired Fins

The dorsal fin (Fig. 13C) is preserved in specimen CPI 83-9-4. According to the position of the first dorsal pterygiophore, the origin of the dorsal fin is anterior to the origin of the pelvic fins. The dorsal fin has at least 13

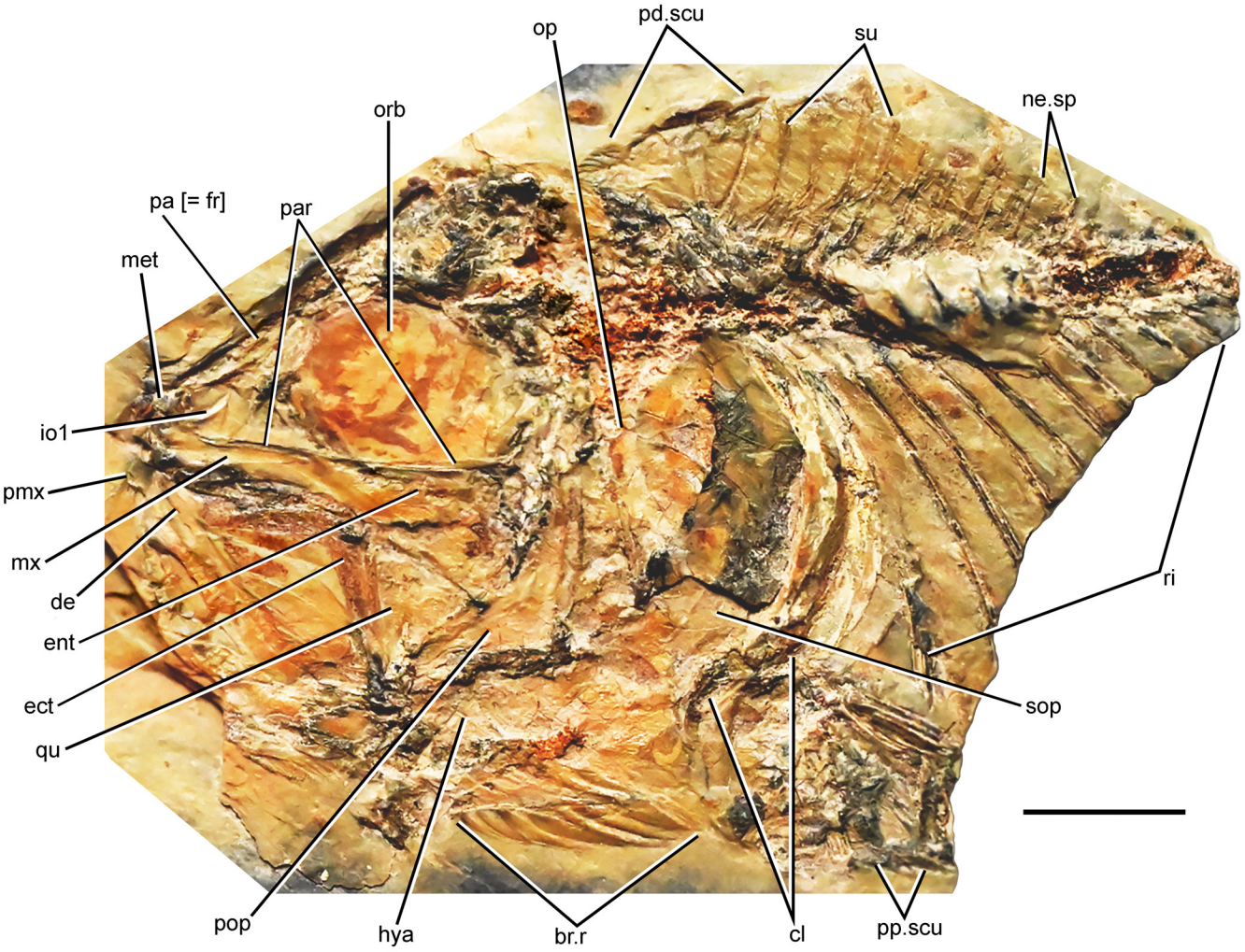


FIGURE 14 — †*Aijaichthys brevis* n. gen. and sp. Head and anterior part of trunk in lateral view (CPI 8309). Scale bar = 3 mm. Abbreviations: *br.b*, branchiostegal bones; *cl*, cleithrum; *de*, dentalosplenial; *ect*, ectopterygoid; *ent*, entopterygoid; hya, hyoid arch; *io1*, infraorbital 1; *met*, mesethmoid; *mx*, maxilla; *ne.sp*, neural spines; *op*, opercle; *orb*, orbit; *pa* [= *fr*], parietal bone [= frontal]; *p.cer*, posterior ceratohyal (imprint); *pd.scu*, predorsal scutes; *pmx*, premaxilla; *pop*, preopercle; *pp.scu*, prepelvic scutes; *qu*, quadrate; *ri*, ribs; *su*, supraneurals.

principal rays, and at least one procurrent ray; it is unclear if other anteriormost procurrent or simple rays are missing. The anterior principal dorsal rays are longer than the following rays, giving the fin a decreasing posterodorsal margin. The dorsal rays are thin, with long bases, and they branch only distally. Thirteen elongate proximal radials are preserved, with the first one being the largest and longest of the series and bearing two or three branches; the following proximal radials decrease in length posteriorly. Each proximal radial appears to be a thin bar, with an expanded, almost triangular distal portion that articulates with a middle radial.

The anal fin is incompletely preserved in only one specimen, showing a few anal pterygiophores and rays (Fig. 13C). The caudal fin and its endoskeleton are not preserved in any specimen.

Scales, Scutes and Supraneurals

Information on the scales is not available. The fish has preserved three series of scutes: predorsal, prepelvic and postpelvic (Fig. 13A–C). The predorsal series extends from just behind the cranium and ends anterior to the first proximal radial (Figs. 12B, 13). About 10 predorsal scutes are preserved in this specimen. Specimen CPI 8309 has the anterior predorsal scutes nicely preserved; as shown by this specimen, the series starts just posterior to the supraoccipital region. The first anterior predorsal scute is thicker and leaf-like in shape, with their associated supraneurals inclined anterodorsally. The third predorsal scute has a thick, triangular-shaped supraneural below that is thicker than the rest of the series. The following

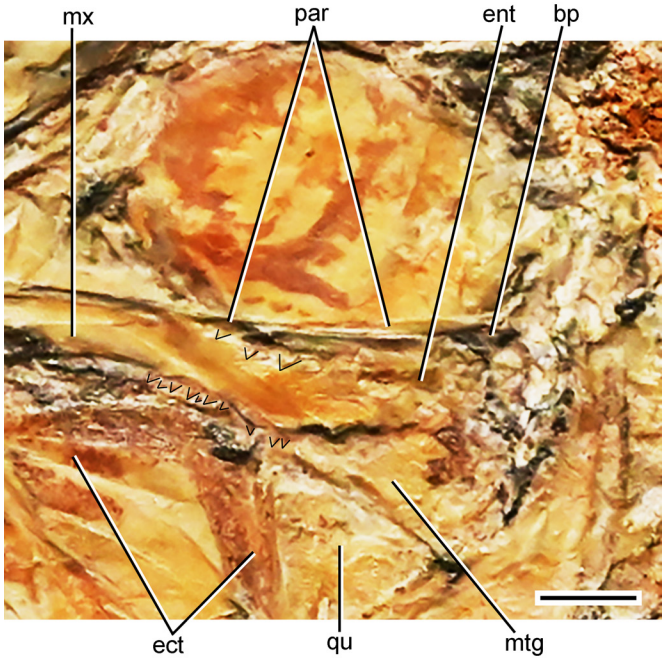


FIGURE 15 — †*Aijaichthys brevis* n. gen. and sp. Section of cranium illustrating the minuscule teeth associated with paraspehnoid and pterygoid bones (CPI 8309). The borders of some teeth are outlines with a thin black line to help with their identification. Scale bar = 1 mm. Abbreviations: *bp*, "basipterygoid" process; *ect*, ectopterygoid; *ent*, entopterygoid; *mtg*, metapterygoid; *mx*, maxilla; *par*, parasphenoid; *qu*, quadrate.

scutes are associated ventrally with supraneurals that are thinner and anteroventrally curved (see description above for †*Ancashichthys peruensis,* and Fig. 14B).

The abdominal series of scutes (Fig. 13B, C) consists of prepelvic and postpelvic scutes that are not as well-preserved as in †*Ancashichthys peruensis* n. gen. and sp. These scutes are formed by an elongate, subrectangular base bearing an anterodorsally oriented process at its anterior margin. The series of abdominal scutes extends along the whole preanal body margin, but it is divided into two series, the pre- and postpelvic ones. The total number of abdominal scutes placed posterior to the cleithrum remains unknown due to incomplete preservation. A few remnants of scutes not associated to ribs are placed anterior to the first rib (Fig. 13B).

FINAL COMMENTS

Taxonomic Assignments

The two newly described fossil clupeomorphs from the Tithonian of Peru (Fig. 3) add new information to the taxonomy, morphology, and biogeographic understanding of the group. Because of their combination of morphological characters, especially the presence of predorsal and abdominal (prepelvic and postpelvic) series of scutes, †*Ancashichthys peruensis* n. gen. and sp. and †*Aijaichthys brevis* n. gen. and sp. are interpreted as clupeomorphs, specifically belonging within the order †Ellimmichthyiformes (*sensu* Alvarado-Ortega et al., 2008; Murray and Wilson, 2015; Nelson et al., 2016). Contrary to previous interpretations, Marramà and Carnevale's (2023) study on double armoured clupeomorphs considered the presence of a large beryciform foramen as the only uniquely derived feature of †Ellimmichthyiformes. They proposed a few other features as plesiomorphies of the order, as for instance, the presence of the "basipterygoid" process of the parasphenoid, entopterygoid teeth, postparietals [= parietals] contacting each other medially, and fine striations or crests on the ventral part of the opercle and three epurals. According to the present information, a large beryciform foramen is present in †*Ancashichthys peruensis* (see Fig. 7), but the condition in unknown in †*Aijaichthys brevis*; however, †*Aijaichthys brevis* has preserved entopterygoid teeth and fine bony crests in the lower part of the opercle (Fig. 14). Information on the skull roof and caudal skeleton is not available yet for these fossil Peruvian clupeomorphs.

In the most recent study on the relationships among clupeomorphs, †ellimmichthyiforms, such as †*Armitagus alticorpus* from the Cenomanian of Lebanon and †*Diplomystus dentatus* from the Eocene of USA, were recovered as sister taxa, but their sister-group relationship to other clupeomorphs changed when different phylogenetic analyses were performed. Consequently, Kevrekidis et al. (2024) concluded that the relationships of †Ellimmichthyiformes should be considered open. The morphological characters mentioned by Kevrekidis et al. (2024) for †Ellimmichthyiformes were specifically checked on the new Peruvian species described herein. These include the presence of the "basipterygoid" process on the parasphenoid, absence of a recessus lateralis, absence of a prootic and pterotic bullae, and postparietal bones [= parietal] that meet in the middle, instead of being separated by the supraoccipital. Most of these could not be checked in the two new Peruvian species because of incomplete preservation, although †*Aijaichthys brevis* n. gen. and sp. has a small "basipterygoid" process on the parasphenoid (Fig. 14). In addition, information on other important morphological characters (e.g., caudal skeleton) is also missing (see descriptions above).

To solve these deficiencies, new specimens are needed, so new field work is currently in progress. Despite these deficiencies, we consider that the unique combination of characters of the new Peruvian clupeomorphs support the interpretations of them representing members of the order †Ellimmichthyiformes and also support the erection of the new family †Anchashichthyidae. Additionally, the morphological differences between †*Ancashichthys peruensis* and †*Aijaichthys brevis* (e.g., body shape, body proportions, some head bones, such as the quadrate, number of vertebrae, number of predorsal and abdominal scutes) are significant, supporting each as a new species (see Diagnoses).

Oldest Clupeomorphs and their Geographical Distribution

Currently, the South American continental slope waters of the Pacific Ocean are inhabited by large schools of clupeomorphs that include engraulids and clupeids. Traditionally, their identification followed the European taxonomic interpretations of the group; thus, fishes, such as *Engraulis ringens*, *Clupea* (*Strangomera*) *bentincki*, and *Sardinops sagax*, were recognized as part of the families Engraulidae and Clupeidae (Mann, 1950; Vildoso et al., 1999; Pequeño et al., 2009). However, recent studies based on DNA sequences of five mitochondrial genome regions (Canales-Aguirre et al., 2021) have yielded a different scenario, and the so-called clupeids are now included in the genus *Strangomera* (still in the family Clupeidae) with two species (*S. bentincki* and *S. fuegensis*). *Strangomera bentincki* has a larger, northern distribution, whereas *S. fuegensis* is restricted to the southern part of the continent, extending to the Falkland Islands and Cape Horn.

According to the available information, the oldest known clupeomorphs were in the Barremian (ca. 126–121 Ma; Lower Cretaceous of Brazil) and are represented by the †ellimmichthyiform †*Pseudoellimma gallae* (de Figueiredo, 2009a). The second oldest occurrence is from the Barremian–Aptian (ca. 121–113 Ma; Lower Cretaceous of Brazil) and is represented by †*Cynoclupea wilsoni* (Malabarba and Di Dario, 2017), a clupeiform. Several other fossil clupeomorphs, from the Cretaceous of Brazil, but of Albian and younger ages, have been known for a long time and support the Atlantic side of South America as a center of radiation for early clupeomorphs. Our new findings from the Pacific side of the continent enlarge the geographical distribution of †ellimmichthyiforms and extends the temporal distribution of the group to the Tithonian, making †*Ancashichthys peruensis* n. gen. and sp. and †*Aijaichthys brevis* n. gen. and sp. the oldest known clupeomorphs, suggesting the southern Paleo-Pacific played a role in the early radiation of the group.

The present results are significant because no fossil clupeomorph has been previously reported from the Pacific slope of South America, which is characterized by significant information on marine stem teleosts of Early–Middle Jurassic age from Chile (see Arratia and Schultze, 1999, and Arratia, 2015 for reviews), and interestingly, a head with gonorynchiform characteristics was reported and illustrated for the Lower Cretaceous of Cerro Islote, Atacama Desert, northern Chile by Arratia and Schultze (1999). Other otomorphs, such as gonorynchiforms, characiforms, and especially catfishes, are well-known from Cretaceous deposits of Brazil and Argentina (see Arratia, 2018 for a review on fossil otomorphs and Arratia, 2026 for a review of fossil catfishes). These previous findings and the ones reported herein from Peru are significant, supporting the hypothesis that South America was a center of origin, radiation and diversification of different otomorphs, a large, economically important clade that is sister to Euteleostei or Euteleosteomopha (Betancur-R., et al. 2017; Arratia, 2018).

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