

## *Scombroclupea javieri* sp. nov., an enigmatic Cenomanian clupeomorph fish (Teleostei, Clupeomorpha) from the marine deposits of the Cintalapa Formation, Ocozocoautla, Chiapas, southeastern Mexico

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### ABSTRACT

*Scombroclupea javieri* sp. nov. is erected based on the description of well-preserved specimens collected in the lower Cenomanian marine outcrop at the El Chango quarry, near Ocozocoautla de Espinosa, Chiapas State, southeastern Mexico. This new species shows the distinctive feature of the superorder Clupeomorpha, the presence of the abdominal scute series, as well as the diagnostic characters of *Scombroclupea*, as the lack of the dorsal scutes and the presence of two supramaxillae, the comb-like dentition in the maxilla, the horizontal laminae in the anterior caudal vertebrae, the flat epineurals and epipleural in caudal region of the trunk, and the finlets present along the anal fin, and differs from the other three nominal species of this genus in meristic data of the fins and vertebrae. *Scombroclupea* was previously thought as an *incertae sedis* members of the order Clupeiformes; however, *S. javieri* displays two primitive features never recorded before in this clupeomorph order and commonly observed in the order Ellimmichthyiformes, this new species has a large beryciform foramen piercing the anterior ceratohyal and its parietal bones are sutured to each other. The review of specimens of *S. occidentalis* and *S. macrophthalmia* confirms that these species share the presence of a large beryciform foramen in the anterior ceratohyal. These characters make it difficult to include *Scombroclupea* as a member of any of the orders Clupeiformes and Ellimmichthyiformes. This record of *Scombroclupea*, the oldest in America and the second in México, widens the geographical Cenomanian distribution of the genus along the Tethys Sea, from Middle East to southern North America.

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### 1. Introduction

The nearly 400 living species of herrings, anchovies, and sardines, and their about 160 extinct allies species, constitute a diverse and widespread teleostean fish group formally named as the superorder Clupeomorpha (Greenwood et al., 1966; Nelson et al., 2016). Members of this group inhabit practically all aquatic environments around the world and its fossil record

dates back to the Early Cretaceous (Grande, 1985; Helfman et al., 2009). For a long time this group of fishes were long treated as a “wastebasket” group (e.g. Berg, 1940; Jordan, 1923; Lecointre and Nelson, 1996; among others), however, Greenwood et al. (1966: 358) and later Grande (1985) recognized their naturalness. Until today, the general aspects of clupeomorphs classification as set by last author, it being grouped into the orders Ellimmichthyiformes and Clupeiformes. Despite the recent achieves on the knowledge of the interrelationships and the arrangement of a natural classification of the clupeomorphs; today, the early diversification of this group still problematic (e.g. Grande, 1985; Zaragüeta-Bagils, 2004; Alvarado-Ortega, 2014; Vernygora et al., 2016). Therefore, any contribution to the knowledge of the fossils

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of this group is relevant to solve these and other problems of its natural history.

Undoubtedly, Mexico is the North American territory with the richest, more diverse and better preserved clupeomorphs fossil record and counts with numerous sites with ages ranging between the Albian to Oligocene (Maldonado-Koerdell, 1949; Ovalles-Damián, 2004; Alvarado-Ortega et al., 2006, 2008; González-Barba and Alvarado Ortega, 2009; Pérez-Sánchez and González-Rodríguez, 2010; among others). This was demonstrated by Than-Marchese and Alvarado-Ortega (2013), who launched a project to study the numerous clupeomorph fossils recently discovered in different locations of Mexico; hence, the aim of the present paper is to describe a peculiar fishes recovered from the Lower Cenomanian marine deposits of the El Chango quarry, previously reported by Than-Marchese et al. (2011, 2015, 2016). Although many of these Mexican fossils still require to be studied accurately; recently, significant strides have been made in this respect. Specimens of *Diplomystus* Cope, 1877, from an uncertain locality in northern Mexico were identified by Aguilera (1896); however, this report is doubtful because, after more than a hundred years, this genus was never found again this country. Applegate (1996) and Chang and Grande (1997) reported the presence of *Diplomystus*-like and *Ellimmichthys* Jordan, 1919, in the Albian limestones of the Tlayúa quarry, Puebla; however, Melgarejo-Damián (2012), Melgarejo-Damián and Alvarado-Ortega (2010) identified four potential new *ellimmichthyiform* species among these, of which they named *Paraclupea seilacheri* Alvarado-Ortega and Melgarejo-Damián (2017). Additionally, the most abundant clupeomorph fish in Tlayúa was named as *Ranulfoichthys dorsonudum* Alvarado-Ortega (2014). *Triplomystus applegatei* Alvarado-Ortega and Ovalles-Damián (2008), later renamed as *Scutatoclupea applegatei* by Bannikov (2015) and a specimen similar to *Paraclupea* Chang and Chou, 1977, were the first clupeomorphs studied from the Cenomanian deposits of the El Chango quarry, Chiapas (Ovalles-Damián, 2004; Alvarado-Ortega et al., 2008). *Scombroclupea occidentalis* Giersch, Frey, Stinnesbeck, Ifrim, and Padilla Gutierrez (2011), was described on with specimens recovered in the Cenomanian deposits of the Loma La Mula site, near Múzquiz, Coahuila.

The El Chango quarry together with its coeval and sister paleontological site, the El Espinal quarry, are real lagerstätten discovered in the first decade of the present century (Ovalles-Damián and Alvarado Ortega, 2002), near Ocozocoautla de Espinosa Municipality, Chiapas, southeastern Mexico (Fig. 1). In these small paleontological sites, a rich and well-preserved fossil assemblage has been recovered from the Cenomanian laminar and parallel limestones strata of the Cintalapa Formation, deposited under marine shallow and tropical marine conditions. The fossil assemblage as far recovered in the El Chango include plants, ammonites, bivalves, arthropods, and fishes (Alvarado-Ortega et al., 2009; Alvarado-Ortega and Than-Marchese, 2012, 2013; Díaz-Cruz et al., 2016; Guerrero-Márquez et al., 2012; Moreno-Bedmar et al., 2014; Vega et al., 2006; among others).

The genus *Scombroclupea* was erected by Kner (1863), to include his species *S. pinnulata* from Comen, today Slovenia, as well as *S. macrophthalma* (Heckel, 1849), previously described as *Clupea macrophthalma* from the Cenomanian deposits of Hakel and Hujula, Lebanon. Subsequently, the last of these species was removed the genus *Clupea* Linnaeus, 1758, and the first species was recognized as its junior synonymous (Woodward, 1901; Patterson, 1967, 1970). Before this paper, the fossil record of *Scombroclupea* included three Cenomanian species with a geographical distribution at both sides of the Tethys Sea, in the Middle East-Europe and North America. The other nominal species of this genus are *Scombroclupea diminuta* Forey, Yi, Patterson, and Davis (2003), recently discovered in deposits of Namoura, Lebanon, and *S. occidentalis* Giersch, Frey,

Stinnesbeck, Ifrim, and Padilla-Gutiérrez (2011), from the marine deposits of the “Loma La Mula” site, in Coahuila, northern Mexico [other authors (e.g. Alvarado-Ortega and Porras-Múzquiz, 2012) named this site as the La Mula quarry and suggest its age as Turonian]. Unfortunately, since Grande (1985) suggested that *Scombroclupea* is an *incertae sedis* clupeomorph, its phylogenetic relationships have never been properly evaluated.

Here we report a clupeomorph that presents characters that place it in the genus *Scombroclupea*, recognizing as fourth new and valid species, as well as the second for America. In addition, the goal of this work is to present the evidence of complex morphological characters that support as *incertae sedis* genus due to its shared distribution with the main groups of Clupeomorpha.

## 2. Material and methods

### 2.1. Preparation methods

Part of the specimens described in this paper were prepared following the acid method and transfer technique (Toombs and Rixon, 1959). They were bathed into an aqueous solution of 5–15% of acetic acid and hardened with Plexygun. Needles and pin vises were used under the stereoscopic microscope to remove the remaining patches of sediments from the skeletons. Prepared specimens were coated with magnesium dust to get black and white photographs of high contrast under white light.

### 2.2. Anatomical abbreviations and measurements

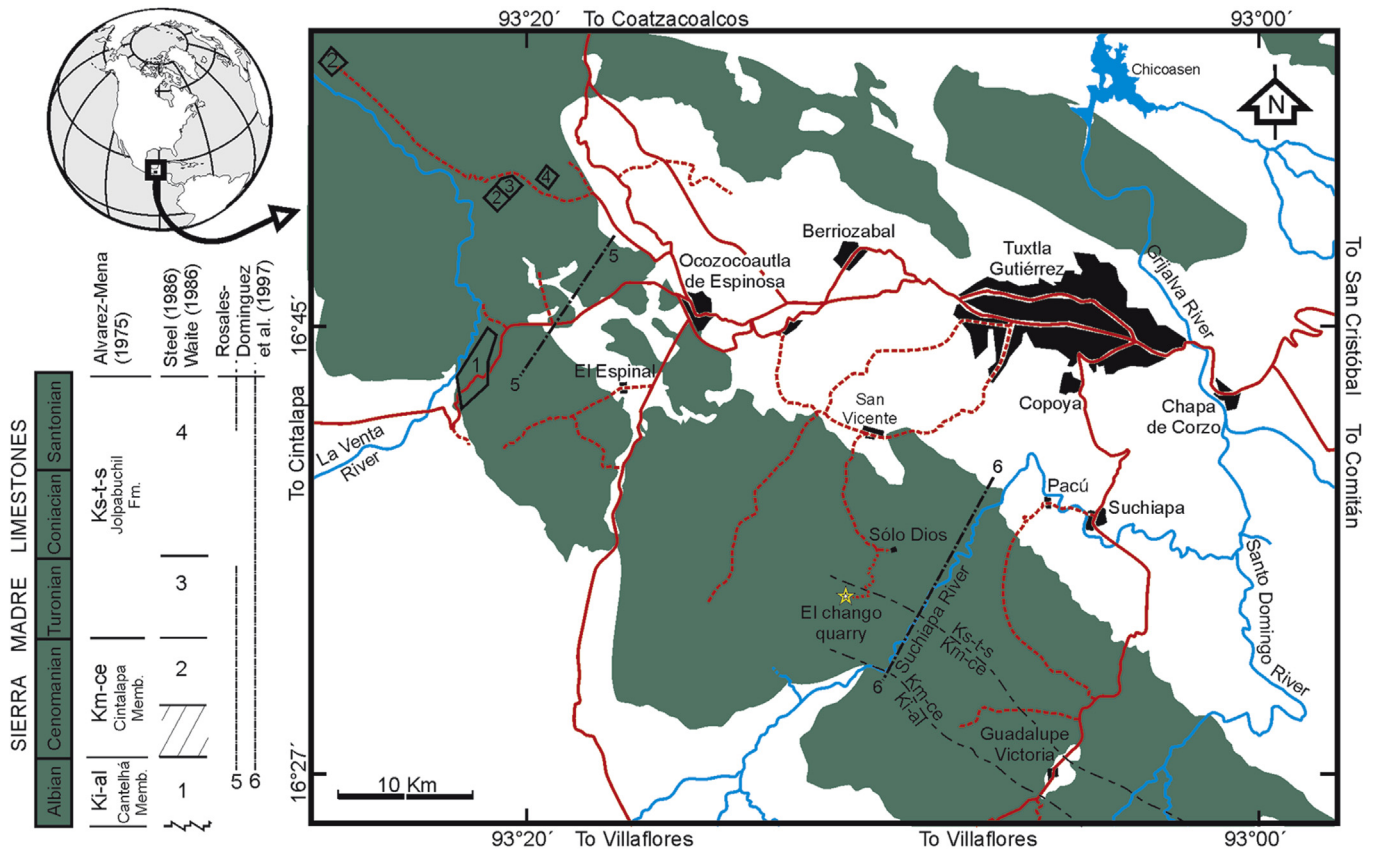
The anatomical nomenclature, abbreviations, and measurements included in the main text, figures, and tables of this manuscript follow those used in similar studies (e.g. Di Dario, 2004; Giersch et al., 2011; Grande, 1985; among others).

### 2.3. Institutional abbreviations

Acronyms of the institutions involved with this work are: CME, Colección de Material Extranjero, IGM; IGM, Colección Nacional de Paleontología, Instituto de Geología, Universidad Nacional Autónoma de México. INAH, Instituto Nacional de Antropología e Historia, México. IHNFG, Museo Eliseo Palacios Aguilera, Secretaría de Medio Ambiente e Historia Natural de Chiapas, México. MNHN, National D'Histore Naturelle, Paris, France. MUZ, Museo de Paleontología de Múzquiz, Coahuila, México.

### 2.4. Comparative materials examined

The specimens examined for comparative purposes are *Paraclupea*-like (Alvarado-Ortega et al., 2008): IHNFG-2331 from the Cenomanian deposits of the El Espinal quarry, Cintalapa Formation, Chiapas, Mexico. *Paraclupea seilacheri* Alvarado-Ortega and Melgarejo-Damián (2017): IGM 4717 (Holotype) as well as IGM 4718 to IGM 4723, from the Albian limestones of the Tlayúa Formation, Puebla, Mexico. *Ranulfoichthys dorsonudum* Alvarado Ortega (2014): IGM 9034 (holotype) as well as IGM 9035 to IGM 9042, from the Tlayúa quarry Puebla, Mexico. *Scombroclupea macrophthalma* (Heckel, 1849): CME 803 from Hakel, Lebanon; and specimens consulted online (<https://science.mnhn.fr/institution/mnhn/search>) are MNHN.F. HAK 1570 from Hadjula, Lebanon, and MNHN.F.HAK 454, MNHN.F.HAK 465D, MNHN.F.HAK 1767, MNHN.F.HAK 1890, MNHN.F.HAK 1998, from Hakel, Lebanon. *Scombroclupea occidentalis* Giersch, Frey, Stinnesbeck, Ifrim, and Padilla-Gutiérrez (2011): MUZ 286, MUZ 302, MUZ 305, MUZ 342, MUZ 345, MUZ 355, MUZ 356, MUZ 505, MUZ 1030 from the La Mula quarry (= Loma la Mula in Giersch et al., 2011), Coahuila,



**Fig. 1.** Locality of El Chango quarry, in Ocozocoautla de Espinosa municipality. The color green is the extension of Cintelapa Formation of Sierra Madre Group. The stars are the principal outcrops of this formation. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Mexico. *Scombroclupea* sp.: MUZ 1106, from the Palestina quarry, Coahuila, Mexico.

### 3. Results

#### 3.1. Systematic paleontology

Superorder Clupeomorpha [Greenwood et al., 1966](#)

Order *incertae sedis*

Family *incertae sedis*

Genus *Scombroclupea* [Kner, 1863](#)

*Scombroclupea javieri* sp. nov.

**Holotype.** IHNFG-5297, a complete specimen of 90 mm standard length exposing its left side ([Fig. 2](#)).

**Paratypes.** IHNFG-2990, a complete specimen preserved in part and contrapart. IHNFG-2992, complete specimen with the scales out of place and scattered on and around the trunk. IHNFG-5298 articulated specimen preserved in part and counterpart, with the head bones dissolved preserved as a preserved as a vague impression. IHNFG-5325, specimen without the posterior ventral part of the head and the anterior part of the abdomen. IHNFG-5326, nearly complete specimen preserved in two parts, large part of the head and the pelvic fins are preserved in the anterior one. IHNFG-5327, incomplete specimen with cranial portion and pectoral fin preserved. IHNFG-5328, complete specimen with the head uncovered ([Appendix, figs. 1-8](#)).

**Locality and horizon.** Cenomanian marine limestones of the Cintelapa Formation exploited at the El Chango quarry, Ocozocoautla de Espinosa Municipality, Chiapas, Mexico ([Fig. 1](#)) ([Alvarado-Ortega and Than-Marchese, 2012, 2013](#); [Moreno-Bedmar et al., 2014](#)).

**Etymology.** The species name honors our friend and colleague Manuel Javier Avendaño Gil, for his valuable contribution to the development of the paleontology in Chiapas.

**Diagnosis.** Fusiform clupeomorph fish with following characters set; frontal ornamented with elongated sinuous ridges in its orbital section; parietals in contact with each other along the midline; wide beryciform foramen presents in the anterior ceratohial; around 11 branchiostegals; the most anterior neural spines are bifid or unfused; anal fin consists of 6 or 7 anal fin rays forming and anterior acuminated lobe and six separated rays or finlets, which together are supported by 12–14 pterygiophores; 16 dorsal fin rays supported by until 18 pterygiophores; parhypural and first preural fused; procurrent rays and principal rays of caudal fin ordered following formula 5+I+9–8+I+5; first hypural and first ural not fused; hypural two and first ural centra fused; two uroneurals; three epineurals; 37–43 total vertebrae.

#### 3.2. Description

##### 3.2.1. General proportions

[Table 1](#) summarizes the measurements and body proportions of *Scombroclupea javieri* sp. nov. In general, the body shape of this fish resembles those of other species of *Scombroclupea*, in which the body is fusiform and laterally compressed, and the unpaired and paired fins are placed on the edge of the trunk. The standard length (SL) of the type specimens ranges between 146 and 91 mm. The head length occupies on average the anterior 24–28% of SL (mean = 25.6%). The relatively short triangular dorsal fin represents 12–15% of SL (mean 13.25%) and rises in the middle of the body between 44 and 52% of SL (mean 47.4%). The small pelvic fin is



Fig. 2. IHNFG-5297 holotype of *Scombroclupea javieri* sp. nov. Scale 10 mm. Best specimens of *Scombroclupea javieri*.

opposed to the posterior half of dorsal fin and rises at 56–60% of the SL (mean 58.25). The elongated anal fin, composed of an anterior acuminate lobe and six separated finlets, occupies 21–24% of SL (mean 22.75) and rises in the posterior third of the body at 72–77% of SL (mean 75.25). The head height is almost equal the maximum height of the body that is in the predorsal section and represents 16–22% of SL (mean 20.4). The caudal peduncle height is and 7.5–9.5% of the SL. The head is triangular and the caudal fin is deeply forked, slightly higher than the trunk, and has a ventral lobe slightly longer than the dorsal lobe.

### 3.2.2. Skull

In *Scombroclupea javieri* the head is triangular, about 1.25 times longer than high, and its preorbital, orbital, and postorbital regions have the same length (Fig. 3). The mesethmoid seems to be five-star shaped, with a short rounded anterior process, probably two posterior projections jointing the frontals, and two wide and rectangular lateral descending processes that ventrally are sutured with the vomer (Fig. 3; Appendix fig. 7A). On each side, the mesethmoid has two shallow facets; that one, on its anterior process, articulates the dorsal anterior tip of premaxilla while the other, on the anterior edge of its lateral descending process, joints with the anterior articular process of maxilla. The nasal bone is an elongated bone.

The frontals are roughly triangular bones that roof about 80% of the skull. These are entirely joined along their middle edges. The interfrontal suture is harmonic above the orbit and somewhat sinuous posteriorly. The frontals joint the mesethmoid anteriorly, the parietals posteriorly, and the pterotic and sphenotic with their lateral postorbital edge. These bones are smooth except in the posterior third, which is ornamented with longitudinal, sinuous, and shallow ridges (Fig. 3; Appendix fig. 7C). The supraorbital sensory canal extends alongside this external edge of these bones; above the orbit, this canal opens in two pores. The temporal foramen is a small cavity formed in the middle of the frontal-parietal suture (Fig. 3).

*Scombroclupea javieri* has a skull with mesoparietal condition (Fig. 3). In lateral dorsal view, each parietal is a wide trapezoidal bone that is concave posteriorly, convex anteriorly, and has a short middle edge and a long ventral border. Both parietals meet to each other in the middle line, separating the frontal from the supraoccipital bone. The supratemporal commissure of the parietal

sensory canal passes alongside the posterior edge of the parietals and opens in some pores located in the middle part of these bones. In dorsal view, the supraoccipital bone shows a small triangular surface from which a petite supraoccipital crest rises.

In all the specimens revised here, the pterotic is partially obscured; however, this forms a large part of the lateral surface of the skull and shows some small pores that form part of the recessus lateralis (Fig. 3; Appendix fig. 7B). Practically nothing can be said about the structure of the posterior surface of the skull but for the small part of the epioccipital bone exposed behind the parietal and exoccipital is above the epioccipital in the holotype. Both bones appear to be rectangular, the latter being slightly concave. The pre-epiotic fenestra is located between the parietal, supraoccipital and epioccipital bones; it is no clear participation of the pterotic bone in this fenestra (Fig. 3). The orbital region of the parasphenoid is a long and broad edentulous bar, flat dorsoventrally, and with no basipterygoid process. The anterior end of the parasphenoid is firstly sutures with a vomer.

### 3.2.3. Upper jaw

The premaxilla (Fig. 3) is a small triangular bone, elongated and three times longer than high. In this bone the anteriorly edge is rounded high, the posterior end is acute, and the alveolar edge is somewhat convex and entirely toothless. The maxillary ascending process is thick and ends in a rounded articular surface.

The maxilla is boomerang like bone, flat and curved (Fig. 3; Appendix fig. 7E). The anterior half that tends to be thickest anteriorly, is projected upward, and bears a couple of rounded and short dorsal articular processes near to the tip. Contrary, its posterior half of this bone is projected backward, is more expanded, uniformly high, and bears the alveolar border; the last one has an elongated and thin line of numerous teeth, which are placed closely on the lingual surface of maxilla and it's generating a pectinate teeth appearance. There are two laminar supramaxillae above the posterior half of the maxilla. The anterior supramaxilla is oval and smaller while the posterior supramaxilla is drop-shaped and posteriorly higher (Fig. 3).

### 3.2.4. Lower jaw

This jaw is a triangular structure in which the ventral border is somewhat convex, the symphysis is shallow, the coronoid process

**Table 1**

Measurements of *Scombroclupea javieri* sp. nov. from El Chango quarry. Based on specimens here described. All measurements are expressed in mm.; proportions of the standard length as (%). Abbreviations: A.f, number of anal fin rays; A.pf, number of anal pterygophores; abd, abdominal vertebrae; a.fin, number of anal finlets; a.v, vertebral number below which anal fin originates; cau, number of preural caudal vertebrae; D.f, number of dorsal fin rays; D.pt, number of dorsal pterygophores; d.v, vertebrae number below which dorsal fin originates; ful.d/v, number of dorsal and ventral procurent caudal rays; HH, skull height; HL, skull length; PA, preanal length; PD, predorsal length; Ph, caudal peduncle height; PV, preventral length; Prep, prepelvic scutes; Postp, postpelvic scutes; Pr, number of pectoral fin rays; Pvr, number of pelvic rays; SL, standard lengths; s.na, supraneural bones; TD, maximum depth of body; TL, total length; v.r, number of pelvic fin rays; v.v, vertebral number below which pelvic fin originates; -, unknown data; \*, at least; ~, approximated; ?, imprecise data.

Specimen	TL	SL	HL (%)	HH (%)	PD (%)	PV (%)	PA (%)	TD (%)	Ph	d.v	a.v	v.v
IHNFG-2990	—	146	35 (24)	~24 (16)	76 (52)	87 (60)	—	34 (23)	—	20	—	23
IHNFG-2992	—	93	26 (28)	20 (22)	45 (48)	—	67 (72)	34 (37)	~7 (7.5)	16	26	—
IHNFG-5297	110	91	24 (26)	20 (22)	42 (46)	52 (57)	70 (77)	24 (26)	8 (8.8)	15	26	19
IHNFG-5298	—	—	—	—	—	—	—	36 (—)	12 (—)	16	27	18
IHNFG-5325	119	92	23 (25)	19 (21)	43 (47)	55 (60)	71 (77)	25 (27)	7 (7.6)	14	24	16
IHNFG-5326	~114	95	24 (25)	20 (21)	42 (44)	53 (56)	71 (75)	23 (24)	9 (9.5)	15	25	17
IHNFG-5327	—	—	—	—	—	—	—	—	—	—	—	—
IHNFG-5328	—	—	22 (—)	19 (—)	—	—	—	—	—	—	—	—

Specimen	Vertebrate	Pr	Pelvic fin		Dorsal fin		Anal fin			a.fin	s.na	Prep	Postp	ful.d/v	
	total/abd/cau		Pvr	Length (%)	D.pt	Length (%)	A.pf	Total rays (Rays + finlets)	Length (%)						
IHNFG-2990	43/24*/19	9*	7*	8*	13*	16*	—	—	—	—	7*	15*	7*	4*+1+9/8*+1+5	
IHNFG-2992	39/24/15	13*	6*	—	16*	ii*+14*	11 (12)	13 (6 + 7)	8*(6* + 2*)	22 (24)	2*	7	15*	6*	4*+1+9/8+1+5
IHNFG-5297	39/22/17	16*	8	~8 (9)	16*	ii+14*	14 (15)	14 (7 + 7)	12 (6 + 6)	19 (21)	6	7*	12	9	4+1+9/8+1+5
IHNFG-5298	40/23*/17	17	6*	11 (—)	18*	ii+14*	18 (—)	14 (7 + 7)	13 (7 + 6)	31 (—)	6*	6?	17	9	5+1+9/9+1+5
IHNFG-5325	37/21*/16	16	8	6 (7)	16*	ii*+15*	~11 (12)	12 (6 + 6)	9*(5* + 4*)	21 (23)	4*	7*	14*	9	4*+1+9/8+1+4
IHNFG-5326	39/22/17	16	7	~7 (7)	15*	iii+14	13 (14)	13 (7 + 6)	13 (7 + 6)	22 (23)	6	6*	16	9	5+1+9/9+1+4*
IHNFG-5327	—	16*	—	—	—	—	—	—	—	—	—	—	—	—	—
IHNFG-5328	—	10*	—	—	—	—	—	—	—	—	—	—	7*	—	—

is high and wide, and the articular process protrudes backward as a small and rounded stout rounded is small. The dentary is V shaped with a deep posterior vertex and the alveolar border short, concave and inclined upward. Dentary bears until three small conical teeth in the anterior region of its alveolar border (Fig 3; Appendix fig. 7D).

The anguloarticular is also triangular and represents the posterior two thirds of the lower jaw. Its anterior end is tightly attached to dentary. This bone forms the lateral external surface of the short and shallow articular process and probably forms the entirely articular facet for the quadrate. The retroarticular is small and occupies the posterior ventral corner of the lower jaw, below the articular process.

3.2.5. Circumorbital bones

Six laminar bones, the dermosphenotic and five circumorbitals, form an open orbital ring; there are supraorbital, but not post-orbital bones (Fig. 3; Appendix fig. 7B). All of them are small rectangular, with rounded borders, and longer than high except for the circumorbital 4 and 5 that covers a small part of the postocular section of the skull. The circumorbital 4 and 5 are about quadrate and higher than long, respectively. The pass of the infraorbital canal forms a longitudinal groove with few branches in the circum-orbitals. Two thin and semicircular sclerotic bones occupy the orbit.

3.2.6. Hyomandibular series

The hyomandibular is hatchet-shaped bone, in which the head is wide and dorsally sinuous whereas the shaft is short, narrow, and slightly curved forward. This bone shows a well-developed opercular process located in the base of the upper third of its posterior edge.

The quadrate is a triangular bone with a stout articular head slightly projected forward and jointing with the lower jaw just below the middle orbit (Fig. 3). The spiny posterior process of the quadrate is as height as main section of this bone. The symplectic is long clove shaped bone distally expanded and projected upward beyond the dorsal edge of the quadrate.

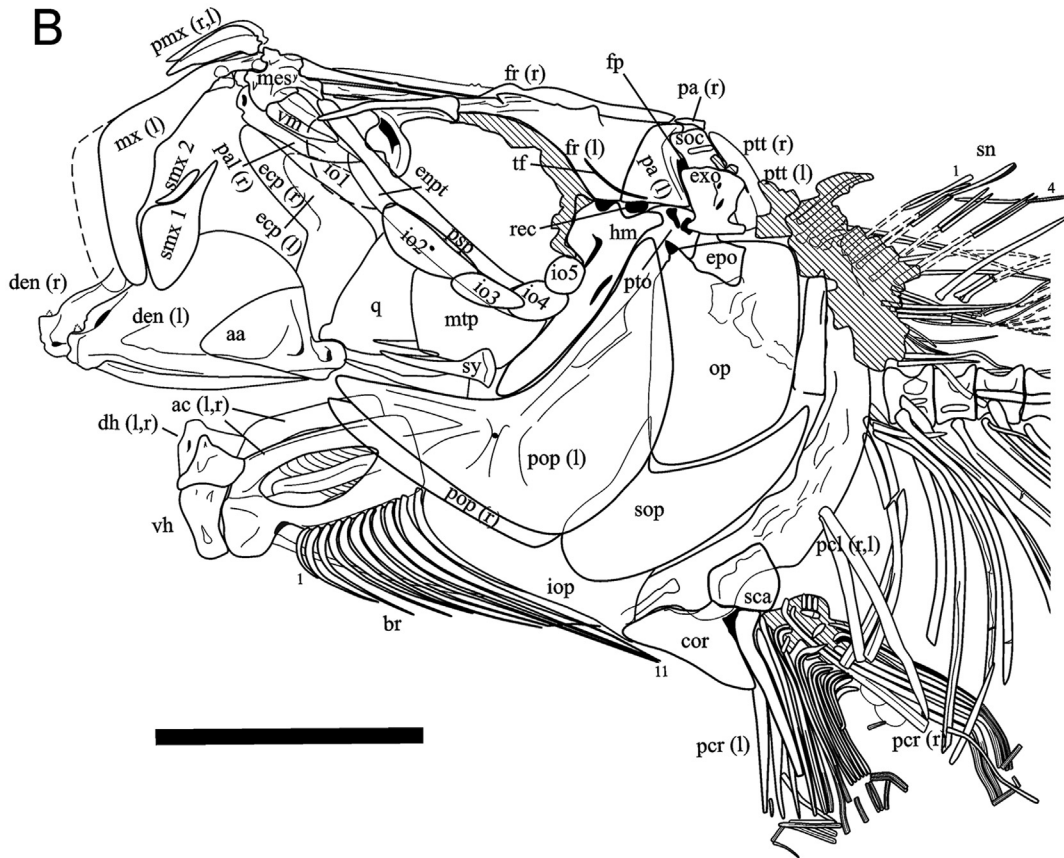
The metapterygoid is a roughly quadrangular bone that occupies large part of the cheek and is located between other bones of the hyomandibular series. The ectopterygoid is a long, curved, and toothless bone that attach the endopterygoid dorsally and the quadrate posteriorly. The endopterygoid is another elongate and toothless bone probably as long as the endopterygoid. The palatine, attached to the anterior ends of the ecto and endopterygoid bones, is triangular and has stout anterior head to articulate ventral edge of the mesethmoid and with the maxillar palatine facet.

3.2.7. Opercular bones

The opercle is a flat and smooth kidney shaped bone, with a straight anterior edge, about 1.5 times higher than long (Fig. 3). The hyomandibular facet is located at the base of the upper quarter the opercular anterior edge. The preopercle is an inverted L shaped bone, slightly higher than long, and strongly expanded posteriorly; in this bone, the height of the vertical limb is about 1.5 times the length of its horizontal limb. Both preopercular limbs form an obtuse angle of about 110°. The preopercular sensory canal has two branches in the horizontal limb. The subopercle is a semicircular smooth bone, as long as the opercle, with a straight dorsal edge, and a triangular dorsal anterior process. Unfortunately, the interopercle is largely obscured in the available specimens; however, this is a flat, smooth and spatula-like bone.

3.2.8. Hyoid arch and branchiostegal rays

Some bones of these series are exposed in the available specimens (Fig. 3). The ventral and dorsal hypohyals are small, rectangular, and tightly attached to the anterior edge of the anterior ceratohyal. A large and oval beryciform foramen pierces the anterior ceratohyal that is elongated, rectangular, and two time longer than high. There are 11 branchistegal rays attached to the ventral part of the anterior ceratohyal; these are flat, curved, and increase the size and expansion in anteroposterior order. An elongated urohyal with a small anterior articular head is present.



### 3.2.9. Axial skeleton

The vertebral column consists of 39–43 preural vertebrae, including 22–24 abdominals and 15–19 caudal vertebrae (Fig. 2, Table 1). Additionally, there are two ural centra. Seventeen pairs of long ribs almost enclose the entire abdominal cavity; these are slightly curved and somewhat expanded proximally. The head of each rib joints the lateroventral cavity of the respective abdominal vertebra but in the last posterior six ones, which develop conspicuous apophysis of increasing size in anteroposterior order to joint with the rib heads. At least in the abdominal region, the neural arche is not fused with the respective centrum and its neural spine is bifid, suggesting that both lateral halves of the neural elements are not fused or fused only in part. Contrary, in the preural region, each centrum seems to be fused with the respective neural and hemal arches, which show stout end simple neural and hemal spines (Fig. 2; Appendix figs. 1–6).

In the anterior twelve preural vertebrae, the lateral surface of the centrum displays a rounded middle longitudinal laminar process (= lateral lamina in Giersch et al., 2011, fig. 7). The anterior and posterior of these lateral laminae tend to be short and smaller; however, those lateral laminae located in the center are the most conspicuous extend up three fourths of the centrum length and laterally little extended. At least, the first seven preural centra develops a couple of short and sharp anterior prezygapophyses that are projected anteriorly to attach with the anterior centrum (Fig. 5B and 6); of these, the neural prezygapophyses is slightly longer than the ventral one.

Long epineurals and epipleurals are present along the vertebral column (Figs. 2 and 5B). The epineurals are associated with the neural arches and spines of all centra, except in the first six preural centra. In front of the dorsal fin, the epineurals are single long bones tilted backward that rises close to the base of the neural spines; beyond, these bones tend to rise in higher levels of the spines and are Y shaped because develop an anterior middle limb. There epipleural are associated with the abdominal centra and the hemal spines of preural centra, except in those of the first seven preural centra. The epipleurals of the abdominal region are single elongated bones strongly tilted backward that rises close to the ribs head and lateral surfaces of the parapophyses; these bones tend to be shorter in the posterior abdominal region. All the epipleurals in the preural region rise near to the base of hemal spine and are Y shaped because also develop an anterior middle limb.

### 3.2.10. Pectoral girdle and fin

The cleithrum is the most conspicuous element in the pectoral girdle; this is an inverted C shaped bone with a broad posterior expansion (Fig. 3). Above this, there is an elongated ovoid supra-cleithrum and a flat, ovoid, long and bifurcated posttemporal bone; who have a short anterior process and a dorsal process is large, curved and some rectangular with acuminate dorsal end. Behind the cleithrum, there is an elongated postcleithrum.

The coracoid and scapula are almost entirely obscure below the cleithrum. At least two or three dog-bone shaped radial bones articulate with the pectoral girdle and the pectoral fin rays. The pectoral fin consists of 16–17 rays distally branched and segmented (Table 1). The first of this ray is the broader and longer; its length is about that of six or seven abdominal centra. The other pectoral rays are progressively shorter.

### 3.2.11. Pelvic girdle and fin

The pelvic girdle consists of two small triangular pelvic bones united by their middle edges. The pelvic fin is small, opposed to the posterior half of the dorsal fin, and located below the vertebrae 8 to 21. This consists of 7 soft rays distally segmented and branched (Fig. 5A, Table 1). The first pelvic ray is longest in this fin being as long as three preural centra; the other rays tend to be progressively shorter.

### 3.2.12. Dorsal fin

This short fin is triangular, lies above the vertebrae 16 to 22, and rises in the middle of the body (Figs. 2 and 4; Table 1). This consists of 18 soft rays, including three unsegmented and unbranched anterior rays that are the shortest but of increasing size. Additionally, this fin has 15 rays distally segmented and branched, of which the third to fifth are the longest and equal the length of six preural centra.

The dorsal fin is internally supported on 18 dorsal proximal radials pterygiophores. The first pterygiophore is the longest, shows an anterior spiny process linked by a laminar wing, and is located between the neural spines of the vertebrae 12 and 13. The posterior pterygiophores are progressively shorter. The medial and distal radials are very small.

### 3.2.13. Anal fin

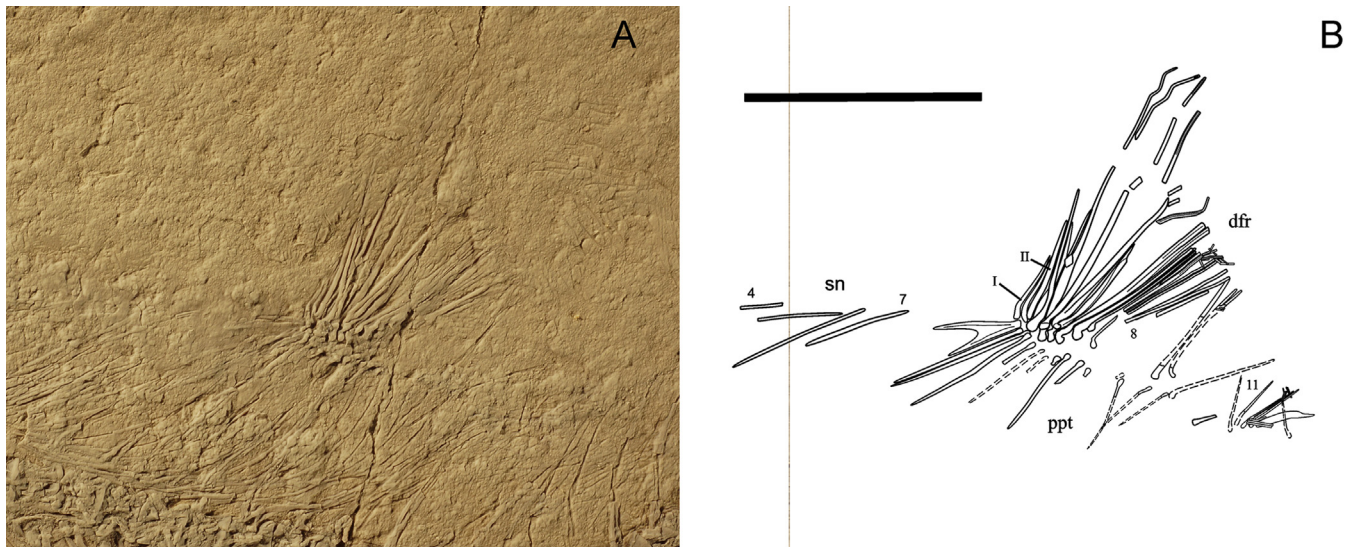
The long anal fin is far back in the trunk, behind the dorsal fin, and lies below the preural centra 26 to 38 (Fig. 5B, Table 1). This fin consists of 12 or 13 soft rays that are supported for 13 to 14 proximal anal radials or pterygiophores. The first anal ray seems to be unsegmented and unbranched, but the other rays are distally branched and segmented. The first anal fin ray is short whereas the second and third are the largest, being almost the length of two preural centra; posterior anal fin rays progressively decrease. The anterior 6 to 7 anal fin rays are closely set forming an acuminate lobe; the posterior 6 rays or finlets are separated by large gaps, which correspond to the presence of enlarged middle anal radials. The distals anal radials are inconspicuous. In IHNFG-5297, the distribution of proximal anal radials (= numbers) and spaces between the hemal spines (= \_) follows formula 1\_2\_2\_1\_1\_2/1\_1\_0\_1\_1\_1\_0\_1.

### 3.2.14. Caudal skeleton

The caudal fin is deeply forked and consists of two triangular and symmetrical lobes, of which the ventral is a little larger than the dorsal. The principal caudal fin rays of both lobes are preceded by five procurrent rays and a single stout, ovoid and flat caudal scute. There are nineteen caudal principal rays, including one segmented and nine segmented and branched in the dorsal lobe plus eight rays segmented and branched and one segmented forming the ventral fin lobe. Hence the caudal fin formula is 5+I+9–8+I+5 (Figs.1 and 6, Table 1; Appendix fig. 8). The four innermost caudal principal rays have proximal flat and branched expanded ends laying over hypurals 2–3.

Neural and hemal spines of the first three preural centra are curved backward to support the caudal fin. The neural spine of preural 2 is distally broad. The pleural centra 2 and 3 are rectangular, about 1.3 times longer than high, and have long thin neural spines, Contrary, the preural 1 and both uralals tend to be progressively smaller and the neural arch and spine on preural 1 is distinctively short, wide, and triangular. The hemal spines on the

**Fig. 3.** Skull and pectoral girdle and fin of *S. javieri* sp. nov. in IHNFG-5297. A) Specimen coated with magnesium smoke. B) Line drawing. Abbreviations: aa, anguloarticular; ac, anterior ceratohyal; br, branchiostegal ray; den, dentary; dh, dorsal hypohyal; ecp, ectopterygoid; enpt, endopterygoid; epo, epoccipital; exo, exoccipital; fr, frontal; hm, hyo-mandibular; io, infraorbital; iop, interopercle; mx, maxilla; mes, mesethmoid; op, opercle; pa, parietal; pal, palatine; pmx, premaxilla; pop, preopercle; psp, parasphenoid; pto, pterotic; ptt, posttemporal; q, quadrate; smx, supramaxilla; soc, supraoccipital; sop, subopercle; vh, ventral hypohyal; mtp, metapterygoid. Scale 10 mm.



**Fig. 4.** Dorsal fin of *S. javieri* in IHNFG-5297. A) Specimen coated with magnesium smoke. B) Line drawing. Abbreviations: dfr, dorsal fin rays; ppt, pterygiophore. Scale 10 mm.

preurals centra are progressively thinner, tilted, and shorter but those of the preurals 1 that bears a longer and thicker hemal spine. The parhypural, fused to preural 1, is even thicker and have anterior and posterior laminar wings. Above the neural arch of the preural 1 there are three long stick like epural bones.

Both ural centra are autogenous but the ural 1 is fused with the hypural 2 and ural 1. The ural 1 also joints the hypural 1. The ural 2 joint the proximal end of at least other four hypurals. All the hypurals are spatuliform but for the hypural 1 that is triangular. The hypurals 2 and 3 are in contact There are two elongated uroneurals laying the dorsal part of preural 1 and ural centra. The uroneural 1 is boomerang shaped, anteriorly bifurcated and fused to preural centrum 1. The small and oblong uroneural 2 is behind the hypural 2 and dorsally projected beyond the dorsal tip of hypural 1. There are no urodermals.

### 3.2.15. Scales and scutes

The trunk is entirely covered with ovoid cycloid scales, 1.5 to 2 times higher than long, and externally ornamented with numerous concentric circulli. The trunk does not show modified scales for the passage of the lateral line. There is a series of 26 abdominal scutes bordering the ventral edge of the trunk from the isthmus to the anus; 17 of them are prepelvics and 9 are postpelvics (Fig. 2 and 5A; Appendix fig. 3–5). These scutes have the shape of a four-pointed star and show a thickened longitudinal band that extends between the anterior and posterior limbs. These scutes are overlapping, the posterior limb of one scute overlies on the anterior limb of the subsequent scute. The lateral limbs of these scutes are spiny, laminar, not overlapping, and in the best case only covers a third of the abdominal cavity.

### 3.3. Comparative remarks

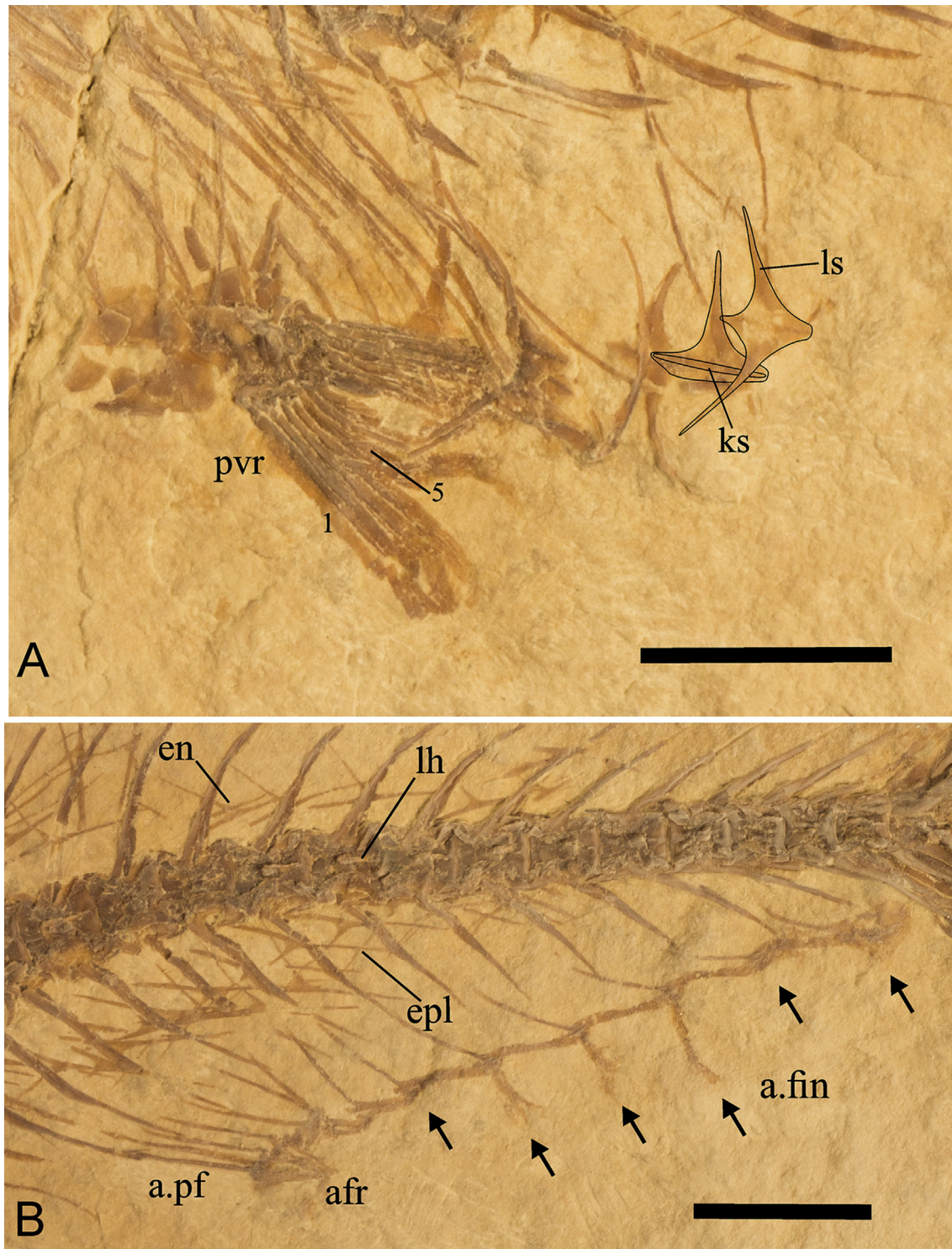
Undoubtedly, *Scombroclupea javieri* is member of Clupeomorpha because it shows five of the seven characters already identified as supporting the naturalness of this superorder (Grande, 1982, 1985; Chang and Maisey, 2003; Forey, 2004; Zaragüeta-Bagils, 2004; Arratia, 1997; Alvarado-Ortega, 2014; Alvarado-Ortega et al., 2008; Murray and Wilson, 2013; among others). These characters include the presence of the abdominal scutes series, the supratemporal commissure passing through the parietals, the pre-

epiotic fossa, the hypural 1 is autogenous while the hypural 2 and ural 1 are fused, and the parhypural fused with preural 1. Although the otophysic connection and the presence of a predorsal scute series are other potential diagnostic character of the clupeomorphs; the first character is not obvious in strongly compressed fossil specimens, as it is the case of the type specimens of *S. javieri*; and the predorsal scutes are secondary lost many taxa (Grande, 1985).

As noted before, the consensual classification of the clupeomorphs suggested by Grande (1985), divides these fishes in two orders, the Clupeiformes and the Ellimmichthyiformes [currently the relationships of *Armigatus* Grande, 1982, and allies is a controversial problem; these have been regarded as a group close to the ellimmichthyiformes (Grande, 1982, 1985), a derived ellimmichthyiform group (Chang and Maisey, 2003; Forey, 2004), a group outside this order (Zaragüeta-Bagils, 2004; Alvarado-Ortega et al., 2008), and a ellimmichthyiform group allocated in its own suborder (Armigatoidei) (Murray and Wilson, 2013)]. Grande's (1985) contribution is to differentiate between orders. Clupeiformes is well-diagnosed on the presence of the recessus lateralis, the lateroparietal skull condition (the parietals are completely separated by the supraoccipital), and the anterior ceratohyal non pierced; and contrary, Ellimmichthyiformes (including *Armigatus* and allies) have no recessus lateralis, the mesoparietal skull condition, a large beryciform foramen pierces the anterior ceratohyal, and develops dorsal scutes laterally expanded (*Armigatus* has ovoid dorsal scutes). In same work, Grande did not include genus *Scombroclupea* in his proposal, however, he without explanation suggested the *incertae sedis* condition of *Scombroclupea* among the clupeomorphs.

The discovery of *S. javieri* provides important anatomy data of the genus *Scombroclupea*; nevertheless, the morphological data recovered in this study agree with Grande's (1985) because the nominal species of *Scombroclupea* show a mixture of characters previously indicated as diagnostic in one or other of the clupeomorph orders. Unlike ellimmichthyiforms and clupeiforms, this genus does not have predorsal scutes but this could be a primitive condition and not result of a secondary loss; as in some clupeiforms, this shows a well-defined recessus lateralis; and additionally, as in ellimmichthyiforms, this genus displays a skull with a mesoparietal condition [firstly discovered in *S. javieri* (Fig. 3)], and

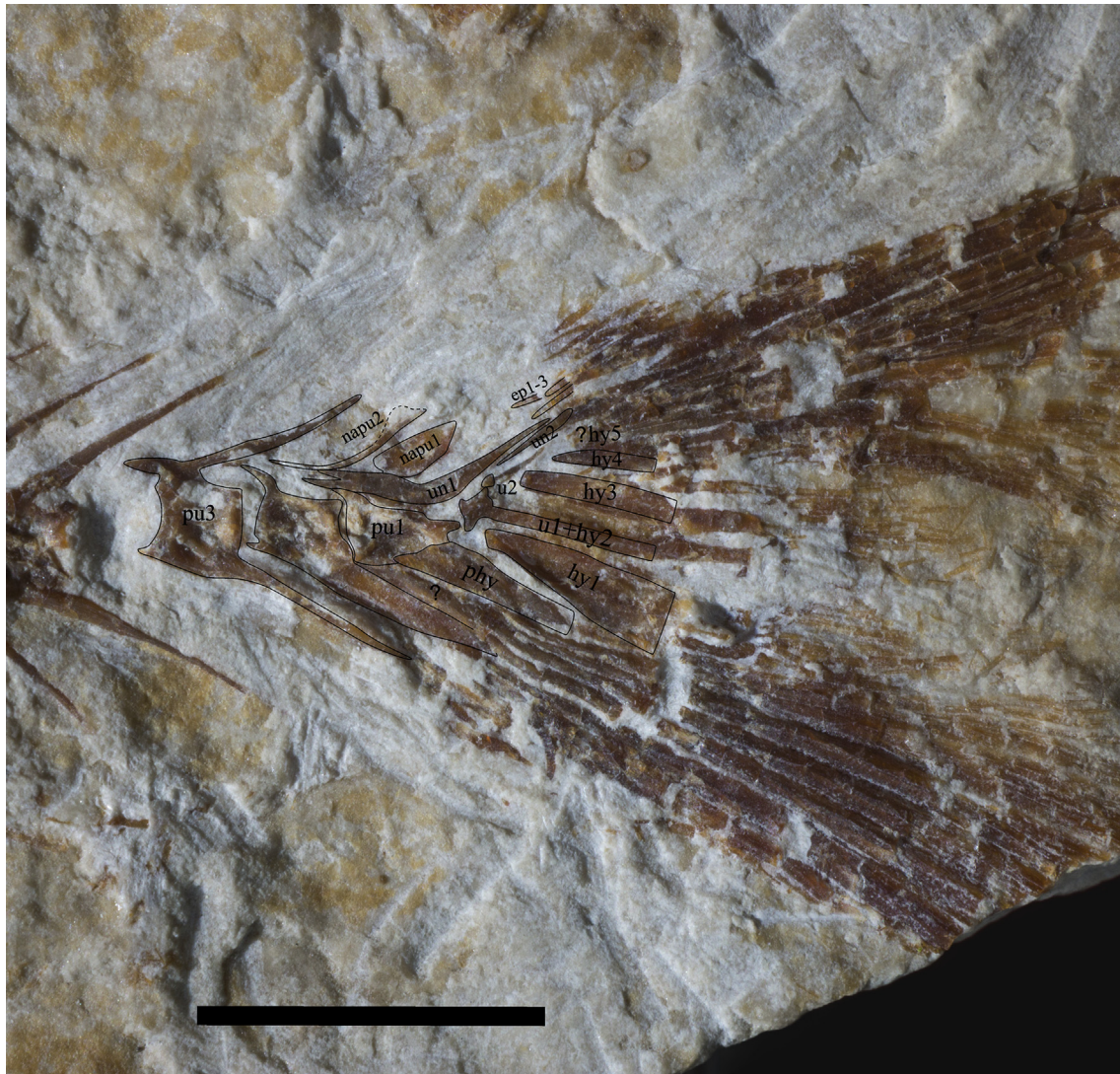




**Fig. 5.** Pelvic girdle, anal fin and scutes close up of *S. javieri* in IHNFG-5297. A) Pelvic girdle and fin, and scutes. B) Anal fin with finlets and caudal trunk. Abbreviators: afr, anal fin rays; a.fin, anal finlets; a.pf, anal pterygiophores; epl, epicentrals; en, epineural; ks, middle keel; lh, horizontal laminae ls, lateral or ascending process; pvr, pelvic fin rays. Arrows show positions of the finlets. Scale 5 mm.

the beryciform foramen anterior piercing the anterior ceratohyal, as seen in *S. javieri* (Fig. 3), *S. macrophthalmia* [noted by Woodward (1901; plate IV fig. 1) and observed here in CME 803, MNHN.F.HAK 465D, and MNHN.F.HAK 454 (Appendix figs. 9–18)], and *S. occidentalis* (see MUZ-480 in appendix figs. 19 and 20).

Although the mesoparietal condition is present in *Scombroclupea*, Ellimmichthyiformes, and *Ranulfoichthys* previously identified as a basal clupeomorph fish that is not clupeiform or ellimmichthyiform (Alvarado-Ortega, 2014); the situation of *Scombroclupea* is peculiar, the middle contact between the parietals is comparatively reduced



**Fig. 6.** Caudal fin of *S. javieri* in IHNFG-2992. Abbreviations: hy, hypural; phy, parhypural; pu, preural centra; napu, neural arch of preural centrum; un, uroneural; u, urohyal; u1+hy2, hypural 2 fused with urohyal 1. Scale 5 mm.

in this genus because its parietals are short and wide whereas in *Ellimmichthyiformes* and *Ranulfoichthys* these bones are more square and show a long parietal contact.

Giersch et al. (2011, p. 74) provided an emended diagnosis of *Scombroclupea* including the lack of dorsal scutes as well as the presence of two supramaxillae, finlets in the anal fin, comb-like dentition on the caudal half of maxilla, horizontal laminae in caudal vertebrae, and flat epineural and epipleural in caudal region. Although the first two of these characters can be considered as primitive among teleosts; the others really are distinctive of this genus. *Scombroclupea javieri* is identified as a member of this genus because it shows all these characters (Figs. 2–6; Appendix figs. 1–8).

Table 2, updated from Giersch et al. (2011, Table 2), summarizes the differences of all nominal species of the genus *Scombroclupea* and supports the singularity of *S. javieri* as a new species. *Scombroclupea javieri* is a distinctive species because its lower jaw is toothed whereas the other species do not have teeth in the lower jaws. The ranges of total vertebrae (39–42) and post pelvic abdominal scutes (7–11) are shared by *Scombroclupea javieri*, *S. macrophthalmalma*, and *S. diminuta*; contrary, *S. occidentalis* has fewer

total vertebrae (35–36) and post pelvic abdominal scutes (6–7). The distal end of the neural spine on preural 2 is distinctively broad in three species, *Scombroclupea macrophthalmalma*, *S. occidentalis*, and *S. javieri* but, this spine is distally sharp in *S. diminuta*. The lateral extension of the largest horizontal laminae on preural centra is unknown in *S. diminuta*, comparatively large in *S. occidentalis*, and similarly small in *S. macrophthalmalma* and *S. javieri*. Finally, although, *S. diminuta* shows a highly variable number of anal finlets (2–6); other species seem to have a constant number of this anal fin components, which are 5 in *S. occidentalis* and 6 in *S. macrophthalmalma* and *S. javieri*.

#### 4. Discussion

Actually, the genus has three valid species: *S. macrophthalmalma* [Líbano (Hakel y Hajula), Slovenia (Komen) y Croatia], *S. diminuta* [Líbano (Namoura)] and *S. occidentalis* [Mexico (Coahuila)]. The *Scombroclupea* diagnosis was amended by Woodward (1901), Forey et al. (2003) and Giersch et al. (2011). The latter defines the genus as follows: 1) two supramaxillae; 2) tiny teeth in the caudal half of the jaw that have a comb-like dentition [Initially observed by

**Table 2**

Measurements and morphology comparative of *Scombroclupea* species, based in Giersch et al. (2011). All measurements are expressed in mm. Abbreviations: pu2, second preural centra.

	<i>Scombroclupea macrophthalmia</i>	<i>Scombroclupea diminuta</i>	<i>Scombroclupea occidentalis</i>	<i>Scombroclupea javieri</i> n. sp.
Number of vertebrae	39–40	39–40	35–36	37–42
Number of anal finlets	6	2–6	5	6
Number of postpelvic scutes	7–10	10–11	6–7	9
Pleural rib/preural vert. radio	0.58	0.59	0.56	0.60
Posterior margin of caudal fin	Straight	Straight	Lobed	Lobed
Neural spine of pu2	Distally broadened	Needle-shaped	Distally broadened	Distally broadened
Maximum lateral extension of horizontal laminae	Reaches 3/4 of vertebral diameter	Unknown	Equals vertebral diameter	Reaches 3/4 of vertebral diameter

Woodward (1901) and removed by Forey et al. (2003), who determined as toothless]; 3) absence of dorsal scutes; 4) transversal processes in some anterior caudal vertebrae forming horizontal laminae [Giersch et al. (2011) reinterpret based on the definition of the transverse process of Baur, 1886 and Rojo, 1991. Named as horizontal laminae by Woodward (1901)]; 5) epineural and epi-pleural intermuscular bones flattened in the caudal region; 6) after anal fin divided into series finlets each of which is formed multi-branched rays.

It is undeniable that the new material reported here is a member of *Scombroclupea* to present the six characters that define the genus mentioned above. Likewise, *Scombroclupea javieri* is the new fourth valid new species of the clade to differentiate itself from the other three species known from the following morphological features: 1) at least one tooth in the dentary bone; 2) preopercle nerve canal has four pores in the horizontal member; 3) neural spines not fused to the thoracic vertebral body and to each other, being bifid; 4) number and arrangement of spines in the dorsal fin: II + 14 soft rays (2–3 non-segmented and non-branched rays, posteriorly 14–16 segmented and branched rays); 5) 12–13 rays in anal fin, 6 finlets in the posterior section; 6) first preural centrum not fused to the first ural centrum; 7) similar size between the centra of the first preural and first ural; 8) absence of interlobal notch between hypural 2 and 3; 9) uroneural first not fused with the first preural centrum; 10) 3 epurals; 11) until 9 postpelvic scutes. These are features that are not observed until now in members of the genus reported by Woodward (1901), Forey et al. (2003), Giersch et al. (2011, pp. S81–S82).

The genus *Scombroclupea* has previously been included in phylogenetic contexts (e.g. Grande, 1985; Giersch et al., 2011) trying to establish affinities within clupeomorphs, however, these have not had strong results. Since Kner (1863) to Giersch et al. (2011), they have kept *Scombroclupea* as a member of Clupeiformes mainly due to the present recessus lateralis, parietals separates by supra-occipital bone and ceratohyal probably absent (Giersch et al., 2011). On the contrary, we have found an opposite characterization of these morphological structures among the clade members. In *S. macrophthalmia* (Woodward, 1901; plate IV fig. 1, CME 803, MNHN.F.HAK 465D, and MNHN.F.HAK 454), *S. occidentalis* (MUZ 480) and *S. javieri* sp. nov. (IHNFG- 5297 and IHNFG-2990) exhibit bercyiform foramen in anterior ceratohyal, and same time, parietal bones are in contact with each other in at least these three species. Therefore, recessus lateralis is the only common feature between the genus and Clupeiformes.

In this sense Grande (1985) included the genus in his review of Clupeomorpha where he defined, although *Scombroclupea* and the members of Ehiravini have finlets in the caudal portion of the anal fin; however, the support of this section of the fin has different arrangements. In Ehiravini the middle and proximal pterygiophores are fused, while in *Scombroclupea* these structures are kept separate. Likewise, Grande (1985) without providing further details,

concludes that *Scombroclupea* is a non-clupeoid, therefore its position is *incertae sedis*. Within Clupeiformes, in this case, the genus has no characters linking it with Denticipitoidei, it is far from being a member of this suborder.

While ellimichthyiform fishes were erected under a single character, lateral expansion of dorsal scutes (Grande, 1985). Almost 30 years later, Murray and Wilson (2013) determined that order is supported by ornamentation of skull roof, anterior ceratohyal pierced, parietals meeting each other, three epurals, basiptyergoid process in parasphenoid and predorsal scutes present. Based on the Murray and Wilson (2013), the first three ellimichthyiform features are shared with at least with the Mexican *Scombroclupea* species and first two of them in *S. macrophthalmia* (CME 803; MNHN.F.HAK 465D); additionally with *S. javieri*, they have in common the epurals number.

This set of plesiomorphic and apomorphic characters present in *Scombroclupea*, which are shared with clupeiforms and ellimichthyiforms, make the genus position within the clupeomorphs difficult to establish based on the phylogenetic proposals currently valid. *S. javieri* (and other *Scombroclupea* spp.) join the group of Mexican species *Ranulfoichthys dorsonudum* and *Paraclupea sheilacheri*, whose interrelation within the clupeomorphs is controversial. Therefore, an exhaustive revision of morphological characters among Clupeomorpha members is necessary to continue with the work of Grande (1985), allowing to delimit more naturally the clusters under the superorder.

#### 4.1. Remarks: Genus *Scombroclupea*

The review of the members of *Scombroclupea* in this work, we propose that at least three structures need a thorough review. The first of these is the development of bercyiform foramen, a controversial structure not easily interpreted. This feature is observed in Heckel's material deposited in the Museum of Natural History of Paris (MNHN.F.HAK 465D and MNHN.F.HAK 454; Appendix figs. 11–14), and later in the review by Woodward (1901, Plate IV Fig. 1), the recognition of this character is evident in specimens of *S. macrophthalmia*. In the same way, in specimens of *S. occidentalis* deposited in the Museo de Paleontología de Múzquiz (MUZ), MUZ-480 (Appendix figs. 19–20), as well as in the material reported here from *Scombroclupea javieri* sp. nov. It emphasizes that the inability to access the *S. occidentalis* type material published by Giersch et al. (2011) (same that is in Germany without date of return), nevertheless in MUZ exists material with similar characteristics. Only in *S. diminuta* formally has not been observed.

The second structure to be revised is the ornamentation of the roof of the skull, which can be observed in material *S. occidentalis* of MUZ and in *S. javieri*, as well as in ellimichthyiforms. It is distinguished as shallow ridges that radiate from the midline in the ocular portion of the frontal. Likewise, in mesoparietal conditions of the skull it observed in material here reported (IHNFG-5297 and

IHNFG-5325) and probability in some specimens of *S. occidentalis* in MUZ; however, fragile nature of the bones difficult to observe such condition.

The last structures to consider are two postcranial elements. One of this is the dorsal fin, that never seen before the fin arrangement with two, until three, unbranched and unsegmented rays and until 15 branched and segmented rays. Comparing the soft rays of the dorsal fins in the other members of *Scombroclupea* there is no differentiation between the rays of the fin, all segmented and branched. The other structure is the neural spines of the thoracic anterior section, which are bifid and not fused together, as well as the neural arches are separated from the centrum. There are suspicions that in specimens of *S. macrophthalmia* (MNHN.F.1767) and *S. occidentalis* (MUZ 480) there is the presence of the postcranial characters mentioned here, they need a review for confirmation.

## 5. Conclusions

*Scombroclupea* is a clupeomorph genus at to have ventral scutes, who is a synapomorphy characters of the clade. *Scombroclupea javieri* sp. nov. is a member of the genus by having a lack of the dorsal scutes and the presence of two supramaxilla, the comb-like dentition in the maxilla, the horizontal laminae in the anterior caudal vertebrae, the flat epineurals and epipleural in caudal region of the trunk and the finlets present along the anal fin, last are interpreted as diagnostic characters of the taxa. Other hand, *S. javieri* differ to *S. diminuta*, *S. macrophthalmia* and *S. occidentalis* as new valid fourth species by the combination of primitive characters (middle condition of parietals) and derivatives (posterior portion anal fin with multiramified finlets, horizontal laminae in caudal vertebrae), distinguished by the dentary toothed, number of soft rays in all fins, 3 epural and 9 postpelvic scutes. This combination of characters provides two aspect: first, it make recognize how difficult it is to establish relationships between species and between genus and clupeomorph fish, since *Scombroclupea* shares defining characters between clupeiforms and ellimmichthyiforms. We recognize as an *incertae sedis* taxa based in morphological data. Second, it is essential to make a strong revision of the morphological characters infra superorder, with the intention of giving natural support to the interior of Clupeomorpha as well as defining the position of *Scombroclupea* in the clade. Some characters to review: beryciform foramen, ornamentation in frontal and middle parietal condition, neural spines not fused with each other and with thoracic vertebral centrum and dorsal scutes, among others.

*Scombroclupea javieri* sp. nov. is a new Mexican fossil fish and it is the second record of the genus found in America Continent. Excluded *S. occidentalis*, all the species of *Scombroclupea* are only known to the Cenomanian deposits, who inhabited the coastal regions in tropical latitudes in the Tethys Sea.

## CRedit authorship contribution statement

**Bruno Andrés Than-Marchese:** Conceptualization, Data curation, Formal analysis, Methodology, Investigation, Project administration, Resources, Validation, Visualization, Writing - original draft, Writing - review & editing. **Jesús Alvarado-Ortega:** Conceptualization, Formal analysis, Funding acquisition, Methodology, Investigation, Project administration, Resources, Supervision, Validation, Visualization, Writing - original draft, Writing - review & editing. **Wilfredo A. Matamoros:** Conceptualization, Investigation, Methodology, Supervision, Writing - original draft, Writing - review & editing. **Ernesto Velázquez-Velázquez:** Conceptualization, Funding acquisition, Resources, Writing - original draft, Writing - review & editing.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cretres.2020.104448>.