

# *Scombroclupea occidentalis* sp. nov. (Clupeiformes, Teleostei) from the Cenomanian (Cretaceous) Plattenkalk deposits of NE Mexico

Samuel Giersch · Eberhard Frey · Wolfgang Stinnesbeck ·  
Christina Ifrim · José Manuel Padilla Gutierrez

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**Abstract** A new species of the clupeid genus *Scombroclupea* is described from the Upper Cretaceous (Cenomanian) Plattenkalk locality “Loma la Mula” in Coahuila, northeastern Mexico. The material provides new osteological data for the genus, which clarify its systematic position. The Mexican *Scombroclupea* points to an occurrence of the genus in the western Tethys and indicates a vicariant event between *S. macrophthalma* from Lebanon and Croatia and the new species described herein. The analysis of the functional morphology of *Scombroclupea* supports the reconstruction of an oscillatory locomotion mode in this genus.

**Keywords** *Scombroclupea* · Western Tethys ·  
Upper Cretaceous · Northeastern Mexico ·  
Functional morphology

## Abbreviations

CPC State collection for Palaeontology of Coahuila,  
Museo del Desierto, Saltillo, Mexico

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S. Giersch (✉) · E. Frey  
Referat für Paläontologie und Evolutionsforschung, Staatliches  
Museum für Naturkunde, Erbprinzenstrasse 13, 76133  
Karlsruhe, Germany  
e-mail: samuel.giersch@smnk.de

W. Stinnesbeck · C. Ifrim  
Ruprecht-Karls-Universität, Institut für Geowissenschaften, Im  
Neuenheimer Feld 234, 69120 Heidelberg, Germany

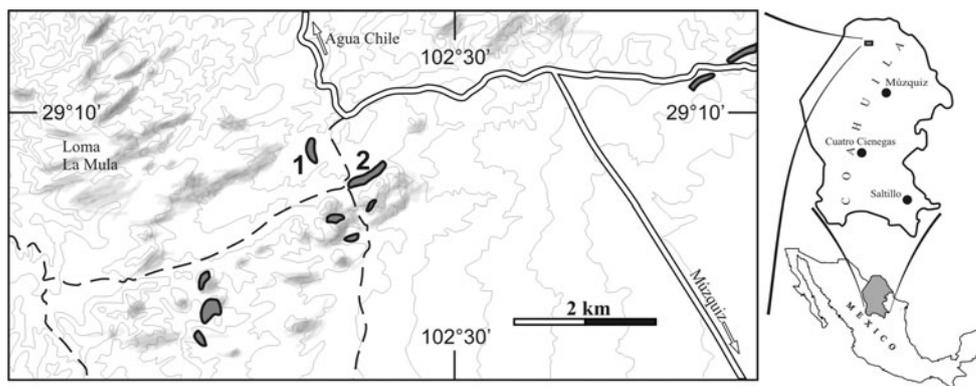
J. M. Padilla Gutierrez  
Museo del Desierto, Prol. Pérez Treviño 3745, Centro  
Metropolitano Parque Las Maravillas, 25015 Saltillo,  
COAH, Mexico

MB.f. Museum für Naturkunde, Berlin, Germany  
SMNK Staatliches Museum für Naturkunde, Karlsruhe,  
Germany  
SMNS Staatliches Museum für Naturkunde, Stuttgart,  
Germany

## Introduction, geological and stratigraphical setting

Fossiliferous Upper Cretaceous pelagic Plattenkalk deposits show a wide regional distribution throughout NE Mexico (Stinnesbeck et al. 2005; Ifrim et al. 2007). Most localities are located in the states of Nuevo León and Coahuila. In particular northern Coahuila is rich of small quarries, which produce laminated limestone with an exceptionally well-preserved fossil content. The fossils described herein were in part discovered by quarry men in a quarry field 170 km northwest of Múzquiz, but some also result from scientific excavations in the same locality on the eastern slope of the “Loma La Mula” mountain (Fig. 1). In this area, at least eight quarries unearth Upper Cretaceous sediments within an area of 20 km<sup>2</sup>. The quarried limestone ranges from Cenomanian to Coniacian ages. In this paper, we describe a new species of the fossil clupeomorph genus *Scombroclupea*. The holotype material of the new species *Scombroclupea occidentalis* sp. nov. was found in a small quarry at 29°09'43.7"N, 102°31'22.5"W (Fig. 1-1). Isolated fish-scales are abundant in the sediments exposed in this locality. However, only a few articulated remains of fishes were found. Ammonites and inoceramids are associated with the fish remains, pointing to a hemipelagic palaeoenvironment. The large size of the inoceramids (shell height up to 200 mm), their shape and the type of ornamentation closely associate the

**Fig. 1** Map of the “Loma La Mula” quarry field within Coahuila, NE Mexico. Dark grey areas display Plattenkalk quarries. 1 and 2 Cenomanian localities that yield *Scombroclupea occidentalis* sp. nov.



specimens with *Inoceramus pictus*, although a precise assignation to species or subspecies level is not possible at present. There are acanthoceratid ammonites present throughout the approximately 2 m high section. Near the base of the section schloenbachiids, baculitids, and turrilitid ammonites, likely *Mariella (Wintonia) bosquensis* (ADKINS 1920) (Kennedy et al. 2005) among them, are present in limestone concretions. According to this invertebrate assemblage, we preliminarily assign a Middle to Late Cenomanian age to the layers of origin of *Scombroclupea occidentalis* sp. nov. described herein.

## Materials and methods

The material of *Scombroclupea occidentalis* sp. nov. is housed in the State collection for Palaeontology of Coahuila in the Museo del Desierto, Saltillo, Mexico. The material, which has been examined for this paper comprises seven specimens: CPC-433a, b, CPC-434, CPC-436, CPC-439, CPC-441, CPC-443 and CPC-444. The comparative material of the type species, *Scombroclupea macrophthalma*, belongs to the following institutions and comprises the following specimens: Staatliches Museum für Naturkunde in Karlsruhe: SMNK-PAL. 6593/1, SMNK-PAL. 6593/2; Staatliches Museum für Naturkunde in Stuttgart: SMNS 12500 and Museum für Naturkunde in Berlin: MB.f. 16169, MB.f. 16172, MB.f. 16173, MB.f. 16174, MB.f. 16179, MB.f. 16182, MB.f. 16183, MB.f. 16184, MB.f. 16186, MB.f. 16189, MB.f. 16190, MB.f. 16191, MB.f. 16194.

Because of the high fragility of skeletons, only CPC-434 was transferred to epoxy resin. All specimens were cleaned with scalpel and steel needles under a binocular microscope (Leica MS5). Drawings and digital photos were made by the corresponding author using a camera lucida and a digital camera Canon EOS 350D. The anatomical nomenclature follows Grande (1985) and Rojo (1991). We dissected caudal parts of recent *Clupea harengus* and *Scomber scombrus* to study the structure and function of body parts, which are responsible for propulsion. A

comparison of these structures with accordant structures in *Scombroclupea* was used for a reconstruction of the locomotion type for this fossil fish.

## Systematic palaeontology

Infraclass	Teleostei MÜLLER 1845 (sensu ARRATIA 1999)
Subcohort	Clupei WILEY & JOHNSON 2010
Order	Clupeiformes GOODRICH 1909
Suborder	Clupeoidei BLEEKER 1859
Superfamily	Clupeoidea (sensu GRANDE 1985)
Family	<i>Incertae sedis</i>
Genus	<i>Scombroclupea</i> KNER 1863

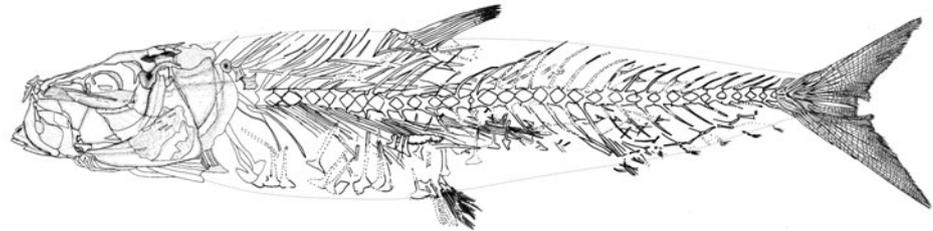
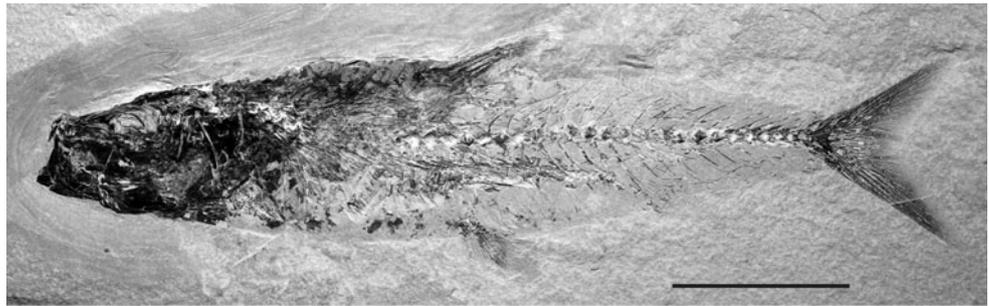
**Remark** The genus *Scombroclupea* includes the type species *S. macrophthalma* and *S. dimiuta* (Forey et al. 2003). The emended diagnosis for the genus mentions edentulous jaws (Forey et al. 2003, p. 283). The re-examination of the type species, *S. macrophthalma*, and the study of the species described herein shows that both species bear a comb-like dentition with minute teeth on the posterior half of the margin of the maxilla (Fig. 6). This confirms the former diagnosis given by Woodward (1901, p. 135), which mentions minute, or absent teeth. Therefore we provide the following generic diagnosis:

Emended diagnosis: clupeoid with two supramaxillae; minute teeth on caudal half of maxilla forming a comb-like dentition; absence of dorsal scutes; transverse processes of the anterior few caudal vertebrae forming horizontal laminae; epineural and epipleural intermusculars in caudal region flattened; anal fin divided posteriorly into series of anal finlets each of which formed by a multibranching fin ray.

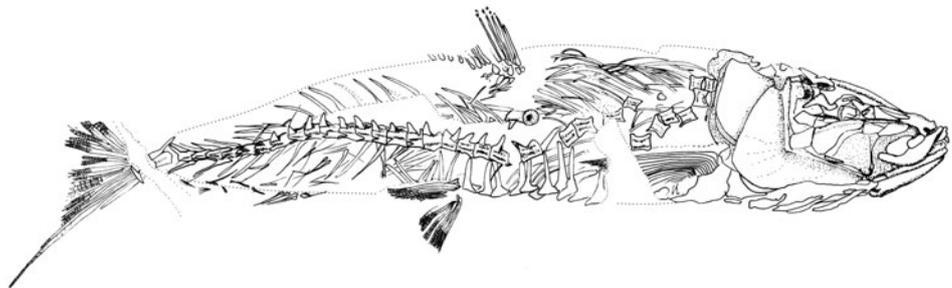
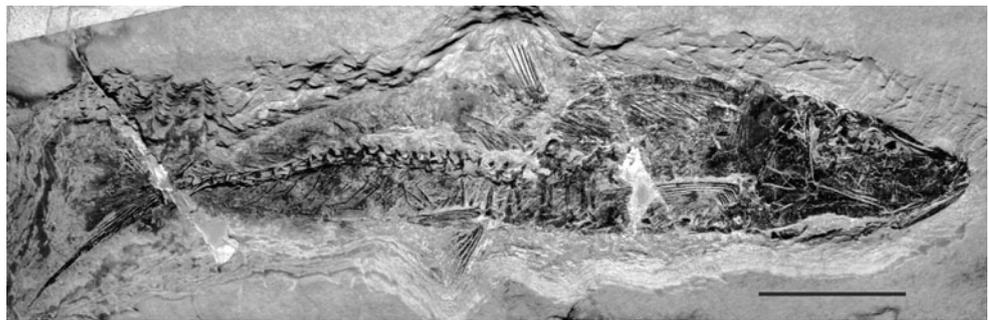
## *Scombroclupea occidentalis* sp. nov. (Figs. 2–11; Tables 1, 2)

**Diagnosis** Large *Scombroclupea* reaching 250 mm standard length (SL); vertebral column consists of 36 preural

**Fig. 2** *Scombroclupea occidentalis* sp. nov. (Cenomanian, Loma la Mula, Coahuila, NE Mexico), CPC-433 (Holotype), main slab. Scale bar 30 mm



**Fig. 3** *Scombroclupea occidentalis* sp. nov. (Cenomanian, Loma la Mula, Coahuila, NE Mexico), CPC-434. Scale bar 30 mm

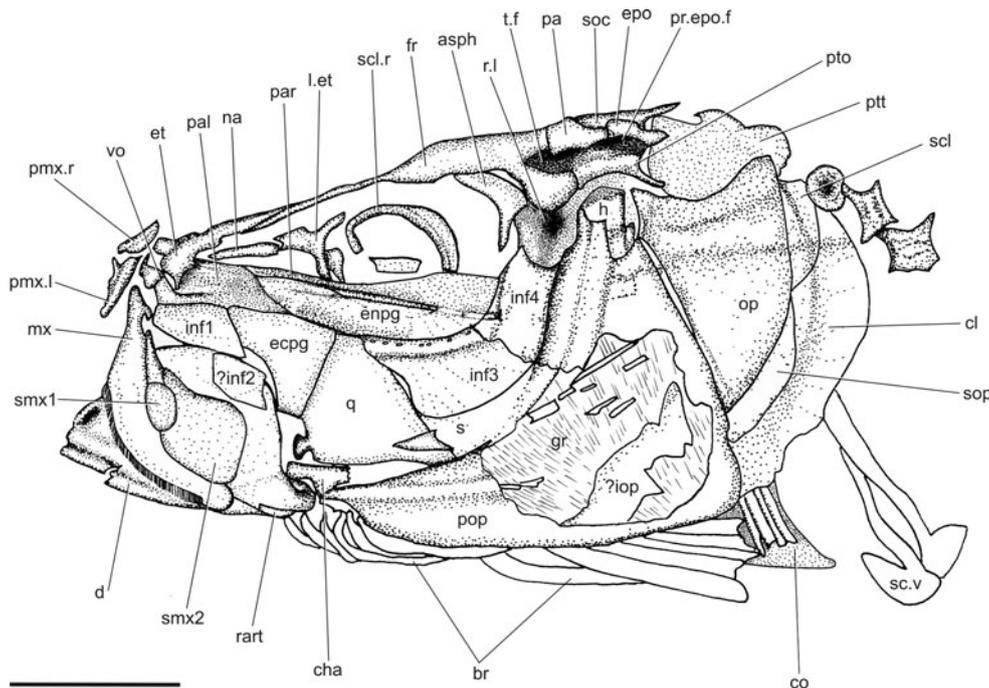


vertebrae, 16 are caudal; vertebrae 14–31 bear lanceolate horizontal laminae; mediolateral length of laminae is about the diameter of the vertebral centrum; 6–7 postpelvic scutes; caudal part of anal fin formed by 5 finlets; epural 1 reaches the dorsal margin of ural centrum 1; trailing-edge of caudal fin with two tuft-like lobes formed dorsally by the 7th lepidotrichium and ventrally by the 8th lepidotrichium.

*Types and material* Holotype: CPC-433a and CPC-433b (slab and counterslab), complete, subadult specimen of 150 mm SL, from Cenomanian deposits at Múzquiz, Coahuila, northeastern Mexico; CPC-434, CPC-436, CPC-439, CPC-441 (Paratypes), from Cenomanian deposits at Loma la Mula, Coahuila, northeastern Mexico.

*Etymology* *Occidentalis* is the Latin word for occidental, belonging to the occident. This refers to the western Tethysian occurrence of the species.

*Description* All specimens are preserved in lateral view. The description is based mainly on the holotype CPC-433a and also on paratype CPC-434. The holotype is almost completely articulated and is visible from its left side (Fig. 2). Only the mandible and the second infraorbital lost contact and shifted 5 mm ventrally. The bones of the nasal and occipital region are badly crushed. However, in most parts the skull is three-dimensionally preserved and allows the reconstruction of most of the skull bones. Ventral scutes are shifted dorsally and the caudal part of the dorsal



**Fig. 4** Skull anatomy of *Scombroclupea occidentalis* sp. nov., CPC-433 (Holotype). Camera lucida drawing in left lateral view. *ang* angular, *asph* autosphenotic, *br* branchiostegal rays, *cbr* ceratobranchials, *cha* anterior ceratohyal, *cl* cleithrum, *co* coracoid, *d* dentary, *ecpg* ectopterygoid, *enpg* entopterygoid, *epo* epiotic, *et* ethmoid, *fr* frontal, *gr* gill rakers, *h* hyomandibula, *?iop* interopercle, *inf*

infraorbital (numbered), *l.et* lateral ethmoid, *mx* maxilla, *na* nasal, *op* opercle, *pa* parietal, *pal* palatine, *par* parasphenoid, *pmx.l/r* left/right premaxilla, *pop* preopercle, *pr.epo.f* pre-epiotic fossa, *pto* pterotic, *ptt* post-temporal, *q* quadrate, *rart* retroarticular, *r.l* recessus lateralis, *s* symplectic, *scl* supraclithrum, *scl.r* sclerotal ring, *sc.v* ventral scutes, *smx* supramaxilla (numbered). Scale bar 10 mm

fin is disarticulated. CPC-434 is visible from its right side. Some abdominal vertebrae and ribs, as well as the posterior ventral scutes are disarticulated. The distal portions of the pectoral, the dorsal, and the caudal fin are lost (Fig. 3).

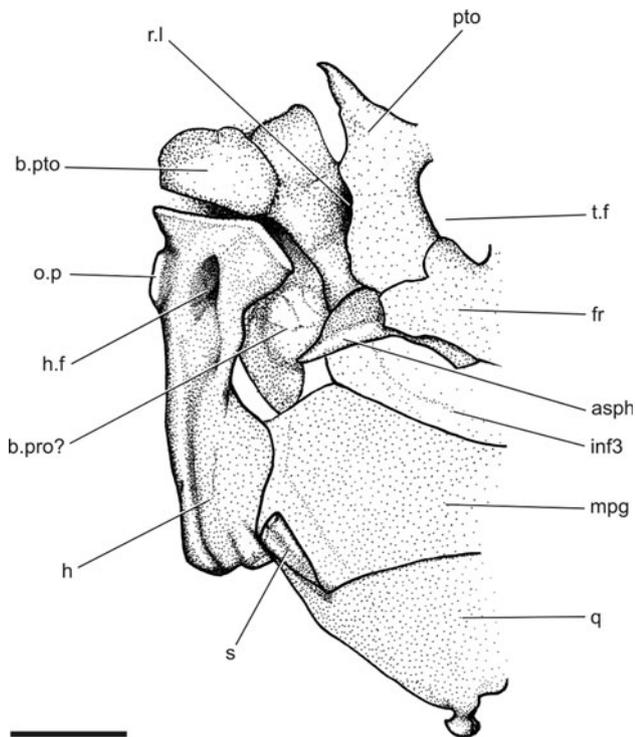
**Dimensions and proportions** The SL of six specimens varies between 145 and 250 mm. The average SL of this fusiform fish is about 200 mm. The skull occupies 28% of SL. The maximum depth of the body is one quarter of SL. The origin of the dorsal fin lays approximately level with the mid-SL. The pelvic fin originates ventral to the caudal half of the dorsal fin. The anal fin originates in the middle between the pelvic fin and the base of the caudal fin.

**Neurocranium** As in most clupeomorphs, the oticooccipital region is short in comparison with the orbital and ethmoid regions and it occupies 25% of the skull length (Fig. 4). The frontal is the largest bone in the skull roof. It runs from the middle of the nasal region up to the middle of the otical region. The frontal is a narrow bar dorsal to the orbit. It carries the anteroposteriorly running sulcus for the supraorbital sensory canal. The frontal broadens posteriorly and splits in lateral and medial parts anterior to the temporal foramen. The temporal foramen (Figs. 4, 5) is surrounded dorsally by the medial part of the frontal and by a short parietal, which measures approximately one-fifth of the frontal in length. The temporal foramen is floored by

the posterolateral portion of the frontal and by the pterotic. The pterotic ends posterolaterally in a spine, which occupies one-third of the total length of this bone. The ventrolateral portion of the pterotic is uniformly concave and borders the hyomandibular fossa laterally. Posterior to this margin, the bone surface of the pterotic shows an anterolateral inflation, which probably indicates the presence of a pterotic bulla (Fig. 5).

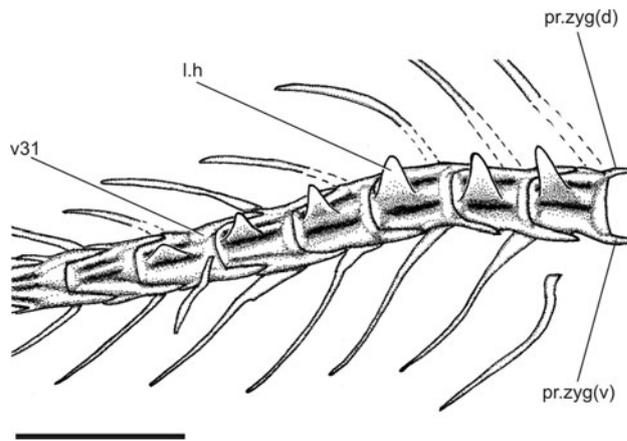
The posterolateral part of the braincase shows a pre-epiotic fossa, which is developed between pterotic, parietal and epiotic posterior to the temporal foramen. The pre-epiotic fossa is roofed by the posterior half of the parietal and the epiotic, which terminates posterior in a short attenuate process. The pterotic forms the ventral margin of the pre-epiotic fossa. The supraoccipital (Fig. 4) separates the parietals and meets anteriorly with the frontals. The supraoccipital does not project beyond the posterior profile of the braincase. The rest of the braincase remains unknown, being crushed or invisible in the available specimens.

The posterodorsal part of the orbit is roofed by a broad and hook-shaped sphenotic (Figs. 4, 5), which terminates laterally with an acuminate, ventrally directed process. The recessus lateralis opens between this process and the pterotic anterior to the dorsal tip of the preopercle.



**Fig. 5** *Scombroclupea occidentalis* sp. nov., CPC-443. Camera lucida drawing of details of the slightly disarticulated skull. *asph* autosphenotic, *b.pro* prootic bulla, *b.pto* pterotic bulla, *fr* frontal, *inf3* third infraorbital, *h* hyo-mandibula, *h.f* hyomandibular foramen, *mpg* metapterygoid, *o.p* opercular process, *pto* pterotic, *q* quadrate, *r.l* recessus lateralis, *s* symplectic. Scale bar 5 mm

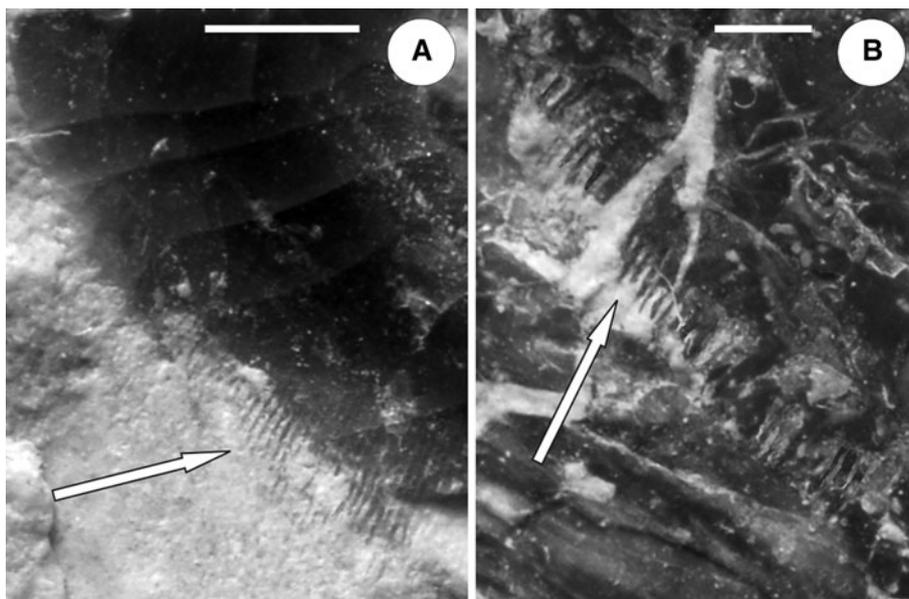
The anterior portion of the orbit is bordered by a short and slender lateral ethmoid (Fig. 4), which bears a laterally directed club-shaped process. The length of the lateral ethmoid is one quarter of the length of the frontal.

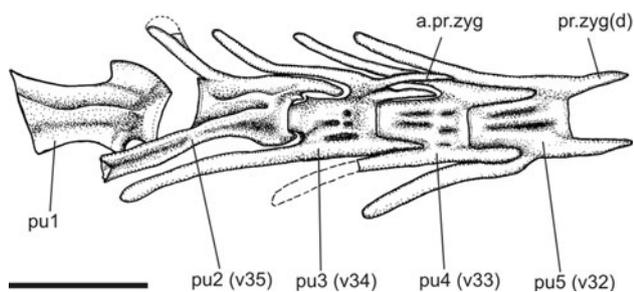


**Fig. 7** *Scombroclupea occidentalis* sp. nov., CPC-434. Camera lucida drawing of caudal vertebrae showing horizontal laminae and elongated prezygapophyses. *l.h* horizontal laminae, *pr.zyg(d)* dorsal prezygapophysis, *pr.zyg(v)* ventral prezygapophysis, *v31* 31st vertebra. Scale bar 10 mm

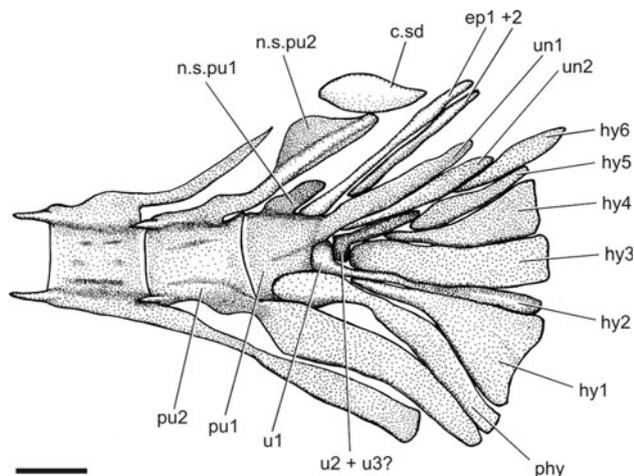
The anterior part of the skull roof is formed by the large ethmoid. The longitudinal dimension of this bone equals half of the length of the frontal. The ethmoid broadens anteriorly and its anterior third diverges into a lateral wing, which has a rounded rectangular outline. The ethmoid terminates anteriorly in an anterodorsally directed knob. The posterior half of the ethmoid is flanked by a rod-shaped nasal, which articulates posteriorly with the lateral ethmoid. Some specimens show part of the vomer that suggests that the bone is edentulous. The parasphenoid is a slender and edentulous rod-shaped bone. On CPC-439 the parasphenoid extends laterally into a pair of short and blunt basisphenoid processes posteriorly adjacent to the orbit. The surface of all skull bones is smooth.

**Fig. 6** Details of the oral margin of the maxilla in *Scombroclupea*. Arrows pointing on the comb-like dentition. **a** *Scombroclupea macrophthalmia* SMNK-PAL. 6539/2. **b** *Scombroclupea occidentalis* sp. nov. CPC-433 (Holotype). Scale bar 0.3 mm

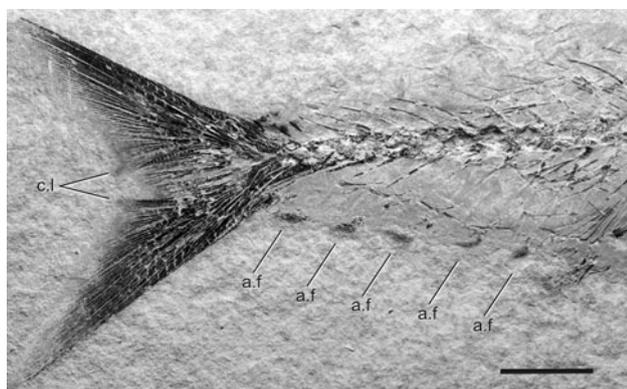




**Fig. 8** *Scombroclupea occidentalis* sp. nov., CPC-434. Camera lucida drawing of preural vertebrae showing accessory prezygapophyses. *a.pr.zyg* accessory prezygapophysis, *lh* horizontal laminae, *pr.zyg(d)* dorsal prezygapophysis, *pr.zyg(v)* ventral prezygapophysis, *pu* preural vertebra (numbered), *v* vertebra (numbered). Scale bar 5 mm



**Fig. 9** Caudal skeleton of *Scombroclupea occidentalis* sp. nov. CPC-433 (Holotype). *c.sd* dorsal caudal scute, *ep* epural, *hy* hypural (numbered), *n.s.pu* neural spine of preural centrum (numbered), *phy* parhypural, *pu* preural centrum (numbered), *u* ural centrum (numbered), *un* uroneural (numbered). Scale bar 2 mm



**Fig. 10** Details of anal and caudal fin of *Scombroclupea occidentalis* sp. nov. CPC-433b (counter slab of the Holotype). *a.f* anal finlet, *c.l* caudal lobe on the trailing edge of the caudal fin. Scale bar 10 mm

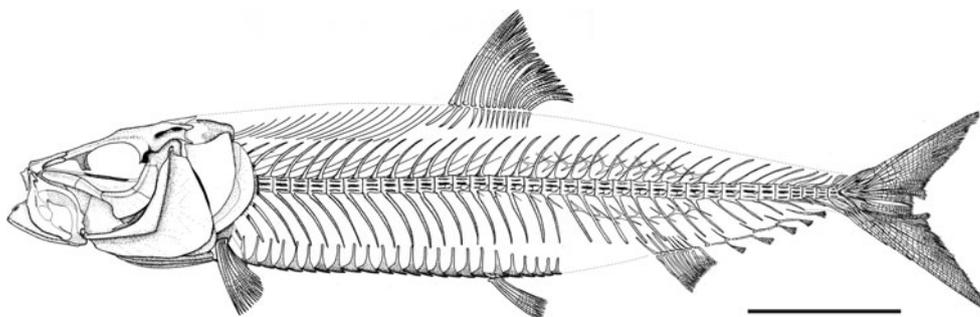
**Suspensorium** The hyomandibula (Fig. 5) has a narrow vertical shaft reinforced by a lateral ridge, which broadens dorsally and terminates into an articular head, which shows an anterior and a posterior articular facet. The anterior facet articulates onto the posteroventral face of the sphenotic, and the posterior one articulates within the ventral groove of the pterotic. Both articular facets merge at the middle of the bone at a blunt angle. Ventrally to the contact point, the hyomandibular head is pierced a hyomandibular foramen. The posterior margin of the bone bears a short rectangular opercular process in its dorsal quarter. The anteroventral portion of the hyomandibula shows a thin membranous wing, which meets with the metapterygoid and the symplectic. The hyomandibular shaft is slightly anteroventrally curved and terminates in a rounded articular surface for the interhyal. Ventral to the orbit, the large metapterygoid (Figs. 4, 5) is mostly camouflaged by the third infraorbital. Its slightly concave anterior margin meets with the quadrate. The outline of the quadrate (Fig. 4) resembles an equilateral triangle. The anteroventral edge is formed by the anteriorly pointing condyle of the mandibular joint. The ventral margin of the bone lies horizontally and ends posteriorly in the posterior process that margins the wedge-shaped symplectic groove ventrally (Fig. 5). The symplectic terminates anteriorly at the level of the centre of the orbit. The jaw articulation is located ventral to the lateral ethmoid. The anterior margin of the quadrate is straight and meets with the longitudinally elongate triangular ectopterygoid, which is slightly smaller than the quadrate. Parts of the small palate are visible ventral to the lateral wings of the ethmoid. The palate and the ethmoid are of equal length. The dorsal margins of the palate, the ectopterygoid, and the metapterygoid contact with the broad entopterygoid, which is twice as long as the palate.

**Jaws** The upper jaw consists of premaxilla, maxilla and two supramaxillae (Figs. 4, 6). The premaxilla is a wedge-shaped bone, which tapers ventrad. Its length equals one-third of the length of the maxilla. At the symphyseal suture between both premaxillae there is a small concave depression ventral to a knob-like process at the antero-dorsal corner of the bone.

The maxilla is a crescent-shaped blade of bone, which tapers anteriorly. At the symphysis, it bears a hooked ethmoid head pointing posterodorsad and a palatal head pointing anteriorly. The vertical anterior third of the oral margin of the maxilla is straight, edentulous, and matches the posterior margin of the premaxilla. The posterior portion of the oral margin bears a comb of approximately 100 min, rod-shaped teeth (Fig. 6b).

The teeth are parallel with each other and they are dorsoventrally orientated independently from the curvature of the ventral margin of the maxilla. There are two supramaxillae. The anterior supramaxilla shows an

**Fig. 11** *Scombroclupea occidentalis* sp. nov.  
Restoration of the skeleton in left lateral view based on the proportions shown in CPC-433 (Holotype). Scale bar 30 mm



**Table 1** Biometric parameters of *Scombroclupea occidentalis* sp. nov.

Number	TL (mm)	SL (mm)	HL (mm)	PD (mm)	PV (mm)	PA (mm)	TD (mm)	D.pt	D.f	A.pf	A.f	a.fin
CPC-433	180	145	43	74	82	115	36		13	12	15	5
CPC-434	245	205	58	108	124	168	42	13	13		15	5
CPC-439		(196)	(52)	(97)	(103)	(144)	40			12	15	5
CPC-436	(230)	(194)	(50)	(92)	(102)		40	14	14	11		5
CPC-441	(230)	(194)	(50)	(92)	(102)	(137)	39			12	15	5
CPC-444	(285)	240	65	128	139	178	56	14	14	12		5

Number	vert	c.v	ful.d/v	HL/SL	PD/SL	PV/SL	PA/SL	TD/SL	d.v	a.v	v.v	p.r	v.r	Prep	Postp
CPC-433	36	16	6/4	0.28	0.51	0.56	0.77	0.24	13	26	16	12	6	19	6
CPC-434	36		?/4	0.29	0.53	0.6	0.82	0.21	15	29	18	17	7		7
CPC-439	36	16		(0.27)	(0.5)	(0.53)	(0.73)	(0.20)	15	28	18	13	7		6
CPC-436	(36)	16	6/4	(0.26)	(0.47)	(0.53)		(0.2)				14	7		7
CPC-441	(35)	15		(0.26)	(0.47)	(0.53)	(0.71)	(0.2)				12	6	18	6
CPC-444	36	15		0.27	0.53	0.57	0.74	0.23	15	26	17		6	17	6

*TL* total length, *SL* standard length, *HL* skull length, *PD* predorsal length, *PV* preventral length, *PA* preanal length, *TD* maximum depth of body, *D.pt* number of dorsal pterygophores, *D.f* number of dorsal fin rays, *A.pf* number of anal pterygophores, *A.f* number of anal fin rays, *a.fin* number of anal finlets, *vert* number of preural vertebrae, *c.v* number of preural caudal vertebrae, *ful.d/v* number of dorsal and ventral procurrent caudal rays, *d.v* vertebral number above which dorsal fin originates, *a.v* vertebral number below which anal fin originates, *v.v* vertebral number below which pelvic fin originates, *p.r* number of pectoral fin rays, *v.r* number of pelvic fin rays, *prep* number of prepelvic scutes, *postp* number of postpelvic scutes

**Table 2** Comparison among characteristics of *Scombroclupea* species

	<i>Scombroclupea macrophthalma</i>	<i>Scombroclupea diminuta</i>	<i>Scombroclupea occidentalis</i> n. sp.
Number of vertebrae	39–42	39–40	35–36
Number of anal finlets	6	2–6	5
Number of postpelvic scutes	7–10	10–11	6–7
Pleural rib/preural vert. ratio	0.58	0.59	0.56
Posterior margin of caudal fin	Straight	Straight	Lobed
Neural spine of pu2	Distally broadened	Needle-shaped	Distally broadened
Maximum lateral extension of horizontal laminae	Reaches ¾ of vertebral diameter	Unknown	Equals vertebral diameter

asymmetrical ovoid outline and rests laterally on the anterior portion of the posterior supramaxilla dorsal to middle portion of the maxilla. The posterior supramaxilla is about three times larger than the anterior supramaxilla. Its anteriorly directed process is weak and runs along the

dorsal margin of the anterior supramaxilla. In the available specimens, the upper jaw covers much of the mandible so that details are not seen. The mandible shows a semicircular outline and is 1.6 times longer than high. The ventral margin of the dentary is straight. The sensory canal runs in

a deep ventrolateral sulcus. The sulcus terminates anteriorly in a concave notch adjacent to the anterolateral corner of the mandible. Dorsal to this notch the symphyseal margin shows an elliptic groove, which opens laterally. The posterior part of the ventral margin of the angular is flanked by a rod-like retroarticular. However, the articular process for the quadrate head is formed by angular only. The mandible is edentulous.

*Hyoid arch and gill arches* Most of these arches are covered by the opercular series. In CPC-433 the anterior part of the anterior ceratohyal is visible ventral to the quadrate (Fig. 4). The berycoid foramen seems to be absent. There are ten spatulate branchiostegal rays. The two anterior most are located anterior to the level of the mandibular joint. Parts of the gill arches are visible in the holotype: the ceratobranchials of the anterior most arch seems to be slightly more slender than the following ones.

*Opercular series* The preopercle is the largest bone of the entire fish. The crescent-shaped bone shows a horizontal limb 1.2 times longer than the vertical limb. The preopercular sensory canal passes through a narrow and deep sulcus, which runs along the anterior margin of the vertical limb and the dorsal margin of the horizontal limb. The opercle is a triangular plate being 1.8 times deeper than long. Its ventroposterior margin is gently rounded ventrally and straight posteriorly. The opercle shows a concave dorsal margin and a straight anterior margin. The opercle overlaps most of the subopercle and the interopercle is entirely covered by the preopercle.

*Infraorbitals* These bones are poorly preserved and partially dislocated in the available specimens. There are at least four infraorbitals. A probably existing fifth infraorbital remains unknown due to the poor preservation. The largest is the third one (Fig. 4), which shows a ventral wing. The S-shaped anterior margin of the wing continues into a gently rounded ventral margin. The orbital margin of third infraorbital is occupied by a slightly curved canal for the infraorbital sensory tube. The tube is pierced by a line of eight elliptic pores. The first and second infraorbitals are narrower than the third but equal in length. The first infraorbital terminates anteriorly at the level of the anterior end of the nasal.

*Girdles and paired fins* The pectoral girdle consists of the post temporal, ventrally followed by the supracleithrum, the cleithrum and the endoskeletal coracoid and possibly a scapula, but the latter is not definitively identifiable on the available material (Fig. 4). Several rod-like bony elements occur next to the supracleithrum, but their original shape and position remains unclear to identify them as postcleithra.

The post temporal is a fragile plate showing an ovoid outline. Its longitudinal diameter equals the width of the opercle. Supracleithrum and cleithrum form a narrow,

crescent-like and anteroventrally inflected arch of which the supracleithrum occupies the dorsal quarter. The coracoid is triangular in lateral view with a ventral margin parallel to the ventral body outline. The pectoral fin counts 12 lepidotrichia and articulates in ventral position. The longest lepidotrichium is as long as the length of seven vertebrae.

The pelvic fin originates ventral to the 17th vertebra and slightly posterior to the mid-length of the body and shows six lepidotrichia. Its length is half that of the pectoral fin. The basipterygium is minute and wedge-shaped and as long as two vertebrae.

*Vertebral column* The vertebral column consists of 36 vertebrae of which 16 are caudal. The centra are hourglass-shaped with three ridges on either side. The length of the centra is 1.2 times their diameter. From the 13th or 14th vertebra to the 31st vertebra, the centra bear laterally expanded ridges forming horizontal laminae (Fig. 7; see remark below). The lateral extension of these lanceolate laminae reaches its maximum size between the 16th and 25th vertebrae and equals the diameter of a vertebral centrum. Then, the lateral extension of the laminae continuously decreases caudally to the 25th vertebra. The dorsal and ventral prezygapophyses (Figs. 7, 8) are long and lie horizontally. Anteriorly, they reach the mid level of the preceding centrum, except on the two posteriormost centra, that show reduced prezygapophyses.

*Remark* A generic feature of *Scombroclupea* is the presence of lanceolate horizontal laminae, which originate from the lateral face of the precaudal centra. Similar structures, which are usually termed “transversal processes”, occur isolated within different orders of fossil and extant teleosts, e.g. in Elopiformes, Syngnathiformes and Aulopiformes (e.g. Springer 1957; Goody 1969; Chalifa 1989; Forey et al. 2003). According to Rojo (1991), in fish anatomy a transverse process is used synonymous to the parapophyse, which is articulated with the epipleurals. In a general sense of vertebral anatomy the term “transverse process” *sensu stricto* characterises a lateral protrusion of the roof of the neural arch (Baur 1886). Apparently the transverse processes in *Scombroclupea* neither are parapophyses nor match the latter definition. So we propose the term “laminae horizontales” referring to the horizontal orientation of these thin bony structures.

*Median fins* The dorsal fin originates dorsal to the 14th vertebra, which is approximately in the middle of the SL. The fin is formed of 15 fin rays and is slightly higher than long. The rays are supported by 13 pterygiophores. The first ray is the longest. The anal fin originates ventral to the 24th vertebra, and reaches the caudal fin. It shows 12 pterygiophores supporting 15 fin rays. The seven anteriormost pterygiophores stand close to each other between the haemal arches of the 24th and 26th vertebrae. The five

posteriormost pterygiophores consist of long proximal radials, which are widely spaced between 26th and the 32nd haemal arch. They support elongated middle radials, which are pointing caudally resulting in widely spaced successive fin rays. The distal radials are missing. They are either no distinct elements because of fusion with the middle radials or they are not preserved because they were cartilaginous. The associated finrays are multibranching at the insertion point and form five triangular finlets (Fig. 10).

**Caudal skeleton and fin** Three preural and two ural vertebrae support the caudal fin. The length of the three preural centra gradually decreases caudad, down to 80% of the average centrum length (Fig. 9). The distal half of the second preural neural spine extends anterodorsad into a semicircular wing. The first preural centrum bears a reduced preural neural arch and is fused with the first uroneural. The caudally following first ural centrum is small and its length equals one-third of the preural centrum length. It rests at the posteroventral edge of the first preural centrum and is medially fused with the latter (Schultze and Arratia 1989). Posteriorly, the first ural centrum is fused with a narrow, rod-like second hypural. Minute and probably fused second and third ural centra are visible. A second uroneural is located just ventral to the first uroneural. The triangular first hypural is the largest in the hypural series. Its proximal end fails to contact the first ural centrum. The rectangular third hypural is horizontally orientated and shows a weak interlobar notch on the distal third of its ventral margin. The fourth hypural shows an elongated triangular outline. Hypurals 5 and 6 are fusiform. Two rod-shaped epurals are located dorsal to the first uroneural. The proximal end of the first epural reaches the dorsal margin of the first preural centrum.

The caudal fin is composed of nine dorsal and ten ventral fin rays. Additionally the caudal fin shows six procurrent dorsal and four procurrent ventral rays. The two principal rays are unbranched. The trailing edge of the caudal fin shows two tuft-like lobes (Figs. 10, 11), which are formed dorsally by the 7th lepidotrich and ventrally by the 8th.

### Systematic discussion

The genus *Scombroclupea* was erected by Kner (1863) for the type species *S. macrophthalma* and was revised by Woodward (1901). Woodward (1901) included the species *S. gaudryi* (Pictet & Humert) and *S. scutata* WOODWARD 1908. However, *S. scutata* from the Lower Cretaceous of Brazil shows distinct morphological differences that separate it from *Scombroclupea* (Figueiredo 2005). Therefore already Woodward (1942) himself erected a new clupeomorph genus, *Scombroclupeoides*, for this species.

Moreover, *S. gaudryi* from the Cenomanian of Lebanon was excluded from *Scombroclupea* by Patterson (1967), who erected the new genus *Gaudryella* (Patterson 1970). The occurrence of a *Scombroclupea*, *S. murlii* in early Eocene deposits from India remains questionable, because diagnostic characters of the fragmentary material are neither described nor figured (Shani and Chowdhury 1971). According to Forey et al. (2003), the genus *Scombroclupea* includes the valid species *S. macrophthalma* and *S. diminuta*.

*Scombroclupea* is characterized by a maxilla that bears two supramaxillae and shows a comblike dentition on its caudal half. Additionally, the postcranium of the genus is characterized by transverse processes of the anterior few caudal vertebrae forming horizontal laminae and a series of flattened epineural and epipleural intermuscular bones in caudal region. However, the most distinct character in *Scombroclupea* is the anal fin that is divided posteriorly into series of finlets each of which formed by a multi-branched fin ray. Showing all these characters, the material from northeastern Mexico described herein unequivocally belongs to *Scombroclupea*.

However, in addition to the distinctly larger SL, the Mexican *Scombroclupea* shows a couple of morphological characters, which separate this material from the published species: the Mexican specimens show 35–36 preural vertebrae and therefore five vertebrae less than the average count of vertebrae in the type species. In *S. macrophthalma* and *S. diminuta* the number of vertebrae varies between 39 and 42. A comparable small variation in the number of vertebrae exists in extant clupeoids (Orton 1916; Ford 1941; Krajnović-Ozretić and Žikić 1978). Hence, we regard the smaller number of vertebrae as a diagnostic character of *S. occidentalis* sp. nov. Moreover, in the Mexican *Scombroclupea*, there are constantly five finlets in the caudal part of the anal fin. In contrast, *S. macrophthalma* and *S. diminuta* show six and two to six anal finlets, respectively. There is a difference in the lateral extension of the lanceolate horizontal laminae. The maximum lateral extension equals the diameter of a vertebral centrum in the Mexican material. In *S. macrophthalma* the maximum extension of laminae is shorter, reaching only three quarters of a vertebral diameter as is seen in MB.f. 16182. The existence of horizontal laminae remains unknown in *S. diminuta*. Additionally, the number of postpelvic scutes is reduced to six or seven in the Mexican species and the trailing edge of caudal fin bears two tuft-like lobes formed dorsally by the 7th lepidotrichium and ventrally by the 8th lepidotrichium. The accordant trailing edges in *S. macrophthalma* and *S. diminuta* are straight. Based on these differences (see also Tables 1, 2), we regard the Mexican *Scombroclupea* as a new species.

*Scombroclupea* is a common fish of Cenomanian localities (see below). However, its systematic position

within the subcohort Clupei remains uncertain due to the high fragility of the skeleton, which prevents the investigation of many details. Grande (1985) questioned an affinity with the suborder Clupeoidei, whereas Forey et al. (2003) argued for including *Scombroclupea* within the suborder Clupeoidei. The Mexican material supports an inclusion of *Scombroclupea* within the superfamily Clupeoidea based on diagnostic characters given by Grande (1985), Di Dario (2002) and Wiley and Johnson (2010):

Subcohort Clupei: Abdominal scutes are present. The second hypural is fused with the first ural centrum. The ventrolateral surface of the pterotic shows a convex portion, which probably represents an ossified pterotic bulla also mentioned by Forey et al. (2003).

Order Clupeiformes: A recessus lateralis is present. The parietals are separated by the supraoccipital. A beryciform foramen in the anterior ceratohyal is probably absent.

Suborder Clupeoidei: The braincase shows a temporal foramen and a preepiotic fossa. The first uroneural is fused with the first preural centrum. The size of the first ural centrum is distinctly reduced compared to the size of the first preural centrum. The parhypural remains separated from the first preural centrum.

Superfamily Clupeoidea: The ratio of pleural ribs to preural vertebrae (approximately 0.58) is within the range given for Clupeoidea (0.47–0.71) by Grande (1985). Additionally, *Scombroclupea* shows an interzygapophysal articulation formed by elongate and horizontally orientated neural and hemal prezygapophyses. This character occurs only within Clupeoidea, Engrauloidea and *Chirocentrus* (Di Dario 2002). *Scombroclupea* does not show any other diagnostic characters of neither engrauloidea nor *Chirocentrus* is therefore assigned to the Clupeoidea.

The only diagnostic character of Clupeidae mentioned by Grande (1985) is the presence of two rod like postcleithra. This character remains unclear in *Scombroclupea* due to the poor preservation. Hence we place *Scombroclupea* as Clupeoidea *incertae sedis*. The relationship of *Scombroclupea* to one of the extant clupeid subfamilies still remains uncertain and is discussed in detail by Forey et al. (2003).

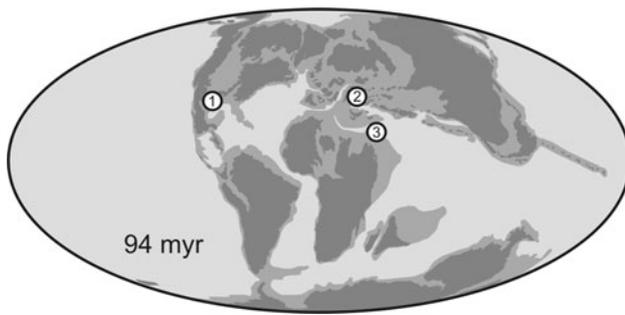
## Functional morphology

Body shape and arrangement of the fins in *Scombroclupea* are strikingly similar to those of extant Clupeidae (Figs. 2, 3, 11). Thus, in analogy to those, an axial carangiform locomotion mode could be assumed for *Scombroclupea* as is seen e.g. in *Clupea harengus*. In carangiform swimming teleosts the thrust generating part of the body is restricted to the caudal third including the caudal fin (Reif 1981). *Scombroclupea* shows features in this body region, which

are unique within Clupeiformes and demonstrate that *Scombroclupea* could have been able to produce a modified carangiform swimming style, probably even a thunniform. This locomotion style is seen in swimmers that can swim permanently at high velocity and is found among Teleostei within Scombridae (e.g. *Scomber*, *Thunnus*). In thunniform swimmers, the thrust is mainly generated by the lateral movement of the tail peduncle and the semi-lunar tail fin. A scombrid construction is characterised by the following features aligned with the style of locomotion: (a) Stiff caudal third of the vertebral column; (b) Trunk converges into a slim tail peduncle (“narrow necking”); (c) Caudal fin shows a large lateral mobility against the tail peduncle; (d) Vertical finlets along the tail peduncle. *Scombroclupea* shows similar characteristics:

(a) Stiff caudal third of the vertebral column. Pre- and postzygapophyses of the vertebrae of Clupeoidea und Engrauloidea are orientated horizontally. The prezygapophyses are prolonged onto the cranially adjacent vertebra to articulate with the stubby postzygapophyses (Di Dario 2002). In *Scombroclupea* the prezygapophyses are long and reach cranial until half of the length of the cranial adjacent vertebra (see Figs. 7, 8). This interdigitation mechanically reduced the lateral excursion of the vertebral column of *Scombroclupea*. Elongated prezygapophyses, which support stiffness, are present within recent Scombridae in the black scipjack *Euthynnus lineatus* and the frigate mackerel *Auxis thazard* (Firestine and Walters 1968). Additionally, Firestine and Walters (1968) described the presence of accessory prezygapophyses in some scombrids. This feature also seems to be present in *Scombroclupea* (Fig. 8). Furthermore, the lateral mobility was reduced by the laminae horizontalia on the caudal abdominal vertebrae of *Scombroclupea*. Such laminae are unknown from extant Clupei, but a comparable structure exists e.g. within Elopiformes: in *Megalops atlanticus* these laminae are connected with the epicentralia, which are embedded in the septum horizontale (Springer 1957). Position and orientation of the laminae in *Scombroclupea* suggest that they were also integrated in the septum horizontale. The bony laminae protruding laterally into the connective tissue certainly reinforced the caudal region of *Scombroclupea*. Extant Scombridae do not possess comparable horizontal laminae, but bear horizontally orientated rod-like epicentralia within the septum horizontale, which are rigidly fused with the lateral faces of the vertebrae by means of ligaments. These epicentralia are braced against each others with ligaments running diagonally inside the septum horizontale and thus cause the stiffness of the tail peduncle of the scombrid construction.

(b) Trunk converges into a slim tail peduncle. The slim tail peduncle as it occurs especially within Scombridae (Helfman et al. 1997), to a lesser extent is also present in



**Fig. 12** Palaeogeographical map of the Cenomanian showing the distribution of *Scombroclupea*. 1 *S. occidentalis* sp. nov., NE Mexico. 2 *S. macrophthalma*, Comen, Slovenia. 3 *S. macrophthalma*, and *S. diminuta*, Lebanon

*Scombroclupea*. In *Scombroclupea* the skeleton of the tail peduncle is morphologically very similar to that of scombrids. The neural spines caudal to vertebra 30 are inclined caudally about 30°–25° with respect to the long axis of the vertebral column. The hemal arches in *Scombroclupea* are inclined even more caudally and run almost parallel to the vertebral columns caudal to vertebra 33 (Fig. 11).

(c) Caudal fin shows a large lateral mobility against the tail peduncle. The concentration of the lateral axial undulation in the posterior end of the caudal peduncle and the caudal fin in the thunniform locomotion style requires a free mobility of the first preural and the ural centra (Firestone and Walters 1968). In *Scombroclupea*, the prezygapophyses of the second preural centrum are reduced and they are absent in the first preural centrum (Fig. 8). The lack of an interdigitation of these two vertebrae indicates a high mobility at the base of the caudal fin.

(d) Vertical finlets along the tail peduncle. The vertical finlets along the dorsal and ventral edge of the tail peduncle posterior to anal and second dorsal fin is one of the most distinct characters in Scombridae. Similarly *Scombroclupea* shows a row of five to six finlets along the ventral edge of the tail peduncle as is suggested by the genus name given by Kner (1863). In *Scombroclupea* the finlets are formed by distally branched lepidotrichia, which forms an obtuse triangle. In contrast, the finlets of extant *Scomber* are supported by five to six straight lepidotrichia, which are basally united at the insertion point of the finlets. Despite their anatomical differences, the outline of the finlets nearly coincides in both groups. Therefore, we assume a hydrodynamical role for the finlets in *Scombroclupea* similar to those in the extant *Scomber*. Many authors suggested that the finlets influence the swimming capacity of the Scombridae by reducing the drag by smoothening the wakes (e.g. Kramer 1960; Walters 1962; Reif 1981). The finlet effect on the circumfluction of the body was experimentally tested with *Scomber japonicus* by Nauen and Lauder (2000, 2001a, b). They demonstrated that

especially the caudal finlets deviate the wake caused by the horizontal circumfluction along the tail peduncle during the lateral oscillation of the caudal fin, and, thus, possibly increases the thrust generated by the caudal fin (Nauen and Lauder 2001a, b). Furthermore it was shown that the wake deviation induced by the finlets is more expressed along the ventral side of the tail peduncle than along its dorsal side (Nauen and Lauder 2001a). Interpreted in terms of the principle of optimal design within functional morphology (e.g. Dullemeijer and Barbel 1977), the occurrence of ventral finlets in *Scombroclupea* seems, thus, to be a consequent step in the development of this construction capable of swimming in a sub-oscillatory to oscillatory locomotion mode.

## Conclusions

The type species *Scombroclupea macrophthalma* KNER 1863 is known from Slovenia (Kner 1863; D'Erasmus 1946; Palci et al. 2008), and Lebanon (Woodward 1901; Forey et al. 2003), i.e. from marine deposits of the central and eastern Tethys. Additionally, *S. diminuta* FOREY, YI, PATTERSON, DAVIES 2003 occurs in the locality Namoura (Lebanon). The material described herein proves the occurrence of *Scombroclupea* within the western Tethys and thus the western Hemisphere (Fig. 12). The global and biostratigraphical distribution pattern of *Scombroclupea* is indicative of a vicariant event between *S. macrophthalma* in the central Tethys and *S. occidentalis* species in the western Tethys. This pattern supports an east–west vicariant event, which is probably a characteristic of Tethyan fish faunas throughout the mid-Cretaceous (Cavin 2008).

Within northeastern Mexico the new species occurs in “Loma la Mula”, northern Coahuila and also in a new Cenomanian locality at Cuatro Ciénegas in Central Coahuila (Fuchs et al. 2010). The distance of about 300 km between both areas suggests a wide regional distribution of this fish during the Cenomanian.

The occurrence of *Scombroclupea* is apparently restricted to Cenomanian deposits and therefore the genus probably represents a biostratigraphically useful index fossil for this Late Cretaceous stage.

The systematic analysis of the genus shows that *Scombroclupea* should be placed within the superfamily Clupeoidea. The construction of *Scombroclupea* suggests that this fish was likely capable for fast permanent locomotion with a sub-oscillatory to oscillatory locomotion mode.

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