

Morphology, relationships and palaeobiology of the Eocene barracudina †*Holosteus esocinus* (Aulopiformes: Paralepididae) from Monte Bolca, Italy

GIUSEPPE MARRAMÀ and GIORGIO CARNEVALE*

Dipartimento di Scienze della Terra, Università degli Studi di Torino, Via Valperga Caluso, 35 10125 Torino, Italy

Received 29 August 2016; revised 31 October 2016; accepted for publication 20 November 2016

The shallow water barracudina †*Holosteus esocinus* Agassiz, 1835, from the Eocene of Monte Bolca, Italy, is re-described in detail. This paralepidid taxon exhibits a unique combination of features, including the following: articular–quadrate joint located below the posterior margin of the orbit; eight branchiostegal rays; small recurved teeth on premaxilla; large, thin and pointed teeth on palate and lower jaw without corrugate pattern or serrate margin; about 19–22 anal–fin rays; about 10–12 pelvic–fin rays; five or six autogenous hypurals; proximal ends of the epaxial caudal–fin rays that extensively overlap the associated hypurals; bony fulcral scales just in front of the dorsal and ventral caudal–fin lobes; and body completely naked, with a broad, uniform, mid-dorsal brown-pigmented band along the back. †*Holosteus esocinus* shares a number of features with the Oligocene †*Pavlovichthys mariae*, and together they constitute the extinct subfamily †Holosteinae, which is redefined herein. A phylogenetic analysis of aulopiform genera using 140 morphological traits supports the monophyletic status of the holosteines as crown group Paralepididae. The peculiar morphology of holosteines resembles in many aspects the body plan of certain modern and extinct ambush predators, suggesting that the morphological adaptations of these Palaeogene fishes can be related, at least in part, to a predatory strategy experimented with by paralepidid fishes uniquely in the context of the massive adaptive radiation of teleost fishes in the aftermath of the end-Cretaceous extinction.

ADDITIONAL KEYWORDS: †Holosteinae – morphospace analysis – northern Italy – osteology – phylogeny.

INTRODUCTION

Fishes of the family Paralepididae, also known as barracudinas (see Fowler, 1936), form a well-defined monophyletic group within Aulopiformes, including about 60 extant species arranged in ten genera (e.g. Davis, 2010). Barracudinas include small- to large-sized (up to 1 m) meso- to bathypelagic predators with a worldwide distribution, from polar to tropical regions (Harry, 1953a; Rofen, 1966; Post, 1986; Thompson, 2003). Although barracudinas have scarce economic and commercial relevance (Thompson, 2003), they represent an important trophic resource for most marine top predators including tunas, swordfishes and whales (e.g. Rofen, 1966; Post, 1986; Young *et al.*, 2006). Extant paralepidids exhibit a distinctive morphology, characterized by the following: an elongated and slender

body, ovoid in cross section or laterally compressed; large, non-tubular eyes, located on the lateral sides of the head; snout very long and pointed and mouth terminal, with a projecting lower jaw; vertebral column with 60 to 121 vertebrae; short-based dorsal fin, usually set in the middle of the trunk; elongated anal fin, with 20–50 rays, its origin being located well behind that of the dorsal fin; presence of adipose fin; pectoral fins inserted low on body flanks, whereas the pelvics are small, originating behind the middle of body and containing 8–12 rays; absence of swim bladder (see Harry, 1953a, b; Rofen, 1966; Post, 1986; Thompson, 2003; Nelson, Grande & Wilson, 2016). Diagnostic osteological features of the family Paralepididae also include two posteriormost branchiostegal rays in close proximity to the corner of the posterior ceratohyal, anteriormost three branchiostegals close to each other on the indentation of the anterior ceratohyal, premaxillary fenestra, palatine with long process for

*Corresponding author. E-mail: giorgio.carnevale@unito.it

articulation with premaxilla and lachrymal anterior to orbit and horizontally oriented (Rofen, 1966; Baldwin & Johnson, 1996; Davis, 2010).

Although barracudinas are the best represented aulopiform family in the Cenozoic record, with the Eocene shallow water species †*Holosteus esocinus* Agassiz, 1835 from Monte Bolca (see Blot, 1980) and the Oligocene †*Holosteus' mariae* (Menner, 1948) from Caucasus and the Carpathians (Prokofiev, 2005; Prikryl, Kania & Krzemiński, 2016), as well as with Miocene and Pliocene species belonging to the extant genera *Lestidiops* and *Paralepis* (Sauvage, 1870; Arambourg, 1925, 1927; Harry, 1953a; Bedini, Francalacci & Landini, 1986; Sorbini, 1988; Carnevale, 2004; Gaudant, 2008), very little is known about the evolutionary history of this group. The Miocene †*Lestichthys porteusi* Jordan, 1921 and †*Trossulus exoletus* Jordan, 1921 from California, formerly referred to Paralepididae (e.g. Jordan, 1921), have been subsequently referred to Hemiramphidae and Euzaphlegidae respectively (David, 1943). The taxonomic position of †*Drimys defensor* Jordan, 1925 from the Miocene of California (Jordan & Gilbert, 1919; Jordan, 1925; Fierstine, Huddlestone & Takeuchi, 2012) is difficult to define, even if its overall morphology and meristic features (e.g. 45 vertebrae) concur to exclude any attribution to Paralepididae (see Ege, 1953, 1957; Harry, 1953a, b; Rofen, 1966; Post, 1987). Finally, the Miocene Mediterranean genus *Parascopelus* referred by Harry (1953a) to Paralepididae is currently regarded as a member of the family Bathysauropsidae (Carnevale, 2007). The divergence of the Paralepididae within Aulopiformes possibly occurred during the Late Cretaceous (Davis & Fielitz, 2010). Although several authors (e.g. Nolf, 1988; Patterson, 1993) have considered the otolith-based species †*Lestidiops ypresiensis* from the Ypresian of France as the oldest fossil paralepidid, articulated skeletal remains of †*Holosteus* have been reported in the latest Paleocene or basal Eocene marine deposits of Denmark (e.g. Bonde, 1997) and certainly represent the earliest confirmed occurrence of this family in the record. Although several specimens of †*H. esocinus* are available for study, very little is known about its anatomy and relationships, with negative implications for our knowledge of the early Cenozoic evolutionary history of barracudinas. The purpose of this article is, therefore, to redescribe in detail the Eocene barracudina †*H. esocinus* from the Eocene of Monte Bolca, Italy and to investigate its relationships and palaeobiology.

The Eocene (late Ypresian, c. 50 Ma; Papazzoni *et al.*, 2014) Konservat-Lagerstätte of Monte Bolca yielded a huge amount of exquisitely preserved fishes, which are housed today in several museums and research institutions around the world. The celebrated fossil fishes from Monte Bolca have been known since the 16th

century for their exquisite preservation and attractive appearance. In the last four centuries, the fish-bearing strata have been extensively exploited, resulting in the collection of about 100 000 specimens from the two main sites of Monte Bolca (Blot, 1969), the Pesciara and Monte Postale. As revealed by a recent taphonomic and quantitative palaeoecological study (Marramà *et al.*, 2016a), the fish-bearing strata of these two sites originated in palaeobiotopes characterized by different environmental conditions. To date, about 250 species (Carnevale *et al.*, 2014), mostly belonging to anguilliforms, atheriniforms, beryciforms, clupeiforms, lophiiforms, pleuronectiforms, tetraodontiforms and several other percomorph groups (e.g. Blot, 1969, 1978; Blot & Tyler, 1990; Tyler & Santini, 2002; Bannikov, 2004a, b, 2006, 2008; Monsch, 2006; Friedman, 2008; Carnevale & Pietsch, 2009, 2010, 2011, 2012; Bannikov & Carnevale, 2010; Marramà & Carnevale, 2015a, b, 2016), have been described from this Lagerstätte. The barracudina †*H. esocinus* is the only aulopiform known from this famous locality. The preservation quality of the examined specimens, as well as the lithology of the associated fossiliferous layers, concurs to suggest that the skeletal material belonging to †*H. esocinus* documented herein is derived from the excavations carried out at the Pesciara site.

MATERIAL AND METHODS

MORPHOLOGICAL EXAMINATION

The present study is based on five well-preserved specimens from the fossiliferous layers of the Pesciara site. The fossils are housed in the collections of the Museum National d'Histoire Naturelle, Paris (MNHN), Museo Civico di Storia Naturale, Verona (MCSNV), and Museo di Geologia e Paleontologia, Università degli Studi di Padova, Padova (MGUP). The material was examined using Wild M5A and Leica M80 stereomicroscopes equipped with camera lucida drawing arms. Measurements were taken using a dial calliper, to the nearest 0.1 mm. Some of the specimens were mechanically prepared using entomological needles in order to reveal fine skeletal details. Standard length (SL) is used throughout. The fineness ratio, a measure of axial elongation, is defined as the total length divided by the maximum depth of the body (Collar *et al.*, 2013). Osteological terminology mostly follows Harry (1953a, b), Rofen (1966) and Baldwin & Johnson (1996). Extinct taxa are marked with a dagger (†) preceding their name.

PHYLOGENETIC ANALYSIS

The phylogenetic analysis was based on the morphological data set of Davis (2010), which in turn is based on the matrices of Baldwin & Johnson (1996) and

Sato & Nakabo (2002). The data matrix contains all 139 characters of Davis (2010), to which we added a new state for Character 84 (number of caudal vertebrae) and a new character (140) in order to describe the main synapomorphy (posteriorly displaced dorsal and anal fins) separating the holosteines from all other aulopiformes (see Supporting Information). The matrix includes all taxa considered by Davis (2010), to which we added the two holosteines †*Holosteus* and †*Pavlovichthys*. The characters were imported into Mesquite 3.03 (Maddison & Maddison, 2008), and the data for the new taxa were added (see Supporting Information). The phylogenetic analysis was performed with TNT 1.5 (Goloboff, Farris & Nixon, 2008), using the heuristic search method. All the characters were considered unordered and given an equal weight. Tree length, consistency index (CI) and retention index (RI) were then calculated for the strict consensus tree and for each character individually (see also Supporting Information).

MORPHOSPACE ANALYSIS

The overall body physiognomy of †*Holosteus* is unique within paralepidids, closely resembling that of pike-like ambush predators. In order to quantify such a physiological similarity, we analysed the morphospace of paralepidids and compared it with that of selected pike-like ambush predators. For the morphospace analysis (Zelditch *et al.*, 2004), images of extant taxa obtained from the online picture repository of FishBase (<http://www.fishbase.org>; Froese & Pauly, 2015) were used. Fossil specimens were selected based on their completeness and degree of taphonomic distortion, in order to minimize preservational artefacts (see Pierce, Angielczyk & Rayfield, 2009). The data set of taxa examined for this study contains members of 17 genera, including all living and extinct paralepidids (including †*Holosteus*) and the five ambush predators considered in the study of Kogan *et al.* (2015), which exhibit a body aspect extremely similar to that of the Palaeogene paralepidids. A total of 15 homologous landmarks and eight equidistant semilandmarks describing the dorsal and ventral profile of the body were digitized using the software package TPSdig 2.05 (Rohlf, 2005) following the scheme applied in studies on the shape variation in modern or extinct fishes. The landmarks and semilandmarks allow us to capture the overall body shape and fin position, which are considered morphological traits directly related to swimming performances and predatory habits in several fish lineages (Webb, 1984; Lombardo & Tintori, 2005; Romano *et al.*, 2012; Maxwell & Wilson, 2013). The non-parametric multivariate analysis of variance (PERMANOVA; Anderson, 2001) and the analysis of similarities (ANOSIM; Clarke, 1993) were performed in order to assess significant

differences in morphospace occupation between groups. Statistical and relative warp (RW) analyses were performed, respectively, through the software packages PAST 3.08 (Hammer, Harper & Ryan, 2001) and TPSrelw (Rohlf, 2003). Detailed information about the generation of shape data, RW and statistical analyses used are provided in Marramà, Garbelli & Carnevale (2016b, c, d).

SYSTEMATIC PALAEOLOGY

ORDER AULOPIFORMES ROSEN, 1973

SUBORDER ALEPISAUROIDEI *SENSU* DAVIS, 2010

SUPERFAMILY ALEPISAUROIDEA *SENSU* DAVIS, 2010

FAMILY PARALEPIDIDAE BONAPARTE, 1835

SUBFAMILY †HOLOSTEINAE PROKOFIEV, 2005

Diagnosis (emended from Prokofiev, 2005): Large-sized paralepidids (most of the specimens reach about 60 cm SL) characterized by a rigid trunk with opposing dorsal and anal-fins posteriorly displaced on the posterior half of the body; dorsal-fin origin located on or slightly behind the vertical of the anal-fin origin; at least 18 dorsal-fin rays; high number of vertebrae (70–112); caudal vertebrae 25–40% of the total number; extended series of epineurals and epipleurals reaching the caudal region; body covered by small scales or totally naked; large and dorsoventrally symmetrical caudal fin; (apparent) absence of adipose fin.

Included genera: †*Holosteus* Agassiz, 1835, †*Pavlovichthys* Menner, 1948.

Remarks: The subfamily †*Holosteinae* was erected by Prokofiev (2005) based on putatively unique synapomorphies shared by †*H. esocinus* Agassiz, 1835, from the Eocene of Monte Bolca and †*'Holosteus' mariae* (Menner, 1948) from the lower Oligocene deposits of Caucasus (Russia) and Carpathians (Romania). According to Prokofiev (2005), these features include a lower jaw joint located in front of the level of the anterior margin of orbit, dorsal-fin origin located behind the anal-fin origin, about 70–100 vertebrae, at least ten branchiostegal rays, large fang-like teeth on the dentary and about 25 rays in both anal and pelvic fins. However, the lack of a comprehensive revision of the Eocene species from Monte Bolca prevented the recognition of the actual nature of their relationships. The exquisitely preserved specimens from the Eocene of Monte Bolca described herein are certainly related to the Oligocene taxon and clearly belong to the subfamily †*Holosteinae*, being characterized by a rigid trunk with both median fins displaced on the posterior half of the body, a dorsal fin with at least 18 rays

whose origin is located slightly behind the vertical of that of the anal fin and a high number of vertebrae (70–110). Three additional synapomorphies were also recognized, including caudal vertebrae of 25–40% of the total number, intermuscular bones extending posteriorly and reaching the caudal region and (apparent) absence of an adipose fin. A number of features, however, provide robust evidence of the separate generic status of the Eocene and Oligocene species (see below).

†*HOLOSTEUS* AGASSIZ, 1835

Type species: †*H. esocinus* Agassiz, 1835.

Diagnosis: Holosteine paralepidid with very elongated body and fineness ratio of 15.0–16.0; head is of about five to six times SL; upper jaw terminating below the ventral margin of the orbit; prominent, non-ossified and horizontally directed projection forming the anterior tip of the lower jaw; articular–quadrate joint located below the posterior margin of the orbit; eight branchiostegal rays; small recurved teeth on premaxilla; large, thin and pointed teeth on palate and lower jaw without corrugate pattern or serrate margins; epineurals and epipleurals extending throughout the vertebral column, being thicker and more ossified in the caudal region; most epineurals bifid or trifid proximally; 106–112 vertebrae of which about 30% are caudal; dorsal fin with 18–20 rays; about 19–22 anal-fin rays; about 10–12 pelvic-fin rays; caudal fin with 19–20 principal rays and about 10–12 dorsal and ventral procurrent rays; five or six autogenous hypurals, of which the first two appear to be partially fused; proximal ends of the epaxial caudal-fin rays that extensively overlap the associated hypurals; bony fulcral scales just in front of the upper and ventral caudal-fin lobes; body completely naked, with a broad, uniform, mid-dorsal brown-pigmented band along the back.

Remarks: †*Holosteus esocinus* was created by Agassiz (1835) based on a nearly complete specimen in the collection of the MNHN, Paris (F.Bol175). Recently, Prokofiev (2005) provided a re-examination of the lower Oligocene paralepidids from the Caucasus and Carpathians. Following the taxonomic interpretations of Daniltshenko (1960), Gorbach (1961) and Constantin (2001), Prokofiev (2005) assigned to the genus †*Holosteus*, the Oligocene barracudina species †*Pavlovichthys mariae* Menner, 1948, also providing a diagnosis of the genus. This Oligocene species differs from †*H. esocinus* by having the articular–quadrate joint located in front of the anterior margin of the orbit, large fang-like teeth with corrugate pattern on lower jaw, more than eight branchiostegal rays, first

and second hypurals not fused and anal and pelvic fins with about 25 rays. Our observations clearly indicate that the generic diagnosis provided by Prokofiev (2005) for the genus *Holosteus* must be restricted to the Oligocene taxon, which, as a consequence, should be referred to a separate genus (see above). The Oligocene species †*Holosteus mariae* is therefore re-assigned to the genus †*Pavlovichthys*, following the principle of priority of the International Commission on Zoological Nomenclature (ICZN, 1999). In his analysis, Prokofiev (2005) indicated the generic name †*Xiphopterus*, erected by Agassiz (1833–1844) for †*Esox falcatus* Volta, 1796, from the Eocene of Monte Bolca as a probable synonym of †*Holosteus*. The examination of the holotype of †*Xiphopterus falcatus* housed in the MNHN, Paris (F.Bol544) allows us to exclude such a hypothesis, considering that except for the similar elongated body, none of the diagnostic characters of the Paralepididae can be recognized in this fish.

Included species: Type species only.

†*HOLOSTEUS ESOCINUS* AGASSIZ, 1835
(FIGS 1–6)

†*Holosteus esocinus* Agassiz, 1835, p. 306; Agassiz, 1844: 85, pl. 43, fig. 5; Bronn, 1856: 683, pl. 52, fig. 8; de Zigno, 1874: 140; Woodward, 1901: 270; Eastman, 1904: 28; Eastman, 1905: 14–15; Leriche, 1906: 381; von Zittel, 1932: 464; Harry, 1953a: 244; Blot, 1980: 353.

†*Xiphopterus falcatus* (Volta, 1796): Frickhinger, 1991: 910; Caltran, Zorzini & Lazzarin, 1998: 81.

Holotype: MNHN F.Bol175, nearly complete articulated skeleton (Fig. 1A), 347.2 mm SL.

Referred material: MCSNV IG.23601 and IG.23602, nearly complete articulated skeleton, in part and counterpart (Fig. 1B, C), 499.4 mm SL; MGUP 11611/2, nearly complete articulated skeleton, in part and counterpart (Fig. 1D, E), 541.0 mm SL; MCSNV B5/T98, incomplete articulated specimen lacking of part of the abdominal and cranial regions, in part and counterpart (Fig. 2A, B); MCSNV VI.N41, partially complete articulated specimen (Fig. 2C), 644.1 mm SL.

Type locality and horizon: Monte Bolca locality, Pesciara site; early Eocene, late Ypresian, middle Cuisian, SBZ 11, *Alveolina dainelli* Zone (see Papazzoni *et al.*, 2014).

Diagnosis: As for the genus.

Description: Counts and measurements for †*H. esocinus* are provided in Tables 1 and 2. The body is

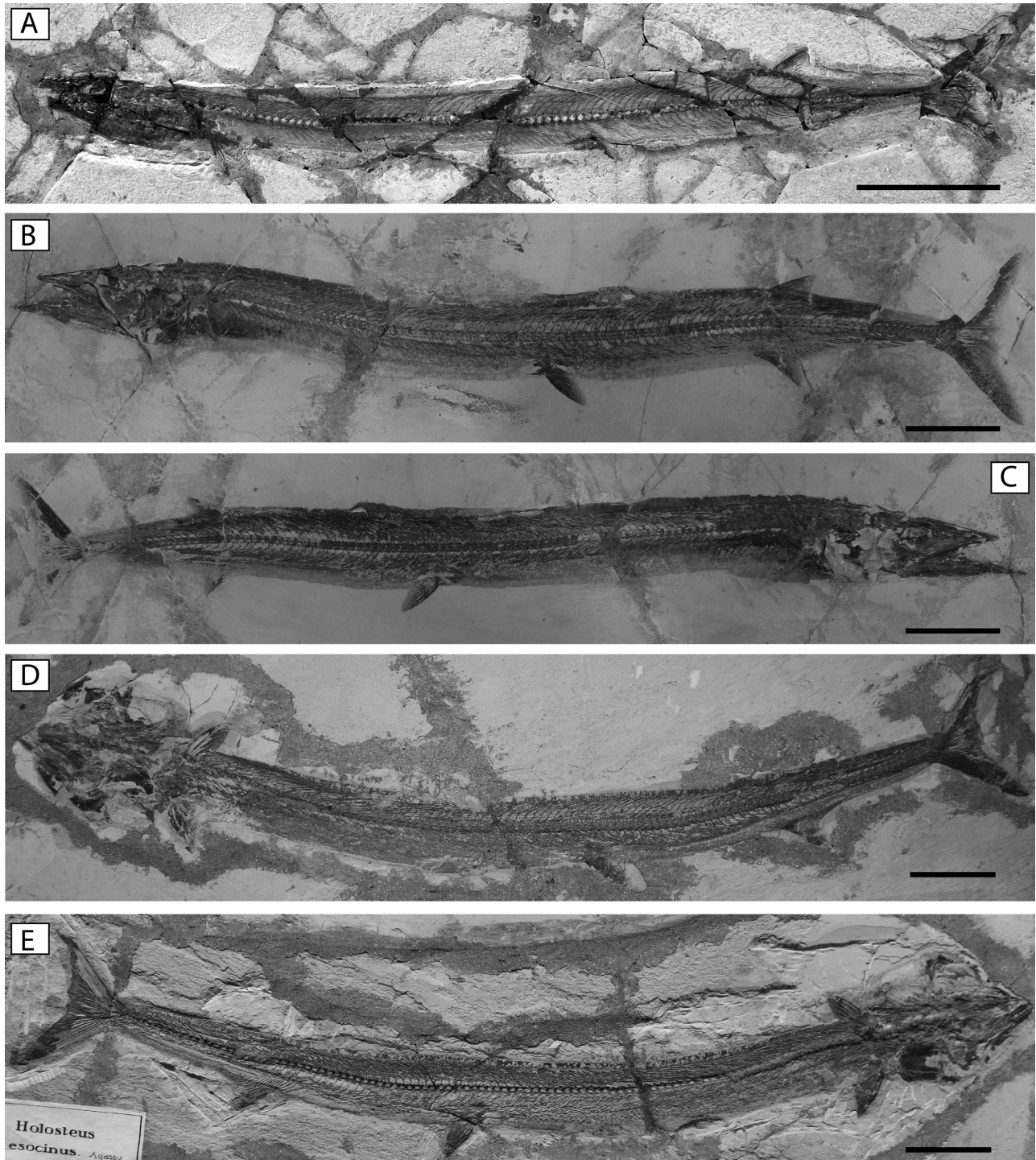


Figure 1. †*Holosteus esocinus* Agassiz, 1835 from the Eocene of Monte Bolca, Italy. (A) MNHN F.Bol175, holotype; (B, C) MCSNV IG.23601/2, part and counterpart; (D, E) MGPUP 11611/2, part and counterpart. Scale bars, 50 mm.

laterally compressed and considerably elongated and slender (Figs 1, 2); it is characterized by a remarkably high fineness ratio (15.0–16.0), which is lower only than that of the extremely elongated *Stemonosudis*.

The head is elongated and nearly triangular in lateral outline, and its length is contained between five to six times in SL. The snout is pointed and long, measuring c. 50% of the head length. The mouth is large, terminal,

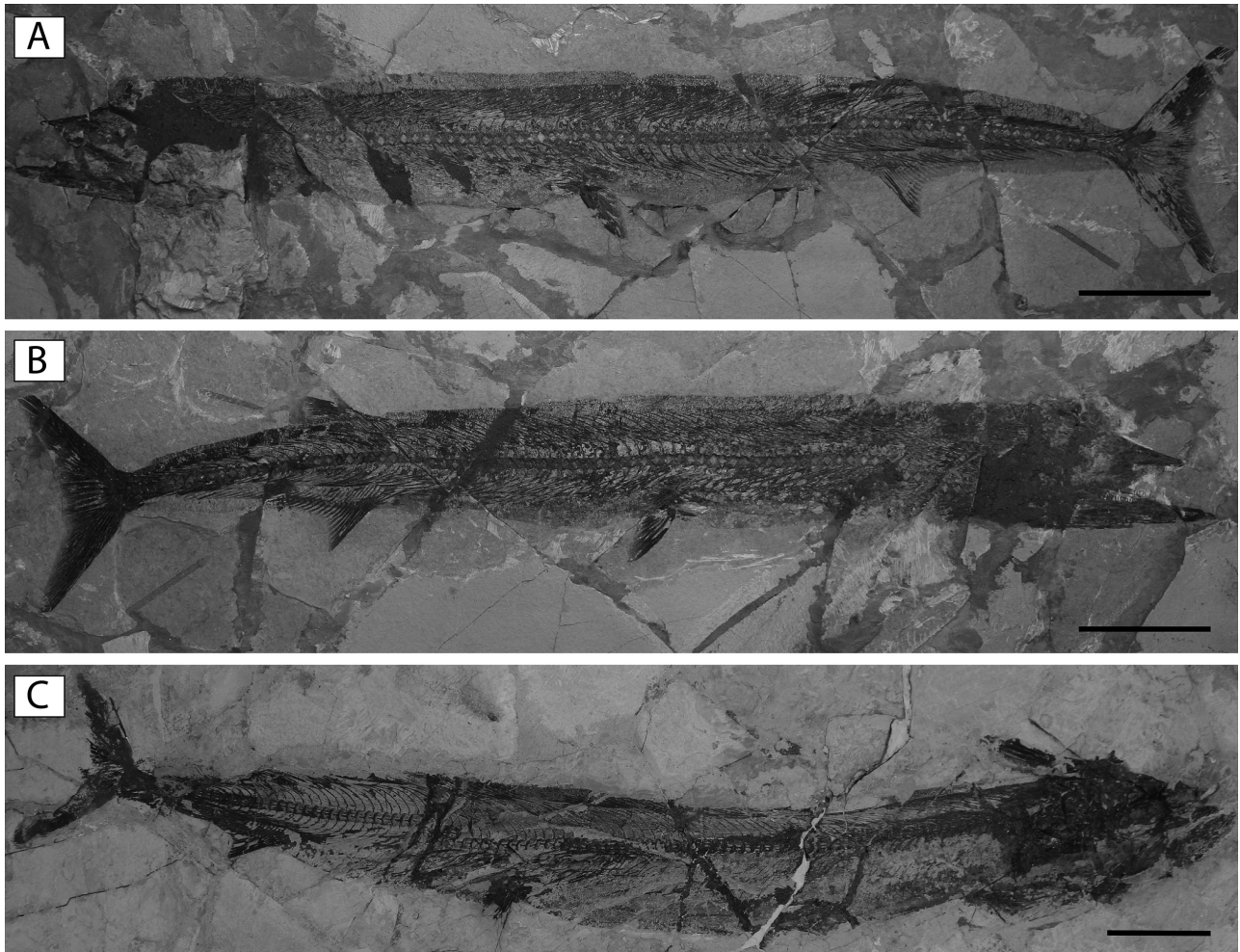


Figure 2. †*Holosteus esocinus* Agassiz, 1835, from the Eocene of Monte Bolca, Italy. (A, B) MCSNV B5/T98, part and counterpart; (C) MCSNV VI.N41. Scale bars, 50 mm.

with a lower jaw projecting well anteriorly to the tip of the upper jaw through a non-ossified prominent and horizontally directed pointed projection. Dorsal and anal fins are displaced to the posterior half of the body, opposite to each other; the dorsal-fin origin is located slightly behind the vertical through the anal-fin origin. The adipose fin appears to be absent. The caudal peduncle is narrow and short (about 9–12% SL). The caudal fin is large, symmetrical and forked, with a concave posterior margin. †*Holosteus esocinus* is totally naked; lateral-line scales seem to be also absent.

The description of the skeletal structures of the neurocranium is primarily based on the specimens MCSNV IG.23601/2 and MGPUP11611/2, in which this region is largely exposed and well preserved (Figs 3A, B, 4A, B), except for the otic region that is largely incomplete and difficult to interpret. The neurocranium is extremely elongated and nearly triangular in

outline. The paired frontals occupy about half of the skull roof length; each frontal articulates anteriorly with the mesethmoid, ventrally with the orbitosphenoid, anteroventrally with the lateral ethmoid, posteriorly with the parietal and posteroventrally with the pterosphenotic and the sphenotic. The parietals are irregular in shape. The supraoccipital forms the posteromedial end of the neurocranium. As in extant paralepidids (Rofen, 1966), the parietals are not fully separated by the supraoccipital (Fig. 4A, B). The sphenotic is subrectangular in outline, devoid of an anterior process. The orbitosphenoid and pterosphenoid form the dorsal and posterior walls of the orbit, respectively. The epioccipital occupies the dorsolateral part of the posterior surface of the neurocranium. The exoccipitals are badly crushed in all the examined specimens, and their morphology is not clearly recognizable. The parasphenoid is slender and almost

Table 1. Morphometric data (measurements as percentage of SL) of †*Holosteus esocinus* Agassiz, 1835, from the Eocene of Monte Bolca

Specimen	Standard length (in mm)	Total length	Maximum body depth	Head length	Head depth	Head fin base	Dorsal fin base	Anal fin base depth	Caudal peduncle length	Caudal peduncle depth	Prepectoral distance	Prepelvic distance	Predorsal distance	Preal distance	Preorbital length	Postorbital length	Orbit diameter
MNHN.FBOL175	347.2	107.2	5.9	18.4	6.9	4.5	?	2.1	?	19.2	61.0	80.6	?	5.6	8.2	1.6	
MCSNV IG.23601/2	499.4	107.0	7.0	18.0	7.8	5.8	7.8	3.2	10.4	19.2	57.7	80.9	79.7	7.0	7.6	2.4	
MCSNV VI.N41	644.1	106.1	7.9	19.6	9.6	4.2	5.2	2.8	9.3	?	63.3	85.9	84.6	?	?	?	
MGPUP 11611/2	541.0	108.3	6.7	15.7	?	4.4	6.7	3.0	11.8	16.8	56.2	78.9	78.2	?	?	?	

Note: Due to the inadequate preservation of the fossil, lacking most of the cranial and abdominal portions of the body, the data for the specimen MCSNV B5/T98 are not reported in the table.

Table 2. Summary of selected morphological features used to discriminate fossil and living genera of the family Paralepididae; includes new data and data from Harry (1953a, b), Rofen (1966), Uyeno, Matsuura & Fuji (1983), Baldwin & Johnson (1996), Fukui & Ozawa (2004), Ditty (2006); Fahay (2007), Froese & Pauly (2015). *Average values

Taxon	Fineness ratio	Abdominal vertebrae	Total vertebrae	Caudal/total vertebrae ratio*	Cleithral strut	Pectoral fin rays	Pelvic fin rays	Dorsal fin rays	Anal fin rays	Caudal fin rays	Epurals
<i>Arctozenus</i>	13.0	37–41	75–85	0.51	Absent	10–13	8–12	8–11	31–34	18–20	1
<i>Dolichosudis</i>	11.0	50	104	0.52	?	12	9	10	38	?	2
† <i>Holosteus</i>	15.5	75–78	106–112	0.30	Present	16–18	10–12	18–20	19–22	19–20	2
<i>Lestidiops</i>	12.0	30–51	75–85	0.49	Present	10–13	9	8–11	27–31	18–20	2
<i>Lestidium</i>	12.2	35–43	77–94	0.56	Present	11–13	9	9–12	27–49	18–20	2
<i>Lestrolepis</i>	15.3	28–34	91–98	0.67	Present	11	9	9–10	41–44	18–20	2
<i>Macroparalepis</i>	13.0	49–62	81–103	0.40	Absent	10–12	9	10–14	19–29	18–20	2
<i>Notolepis</i>	10.9	37–45	75–95	0.52	?	9–13	9	?	20–34	?	2
<i>Paralepis</i>	10.1	28–41	60–77	0.54	Absent	14–17	9	9–12	20–26	18–20	2
† <i>Paulovitchthys</i>	10.0	56	70–90	0.29	?	18–22	24–25	18	25	19	3
<i>Stemonosudis</i>	25.0	29–56	84–121	0.59	Present	10–13	8–9	8–11	31–50	18–20	2
<i>Uncisudis</i>	15.3	37–39	75–80	0.51	Present	11–13	9	9–11	28–31	18–20	2

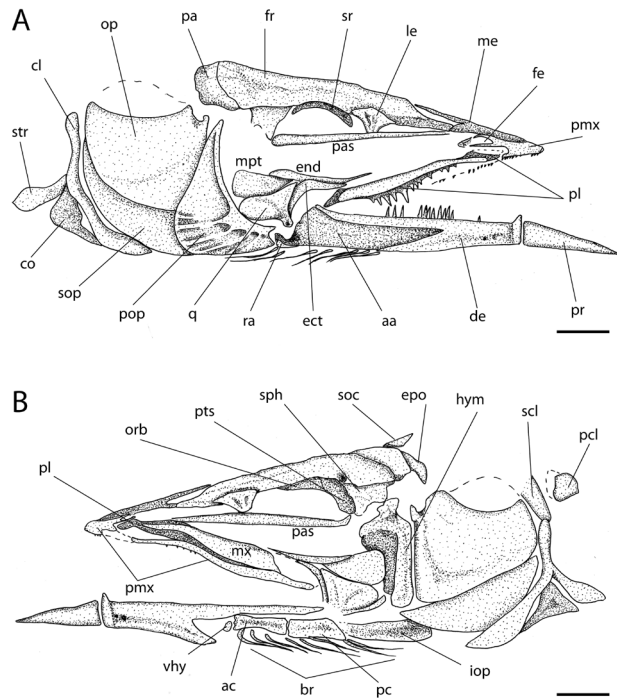


Figure 3. †*Holosteus esocinus* Agassiz, 1835. Reconstructions of the head based on the paratype. (A) MCSNV IG.23602; (B) MCSNV IG.23601. Scale bars, 10 mm. Abbreviations: aa, anguloarticular; ac, anterior ceratohyal; br, branchiostegal rays; cl, cleithrum; co, coracoid; de, dentary; ect, ectopterygoid; end, endopterygoid; epo, epioccipital; fe, premaxillary fenestra; fr, frontal; hym, hyomandibula; iop, interopercle; le, lateral ethmoid; me, mesethmoid; mpt, metapterygoid; mx, maxilla; op, opercle; orb, orbitosphenoid; pa, parietal; pas, parasphenoid; pc, posterior ceratohyal; pcl, postcleithrum; pl, palatine; pmx, premaxilla; pop, preopercle; pr, non-ossified projection of dentary; pts, pterosphenoid; q, quadrate; ra, retroarticular; scl, supracleithrum; soc, supraoccipital; sop, subopercle; sph, sphenotic; sr, sclerotic ring; str, cleithral strut; vhy, ventral hypohyal.

straight, extending for most of the basicranial length. The vomer is not clearly visible. The mesethmoid is thin and elongated; it extends posteriorly and partially overlies the anterior portion of the frontals. The lateral ethmoids are large and fan-shaped, with a broad dorsal portion.

The specimen MGPUP 11611/2 shows a complete and well-preserved infraorbital series (Fig. 4A, B) comprising eight elements. The lachrymal is very large and irregular in shape. As in extant paralepidids, this bone is located horizontally on the snout, anterior to the orbit, and extends along the upper border of the maxilla (see Baldwin & Johnson, 1996); it is ornamented with a few radial grooves along its dorsal margin. The second and third infraorbitals are small

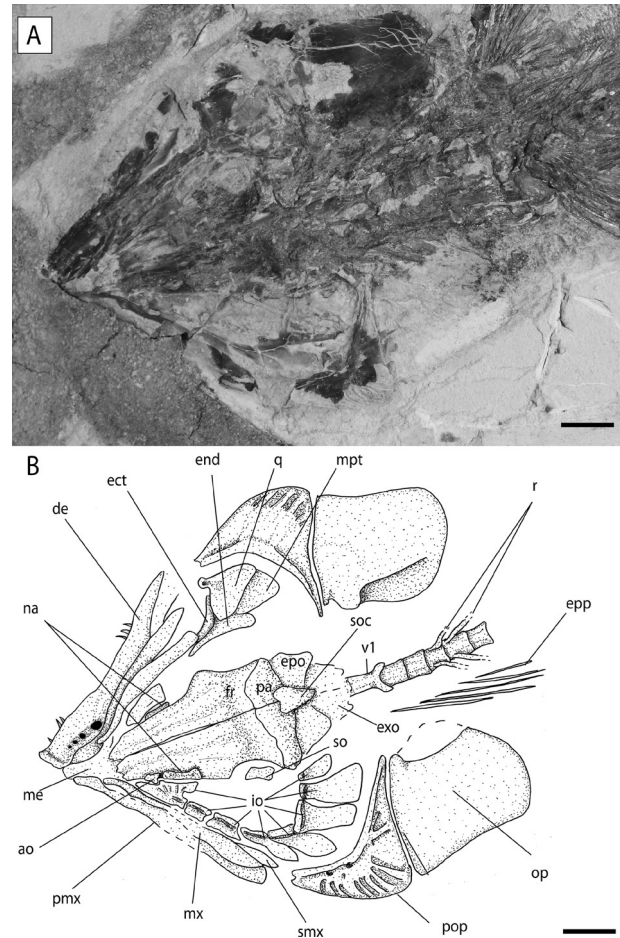


Figure 4. Detail (A) and reconstruction (B) of the head of †*Holosteus esocinus* Agassiz, 1835, based on the specimen MGPUP 11612. Scale bars, 10 mm. Abbreviations: ao, antorbital; de, dentary; ect, ectopterygoid; end, endopterygoid; epo, epiotic; epp, epipleurals; exo, exoccipital; fr, frontal; io, infraorbitals; me, mesethmoid; mpt, metapterygoid; mx, maxilla; na, nasal; op, opercle; pa, parietal; pmx, premaxilla; pop, preopercle; q, quadrate; r, ribs; smx, supramaxilla; so, supraorbital; soc, supraoccipital; v1, first vertebra.

and triangular. The posterior process of the posterior five infraorbitals is well developed with a lanceolate or subquadrangular outline. The antorbital is small, is irregular in shape and lies dorsal to the lachrymal. The nasal is subrectangular in outline and anteroposteriorly elongated. A unique subtrapezoid supraorbital is also recognizable in MGPUP 11611/2. The sclerotic ring is partially visible in MCSNV IG.23601/2 (Fig. 3A).

The premaxilla is elongated, not protractile and closely attached to the maxilla throughout its length, thereby excluding it from the mouth gape (Figs 3B, 4A, B). It has a moderately developed and posteriorly directed ascending process with a wide ovoid

premaxillary fenestra. Anteriorly, the premaxilla bears small and pointed retrorse teeth. The edentulous maxilla is thin, anteroposteriorly elongated, with a broad posterior margin. A single short supramaxilla closely associated with the posterodorsal margin of maxilla is well expanded in specimen MGPUP 1161/2 (Fig. 4A, B). The dentary is slender with a nearly straight dorsal margin; three to four foramina of the laterosensory system are visible in the anterior portion of the dentary (Fig. 4A, B). The lower jaw teeth are large, without a corrugate pattern or serrate margins. †*Holosteus esocinus* is characterized by a vertical, moderately developed symphysis, probably accommodated between the two contralateral premaxillae when the mouth was closed (see Harry, 1953a). Anterior to it, there is a long, non-ossified and horizontally directed extension, projecting well beyond the anterior tip of the upper jaw (Fig. 3A, B); a similar structure characterizes many derived alepisauroids (Harry, 1953a, b), although it is extremely elongated in †*H. esocinus* with its length being contained about five to six times in head length. The anguloarticular is robust, triangular in shape and penetrates the dentary for about the half of its length. The retroarticular is small and curved.

The palatine is robust and elongated; as in all the alepisauroid fishes, the palatine supports a remarkable series of well-developed pointed teeth (Fig. 3A); the palatine teeth are long, without serrations or corrugate pattern and increase in size posteriorly in the series. As in other paralepidids (see Baldwin & Johnson, 1996), the palatine terminates anteriorly with a long process articulating with the premaxilla. The quadrate is fan-shaped, with a slight concavity along the dorsal margin; the quadrate-articular joint is located just below the posterior margin of the orbit, in a position that significantly differs from that characteristic of the Oligocene †*P. mariae* in which this articulation lies anterior to the orbit (see Prokofiev, 2005). The symplectic is not clearly recognizable. The metapterygoid is subtriangular in shape, with rounded margins; it does not extend anteriorly as in synodontids (Baldwin & Johnson, 1996), and its posterior margin articulates with the hyomandibula. The ectopterygoid is slender and gently curved. The endopterygoid is anteroposteriorly elongated. There is no trace of pterygoid teeth. The hyomandibula is short, robust and oriented vertically; it bears two dorsal articular heads and a distinct opercular process emerging dorsally from its posterior margin.

The preopercle is large and crescent-shaped, with the vertical arm slightly longer than the ventral one; the corner formed by the junction of the two arms of the preopercle is ornamented with several radial striae. The opercle is the largest bone of the opercular series; it is subrectangular in outline, about 1.5 times

broader than deep, with a robust condyle for the articulation with the hyomandibula. The subopercle is long, with a rounded posterior margin. The interopercle is long and slender.

The hyoid apparatus is located just under the orbital region (Fig. 3A, B). The anterior ceratohyal is slender, is subrectangular in shape, constricted in the middle and characterized by an indented ventral margin. The posterior ceratohyal is about the same length as the anterior ceratohyal and robust. There are eight branchiostegal rays, four of which articulate with the anterior ceratohyal; the first three branchiostegals are closely associated with each other along the anterior side of the indentation. The posterior two branchiostegals associated with the posterior ceratohyal are very close to each other and insert on the posteroventral corner of the bone. The ventral hypohyal is small and subquadrangular in shape. The dorsal hypohyal as well as the gill arches are not recognizable in the available specimens.

The vertebral column consists of 106–112 vertebrae, of which 75–78 are abdominal and 31–34 are caudal; caudal vertebrae represent about 30% of the total number. The vertebral centra are subquadrangular, slightly higher than long. Pre- and postzygapophyses are weakly developed throughout the entire vertebral column. Neural and haemal spines of the posterior 25–28 caudal vertebrae are thick and robust with a proximal broad laminar expansion, especially on the posteriormost 10–12 caudal vertebrae. There are about 75 pairs of well-ossified pleural ribs, the first of which seems to originate on the fourth vertebra.

Intermuscular bones are well developed and extend from the abdominal to the caudal region. Epineurals originate laterally on the neural arches; it is unclear whether these are fused to the arches on the anterior vertebrae or not. The epineurals are forked proximally (most of them are bifid and in a few cases trifid; Fig. 5A) from vertebrae 12–15 to the end of the abdominal region, thereby resembling the condition of certain primitive ipnopoids and chlorophthalmoids (see Patterson & Johnson, 1995; Baldwin & Johnson, 1996); most of the branches of the forked epineurals appear to be autogenous, unattached to the axial skeleton. Epineurals are long and thin, reaching the dorsal margin of the body; those of the caudal region are more robust and thick. Like in extant paralepidids, epipleurals seem to originate on the first vertebra, and at least the two anterior are autogenous (Fig. 4A, B). †*Holosteus esocinus* shows an extended series of epipleurals associated with all the abdominal vertebrae and most of the caudal vertebrae, resembling the condition of *Paralepis* and *Arctozenus* (Baldwin & Johnson, 1996). The epipleurals of the abdominal region are thin and long, reaching the ventral margin of the body. All the epipleurals are attached to the axial skeleton

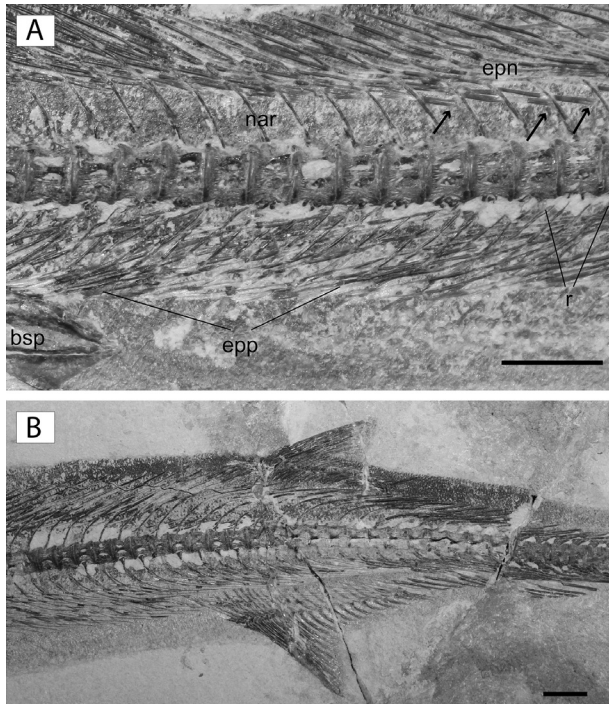


Figure 5. †*Holosteus esocinus* Agassiz, 1835. (A) Detail of the abdominal region of MCSNV IG.23602. Scale bar, 10 mm. Abbreviations: bsp, basipterygia; epn, epineurals; epp, epipleurals; nar, neural arches; r, ribs. The arrows indicate the proximal fork of some epineurals. (B) Detail of the caudal region of MCSNV IG.23601. Note the posterior displacement of the dorsal fin, whose origin is located just posteriorly to the anal fin insertion. Note also the thick and robust neural and haemal arches of the posteriormost caudal vertebrae.

and are not forked distally or proximally. As in extant paralepidids, there are no epicentrals in †*H. esocinus*.

The caudal skeleton is consistent with that of most extant paralepidids (Fig. 6A, B), although some unique features can be recognized. The first preural and first ural centra appear to be fused to each other. The second ural centrum is small and subtriangular in shape. There are six autogenous hypurals, of which the first and the second are fused into a single plate, resembling the condition observed in *Arctozenus* and *Lestrolepis* (see Fujita, 1990; Baldwin & Johnson, 1996). The autogenous parhypural is long and slender. Two autogenous uroneurals are recognizable, of which the anterior one is the largest. There are two thin and slender epurals. There are no urodermals. The caudal fin is large and externally symmetrical, with a nearly concave posterior margin; it contains 19–20 caudal-fin rays with segmentation beginning on the proximal half of each ray; the proximal portion of the principal caudal-fin rays is not modified in any way. The proximal ends of most of the caudal-fin rays of the upper

lobe extensively overlap the associated hypurals, resulting in a sort of epaxial hypurostegy (Fig. 6A, B). There are about 10–12 upper and 10–12 lower procurrent rays. There are two well-developed bony fulcral scales, nearly ovoid in shape located just in front of the upper and ventral caudal-fin lobes, resembling the condition characteristic of certain aulopoids and chlorophthalmoids (Sulak, 1977; Russell, 1999).

The number and morphology of supraneurals is unclear. The dorsal and anal fins are displaced to the posterior half of the body, just in front of the caudal-fin (Figs 1, 2, 5B). The dorsal-fin origin is located slightly behind that of the anal fin; the dorsal fin is triangular in shape and contains 18–20 distally segmented rays decreasing in size posteriorly. There is no trace of an adipose fin between the dorsal fin and caudal fin. The anal fin has a long base and contains 19–22 distally segmented rays; as in all alepisauroids, its outer margin is deeply indented anteriorly. Dorsal- and anal-fin rays are supported by a similar number of pterygiophores; the posterior pterygiophores of both the dorsal and anal fins do not appear to be fused or proximally modified.

The post-temporal is not recognizable in the available material. The supracleithrum is spatulate, laminar and subtriangular in shape. The cleithrum is crescent-shaped with a broad ventral arm. It bears a distinctive paddle-shaped projection (=cleithral strut of Baldwin & Johnson, 1996) along its posterior margin; the presence of such a projection typically characterizes the most derived paralepidids (Davis, 2010; Fig. 3A, B; Table 2). The number of postcleithra is unclear, but at least one is visible along the posterior margin of the supracleithrum; its position and size, as well as its subcircular shape, are reminiscent of the first postcleithrum of *Paralepis atlantica* and *Stenomosudis rothschildi* (see Rofen, 1966; Baldwin & Johnson, 1996). The coracoid is robust and large. The cleithrum–coracoid articulation is located near the anteroventral end of the cleithrum. At least three or four proximal radials can be recognized. The pectoral fin sits low on the body flanks and contains 16–18 rays, with their proximal portions (=spurs of Sato & Nakabo, 2002) being almost equal in size; the first pectoral-fin ray is the longest of the series. As in extant paralepidids, the pectoral-fin base seems to be horizontally oriented and inserts along the ventrolateral surface of the body.

The pelvic fins are abdominal and displaced slightly behind the mid-length of the body, well anterior to the dorsal fin origin. There are 10–12 pelvic-fin rays. The basipterygia are elongated, joined to each other medially and without any trace of posterior or lateral pelvic processes.

The body is totally naked without any evidence of body or lateral-line scales. Because of the lack of

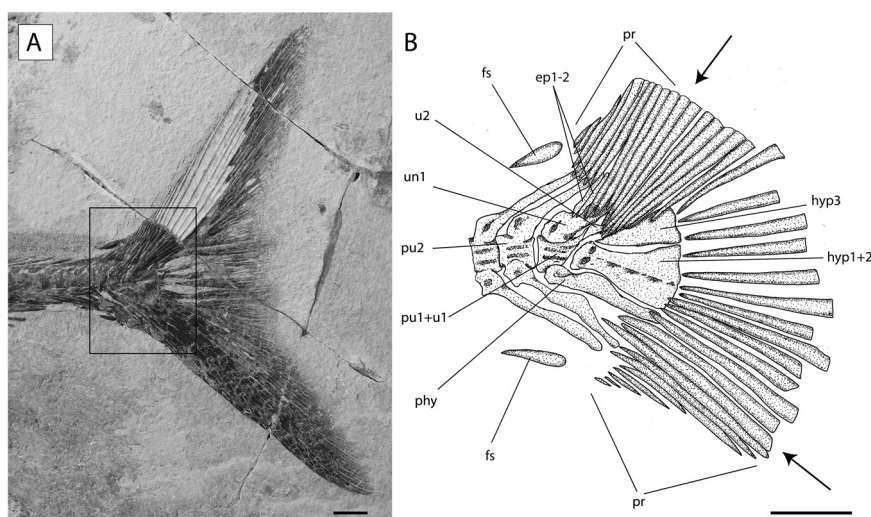


Figure 6. Caudal fin of †*Holosteus esocinus* Agassiz, 1835. (A) Detail of MCSNV IG.23601. (B) Reconstruction of the caudal skeleton, right side, lateral view. Scale bars, 10 mm. The arrows indicate the external dorsal and ventral principal caudal fin rays. Abbreviations: ep, epurals; fs, bony fulcral scale; hyp, hypural; phy, parhypural; pr, procurrent rays; pu, preural centrum; u, ural centrum; un, uroneural.

body squamation, the pigmented peritoneal membrane is clearly visible in well-preserved specimens (e.g. MCSNV IG.23601/2). †*Holosteus esocinus* has a broad, uniform, mid-dorsal brown-pigmented band along the dorsum, extending from the head to the caudal fin, similar to the body pigmentation pattern of the naked genera like *Lestidium* (Harry, 1953b). There is no evidence of pigmentation along the ventral surface of the body. There are no traces of preserved chromatophores.

DISCUSSION

COMPARATIVE REMARKS

The analysis of osteological, morphometric and meristic features of †*H. esocinus* has revealed the presence of several diagnostic characters of the superfamily Alepisauroidea, including four branchiostegal rays on anterior ceratohyal, absence of endopterygoid teeth, unmodified proximal portion of the principal caudal fin rays, palatine as the dominant tooth-bearing bone, pectoral fins inserting low on the body flanks and pelvic fins abdominal, articulation between cleithrum and coracoid near the anteroventral end of the cleithrum and margin of the anal fin deeply indented anteriorly (see Baldwin & Johnson, 1996; Davis, 2010). A number of features support the assignment to the family Paralepididae, including two posteriormost branchiostegal rays in close proximity on the posteroventral corner of the posterior ceratohyal, three anteriormost branchiostegals inserting close to each other along the anterior side of the indentation of the anterior

ceratohyal, snout length about 50% of the head length, premaxillary fenestra, palatine with long process for articulation with the premaxilla, eight infraorbitals with lachrymal horizontally oriented and placed anterior to the orbit, absence of epicentrals, epineurals originating on the neural arches and pelvic-fin origin anterior to the dorsal-fin origin (Baldwin & Johnson, 1996; Davis, 2010). Further characters considered as diagnostic of the paralepidids (Harry, 1953b; Rofen, 1966) and observed in †*H. esocinus* include, among the others, parietals not fully separated by the supraoccipital, long and pointed lower jaw with a well-developed symphysis articulating with an extremely elongated and non-ossified projection; premaxilla not protractile and well attached to maxilla; single supramaxilla; numerous and well-developed procurrent rays; and high vertebral number.

Although the osteological, morphometric and meristic features of †*H. esocinus* are consistent in providing support to the inclusion of this Eocene species within the family Paralepididae, the presence of a series of unique and unusual morphological traits can justify its assignment (together with the species of the Oligocene genus †*Pavlovichthys*) to the separate subfamily †Holoosteinae, including median fins posteriorly displaced, with the dorsal-fin origin slightly behind the anal-fin origin; caudal vertebrae about 30% of the total (modern paralepidids have 40–60% of caudal vertebrae; Baldwin & Johnson, 1996; Davis, 2010); high number of dorsal-fin rays (not less than 18); and (apparent) absence of adipose fin.

The phylogenetic relationships of extant paralepidids and other aulopiform fishes have been recently

investigated by Davis (2010) based on molecular and morphological characters, the latter derived from the data sets assembled by Baldwin & Johnson (1996) and subsequently implemented by Sato & Nakabo (2002). Based on these analyses, Davis (2010) recovered a monophyletic Paralepididae with the exclusion of the genus *Sudis*. The latter is currently regarded as the sole genus of the family Sudidae, representing the sister group of a large clade comprising the families Paralepididae (*Arctozenus*, *Dolichosudis*, *Lestidiops*, *Lestidium*, *Lestrolepis*, *Macroparalepis*, *Paralepis*, *Stemonosudis* and *Uncisudis*) and Alepisauridae (*Alepisaurus*, *Anotopterus*, *Magnisudis* and *Omosudis*). Davis (2010) recovered a monophyletic clade formed by *Macroparalepis*+ (*Paralepis* + *Arctozenus*), which share the following features: pelvic fins beneath or behind the vertical through the dorsal fin origin, most epipleurals with free dorsal branches, intermuscular bones on the five anterior abdominal vertebrae forked proximally and body and lateral-line tube-like scales present and well ossified. None of these characters has been observed in the specimens described herein. As discussed above, †*H. esocinus* clearly exhibits the presence of abdominal pelvic fins inserting well anterior to the dorsal-fin origin, epipleurals articulating to the centra, as well as the presence of a cleithral strut and absence of body scales, a condition shared with the paralepidids *Lestidiops*, *Lestidium*, *Lestrolepis*, *Stemonosudis* and *Uncisudis* (see Baldwin & Johnson, 1996; Davis, 2010). Therefore, these characters reveal the existence of a close affinity between these derived paralepidid genera and †*Holosteus*, which clearly differs from them in having an extended series of intermuscular bones, other than the previously discussed holosteine synapomorphies.

†*Holosteus* differs from all paralepidid genera in its unique combination of meristic features (see Table 2). It can be separated from *Arctozenus*, *Lestidiops*, *Lestidium*, *Lestrolepis*, *Notolepis*, *Paralepis*, *Uncisudis* and †*Pavlovichthys* for the higher number of vertebrae (106–112 vs. 45–98). Moreover, it can be easily separated from *Arctozenus*, *Macroparalepis* and *Paralepis* for the presence of the cleithral strut and differs from all extant paralepidids by the lower caudal/total vertebrae ratio (30% vs. 40–67%), higher fineness ratio (15.5 vs. 10.1–15.3; *Stemonosudis* is the only paralepidid genus with a higher fineness ratio, 25.0) and higher number of dorsal-fin rays (18–20 vs. 8–14). Additionally, the number of anal-fin rays is useful to separate †*Holosteus* (19–22) from *Arctozenus*, *Dolichosudis*, *Lestidiops*, *Lestidium*, *Lestrolepis*, *Stemonosudis* and *Uncisudis* (27–50). Finally, †*Holosteus* exhibits bony fulcral scales (exclusively present in certain members of the families Aulopidae and Synodontidae among Aulopiformes; Russell, 1999) and epineurals forked proximally in most of the abdominal

and caudal vertebrae, showing a condition similar to that observed in certain chlorophthalmoids (Patterson & Johnson, 1995; Baldwin & Johnson, 1996).

PHYLOGENETIC RELATIONSHIPS

The analysis of 140 morphological characters coded for 45 taxa (see Appendix) produced a single tree of length 463 steps with a moderately high CI (= 0.48) and high RI (= 0.76; Fig. 7). Since our analysis is exclusively based on morphological data, the tree is more consistent with the results of Baldwin & Johnson (1996) and Sato & Nakabo (2002), rather than with those of Davis (2010). The monophyly of Aulopiformes as recognized by Rosen (1973), Baldwin & Johnson (1996), Sato & Nakabo (2002) and Davis (2010) is confirmed, supported herein by five synapomorphies: presence of a second epibranchial with an enlarged uncinat process (ch. 1[1]); medial processes of the pelvic girdle joined medially by cartilage (ch. 103[1]); presence of adipose fin (ch. 130[0]); absence of swim bladder (ch. 133[1]); and single or multiple unpaired peritoneal pigment sections in larvae (ch. 137[1]). Three main clades can be recognized within the Aulopiformes: Synodontoidae (Paraulopidae, Aulopidae, Pseudotriconotidae and Synodontidae), Giganturoidei + Chlorophthalmoidei [*Bathysauroides*, *Bathysauridae* and *Giganturidae*]

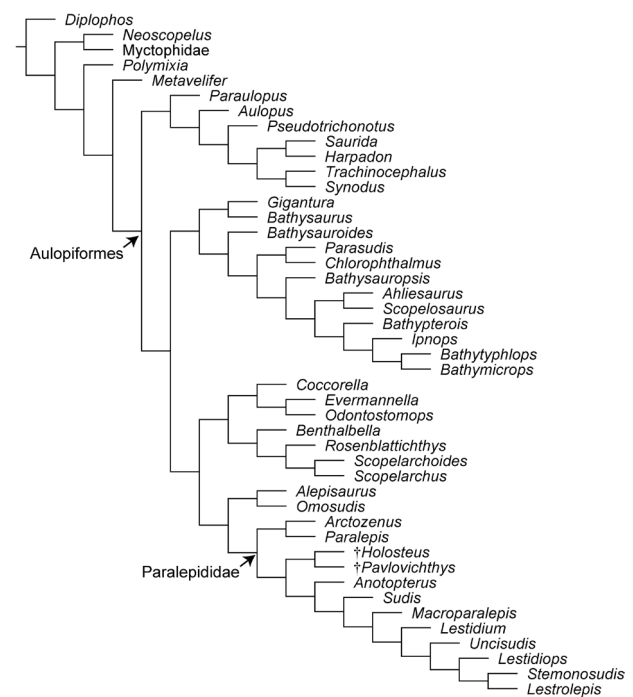


Figure 7. The single tree retrieved in TNT 1.5 based on 140 morphological characters and 45 taxa, showing the hypothetical relationships of †*Holosteus* and †*Pavlovichthys* within Aulopiformes.

+ (Chlorophthalmidae, *Bathysauropsis*, Notosudidae and Ipnopidae)] and Alepisauridae (Alepisauridae, Paralepididae, Evermannellidae and Scopelarchidae).

The relationships within paralepidids are consistent with those of Baldwin & Johnson (1996), and eight characters support their monophyly: first basibranchial usually elongated, comprising a short ossified anterior segment followed by a long posterior cartilage (ch. 24[2]); the two posteriormost branchiostegals close to each other, inserting along the posteroventral corner of the posterior ceratohyal (ch. 36[2]); snout length greater than 50% of head length (ch. 55[1]); presence of a premaxillary fenestra (ch. 56[1]); palatine with a long process for articulation with premaxilla (ch. 57[1]); cartilaginous facet of the palatine for articulation with lateral ethmoid located on the posterior portion of the palatine (ch. 59[1]); lachrymal anterior to the orbit and oriented horizontally (ch. 61[1]); and pelvic girdle with transverse keel separating the ventral surface of the medial process area (ch. 110[1]). In agreement with Baldwin & Johnson (1996), but contrary to the results of Davis (2010), our analysis places *Anotopterus* and *Sudis* within the Paralepididae since these genera share all the paralepidid synapomorphic characters. These two taxa also share with the most advanced paralepidids the absence of body and lateral-line scales (ch. 123[1]), epipleurals not extending posteriorly beyond the fifth abdominal vertebra (ch. 75[1]), and body transparent and glassy in life (ch. 125[1]). The phylogenetic placement of †*Holosteus* and †*Pavlovichthys* within the crown group Paralepididae is evident in our analysis. The monophyletic status of the †Holosteinae is supported by three characters: caudal vertebrae between 25 and 40% of the total number (ch. 84[3]); absence of adipose fin (apparently; ch. 130[1]); and dorsal fin posteriorly displaced, with dorsal-fin origin opposite to or slightly behind the anal-fin origin (ch. 140[1]). †*Holosteus* and †*Pavlovichthys* form a monophyletic clade representing the sister group of all the other Paralepididae, except for *Arctozenus* and *Paralepis*. The sister group relationship between holosteines and the most advanced paralepidids is supported by three synapomorphies, including: first rib originates on the fourth vertebra (ch. 88[1]), pelvic fins abdominal, inserting anterior to vertical through dorsal-fin (ch. 112[1]) and presence of a cleithral strut (ch. 114[1]).

MORPHOSPACE ANALYSIS AND PALAEOBIOLOGICAL NOTES

The RW analysis detected 16 RW axes, with the first four together accounting for about 92% of the overall variation. The morphological diversification across taxa can be examined through the analysis of the distribution of genera in the morphospaces defined

by the RW axes (Fig. 8). The first two RWs explain about 73% of the overall shape variance. The first axis describes the relative position of the dorsal-fin origin along the back as well as the size of the caudal fin. For example, negative scores of RW1 are related to genera with posterior displacement of the dorsal fin and a large caudal fin (e.g. †*Holosteus* and *Esox*), whereas taxa with the dorsal fin located at about mid-length of the body and small caudal fin lie on positive values (e.g. *Arctozenus* and *Uncisudis*). RW2 explains the variation of the location of the pelvic-fin insertion, so that negative scores are related to taxa with a posterior placement of the pelvic fins (e.g. *Arctozenus* and †*Pavlovichthys*), and genera having a more anterior pelvic fin origin (e.g. *Esox* and *Lestrolepis*) lie on positive scores. Along RW3, the main shape variation is related to the body elongation; negative values are exhibited by taxa with high body depth (e.g. *Ctenolucius* and *Esox*), whereas positive values are related to taxa with a very slender and elongated body (e.g. †*Holosteus* and *Stemonosudis*). RW4 explains the snout length and the caudal-fin shape; the most extreme negative values are occupied by very long-snouted fishes with a caudal fin with considerably convex posterior margin (e.g. *Lepisosteus*), whereas in the positive scores lie taxa with a comparatively short snout and a posteriorly concave or nearly forked tail (e.g. †*Holosteus* and *Esox*). The morphospace analysis detected two distinct groups that are significantly separated based on the dorsal fin position and relative size of the caudal fin along the first axis, in this case with the positive scores exclusively occupied by modern paralepidid fishes; the second group, which comprises †*Holosteus* and †*Pavlovichthys*, lies on negative scores of RW1 and solely includes long-bodied ambush predators, thereby suggesting that the general body plan of holosteine fishes mostly resembles the condition of ambush predators rather than that of living barracudinas. The quantitative morphospace occupation of holosteines is also supported by nonparametric tests PERMANOVA and ANOSIM (Table 3), both indicating that †*Holosteus* and †*Pavlovichthys* occupy a significantly different portion of the morphospace with respect to extant paralepidids ($P < 0.05$), in a position not significantly different from that of long-bodied ambush predators ($P > 0.05$).

As evidenced by the morphological and morphospace analyses (see Fig. 8), the overall physiognomy of the body of †*Holosteus* is unique within paralepidids, mimicking the typical condition of pike-like ambush predators, with a long and slender body, elongated skull, antorbital elongation of jaws, posteriorly displaced and opposite median fins, short and narrow caudal peduncle, large and symmetrical caudal fin and squamation reduced or absent (e.g. Tintori, 1990; Moyle & Cech, 2003; Romano *et al.*, 2012; Maxwell & Wilson,

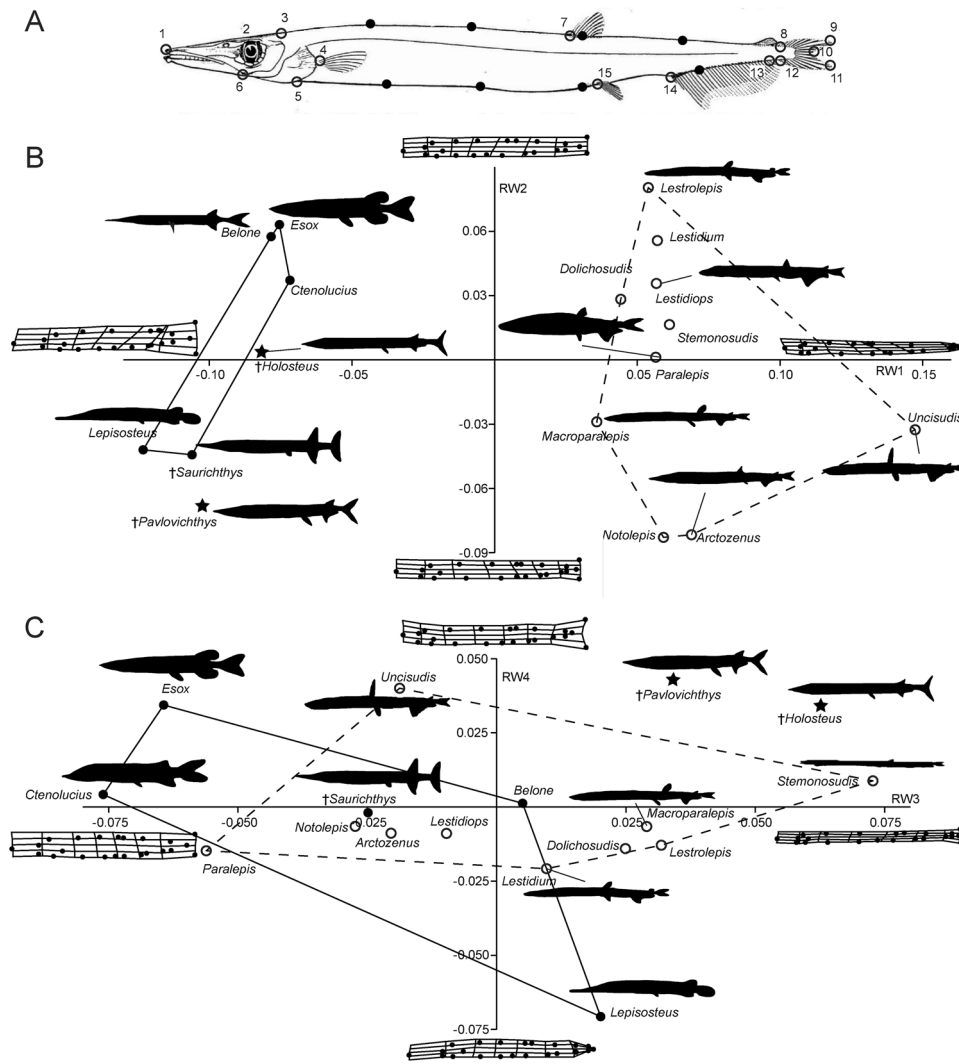


Figure 8. Morphospaces of selected taxa built on the first four RW axes explaining the greatest shape variance. (A) Landmarks and semilandmarks configuration used for the analysis of the body shape variation (*Notolepis* in the example; modified from Harry, 1953a). Semilandmarks are represented by full circles, landmarks by open circles with crescent numeration starting from snout: 1 – anterior tip of premaxilla; 2 – orbit centre; 3 – posterodorsal tip of the skull roof (supraoccipital); 4 – insertion of the first pectoral-fin ray; 5 – ventral tip of the pectoral girdle; 6 – lower jaw joint; 7 – anterior insertion of dorsal fin; 8 – dorsal insertion of the caudal fin; 9 – distal tip of the principal ray of the dorsal caudal-fin lobe; 10 – fork between dorsal and ventral lobes; 11 – distal tip of the principal ray of the ventral lobe of caudal fin; 12 – ventral insertion of the caudal fin; 13 – posterior insertion of the anal fin; 14 – anterior insertion of the anal fin; 15 – insertion of the pelvic fins. (B) Morphospace plotted on the first two RW axes explaining 72.6% of the overall shape variation. (C) Morphospace built on the third and fourth RW axes, together accounting for 19.6% of the variance. Deformation grid plots illustrate the shapes lying at extreme values along each axis, and the silhouettes represent some representatives of each group in the morphospace. Full circles enclosed by full polygons represent ambush predators, whereas open circles enclosed by dotted polygons represent living paralepidids. The stars mark the position of the two holosteines.

2013; Kogan *et al.*, 2015; Kogan & Romano, 2016). An additional diagnostic feature of the fast-start predator morphotype is related to the rigidity of the trunk, stiffened by long neural spines or zygapophyses (as in *†Saurichthys*; e.g. Tintori, 1990, 2013; Romano *et al.*, 2012), by strong squamation consisting of rhombic

ganoid scales (as in lepisosteids; Wiley, 1976) or, alternatively, by a robust series of intermuscular bones throughout the vertebral column, as in *†Holosteus* and *†Pavlovichthys*. Moreover, the ambush predator body plan is also characterized by stiffened fins, through unsegmented rays in ‘paleopterygian’ fishes (Schmid

Table 3. Nonparametric tests used to assess significant differences in morphospace occupation between the three groups

PERMANOVA	Ambush predators	Holosteines	Extant paralepidids
P-values			
Ambush predators		0.0936	0.0006*
Holosteines	0.0936		0.0159*
Extant paralepidids	0.0006*	0.0159*	
F-values			
Ambush predators		1.974	11.900
Holosteines	1.974		8.085
Extant paralepidids	11.900	8.085	
ANOSIM	Ambush predators	Holosteines	Extant paralepidids
P-values			
Ambush predators		0.1446	0.0004*
Holosteines	0.1446		0.0154*
Extant paralepidids	0.0004*	0.0154*	
R-values			
Ambush predators		0.291	0.928
Holosteines	0.291		0.950
Extant paralepidids	0.928	0.950	

Note: The significance is computed by permutation of group membership, with 9999 replicates. Euclidean distances were chosen as a measure unit. The asterisk (*) indicates significant comparisons ($P < 0.05$), thereby suggesting that groups exhibit considerably different morphospace occupation.

& Sánchez-Villagra, 2010; Romano *et al.*, 2012) or with the support of robust bony fulcral scales in front of the median or caudal fins as in lepisosteids (Wiley, 1976). As discussed above, epineurals and epipleurals extend along the entire vertebral column in †*H. esocinus*, being also more robust and thickened in the caudal region. In our opinion, these features, as well as the partial fusion of the hypurals, epaxial hypurostegy and presence of bony fulcral scales in front of the caudal fin lobes support the hypothesis of a fast-start (ambush) predation strategy for this Eocene fish.

The highly successful morphotype of ambush predators evolved independently multiple times during actinopterygian evolution. The first-documented appearance of fishes adopting an ambush style of predation in the fossil record apparently occurred slightly after the Permian–Triassic boundary with the appearance of the genus †*Saurichthys* (family †Saurichthyidae), a highly successful representative of ‘paleopterygian’ fishes, with worldwide distribution in both marine and freshwater ecosystems (e.g. Tintori, 1990, 2013; Tintori *et al.*, 2014; Kogan & Romano, 2016). Subsequently, other fish lineages, including the Cretaceous aulopiform family †Dercetidae, and certain Eocene syngnathiforms (†*Parasynarcualis*) and atheriniforms (†*Mesogaster*, †*Latellagnathus*, †*Rhamphognathus*), exhibited features that were related to the ambush activity (e.g. Bannikov, 2008; Maxwell & Wilson, 2013; Kogan *et al.*, 2015); today,

these kind of predators are represented by gars, pikes, barracudas and several other fishes (Maxwell & Wilson, 2013).

It has been demonstrated experimentally that the peculiar body plan arrangement and conspicuous abdominal muscle mass of ambush predators allow these fishes to generate rapid acceleration performance (Webb, 1978) and, at the same time, to minimize the flow disturbance caused by surrounding water, avoiding detection by the lateral-line sensory system of their prey (Webb & Skadsen, 1980; Webb, Hardy & Mehl, 1992; Kogan *et al.*, 2015). In particular, the posterior displacement of dorsal and anal fins seems to cause a delay in the escape response of prey, giving the illusion that the predator is distant (Dill, 1974; Webb, 1982). Moreover, the rigidity of the trunk, resulting from the development of pre- and postzygapophyses, peculiar neural arch structure (e.g. in †*Saurichthys*; Tintori, 2013) or, alternatively, robust intermusculars (as in †*Holosteus*), could also be related to an increase in elasticity of the whole body in order to ensure a high acceleration during the initial phase of the ambush (Gozzi, 2004).

Maxwell & Wilson (2013) demonstrated that convergent evolution of the body plan of the ambush predators is associated with the posterior displacement of median fins, which in turn is strongly related to the preferential addition of abdominal vertebrae. Several studies (e.g. Baldwin & Johnson, 1996; Davis, 2010)

pointed out that one of the diagnostic characters of Paralepididae is the very high number of caudal vertebrae, representing between 40 and 60% of the total number. †*Holosteus* and †*Pavlovichthys* are unique among paralepidid fishes in having both a posterior displacement of median fins and a significant reduction of the relative number of caudal vertebrae (25–40% of total number) due to the increased number of abdominal elements. This latter feature also characterizes certain modern ambush predators like belonids, esocids, fistulariids, lepisosteids and sphyraenids (Maxwell & Wilson, 2013). The Eocene barracudina †*H. esocinus*, therefore, supports the hypothesis that convergent evolution of the ‘ambush predator’ body plan is often associated with the same changes in axial skeletal configuration, mainly with a posterior displacement of median fins and preferential addition of abdominal vertebrae, confirming the existence of a conservative anatomical module occurring independently in different fish lineages (Maxwell & Wilson, 2013).

Today, heterogeneous tropical habitats associated with reefs (e.g. sand/seagrass beds) represent the ideal environments for diverse and speciose fish assemblages. Large pike-like predators are often associated with these structurally complex shallow water contexts, where the ambush strategy is one of the highly successful types of predation (e.g. Schultz & Kruschel, 2010). Several studies concur to suggest that the Eocene Pesciara limestone deposited in a moderately depressed coastal tropical shallow water intraplatform basin in which different habitats like sand/seagrass beds, open sea and reefs concurred to create a heterogeneous biotope (e.g. Landini & Sorbini, 1996; Papazzoni & Trevisani, 2006) in which zooplanktivorous fishes (clupeids) represented the main trophic resource for most predators (Marramà *et al.*, 2016a), possibly including those with ambush strategy.

Modern barracudina fishes are meso- to bathypelagic predators (Harry, 1953a; Rofen, 1966; Post, 1986; Thompson, 2003). Adult stages of certain barracudina species live at depths up to 4000 m, where they have been observed swimming more or less vertically in order to improve their visual and lateral-line sensibility (Rofen, 1966; Janssen, Pankhurst & Harbison, 1992). †*Holosteus* can be considered as the first-documented evidence of ambush predator strategy within the Paralepididae, as well as the only member of this family that lived in a shallow water environment. Taphonomic considerations, including the extreme rarity of mass mortality layers in the Pesciara succession in which pelagic cruising swimmers generally moving in large schools are often preserved (Wu *et al.*, 2011), might suggest that †*Holosteus* was a solitary predator.

CONCLUSION

The analysis of the fossil record suggests that the holosteines probably diversified during the Paleocene, as indicated by the late Paleocene and early Eocene material from Italy and Denmark (Bonde, 1997). The group persisted up to the Oligocene, as revealed by the numerous fossils collected in the Rupelian deposits of Poland, Romania and Russia (Prokofiev, 2005; Pŕikryl *et al.*, 2016). The excellent preservation of the Eocene specimens from Monte Bolca allowed a detailed reinterpretation of the morphology of †*Holosteus* and the identification of the synapomorphies of this peculiar predatory lineage. The osteological analysis was the initial input to compare, through a geometric morphometric approach, the morphospace occupation of holosteines with that of extant paralepidids and pike-like ambush predators. The morphometric analysis seems to suggest that the early radiation of barracudinas was also characterized by the emergence of unique short-lived body morphology in many ways convergent with that of many shallow water ambush predators. As discussed above, the shallow water lifestyle of †*Holosteus* is remarkably different from the meso- and bathypelagic adaptations of other paralepidids and, more generally, of alepisauroid fishes. The early Paleocene emergence of a predatory shallow water taxon within a typical deep-water lineage is particularly intriguing if considered in the frame of the coeval extensive radiation of a number of teleost lineages of modern type. Several lines of evidence concur to suggest that such a remarkable radiation took place to fill the functional roles vacated by victims of the end-Cretaceous extinction (Friedman, 2009; Marramà *et al.*, 2016b). The origin of the shallow water holosteine paralepidids was therefore coincident with the diversification of scombroids, xiphioids, sphyraenids and carangoids that together represent modern analogues of moderate- to large-bodied Cretaceous predatory fishes (see Friedman, 2009), including pachycormids, pachyrhizodontids, ichthyodectiforms and certain aulopiformes (enchodontids, cimolichthyids and the ambush predator dercetids).

ACKNOWLEDGEMENTS

Roberto Zorzini and Anna Vaccari (MCSNV), Mariagabriella Fornasiero (MGPUP) and Gaël Clément (MNHN) are thanked for permission to examine material under their care and logistic support. Thanks are also due to Jocelyn Falconnet (MNHN) for the photographs. We are grateful to Franco Chilese (Verona) for his hospitality during the visit to Verona by the senior author. The manuscript was improved by the constructive comments provided by Alison M. Murray (Department of Biological Sciences, University of Alberta, Edmonton)

and an anonymous reviewer. The research was supported by the SYNTHESYS grants (FR-TAF-5419 to G. M.) and by grants (ex-60% 2015 and 2016 to G. C.) of the Università degli Studi di Torino.

REFERENCES

- Agassiz L. 1835.** Kritische Revision der in der Ittiolitologia Veronese abgebildeten fossilen Fische. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde* Jahrgang 1835: 290–316.
- Agassiz L. 1833–1844.** *Recherches sur les Poissons Fossiles*. Neuchâtel: Petitpierre, 1420 pp.
- Anderson MJ. 2001.** A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26: 32–46.
- Arambourg C. 1925.** Révision des poissons fossiles de Licata (Sicile). *Annales de Paléontologie* 14: 39–132.
- Arambourg C. 1927.** Les poissons fossiles d'Oran. *Materiaux pour la Carte géologique de l'Algérie, 1^{er} Série-Paléontologie* 6: 1–218.
- Baldwin CC, Johnson GD. 1996.** Interrelationships of Aulopiformes. In: Stiassny MLJ, Parenti LR, Johnson GD, eds. *Interrelationships of fishes*. San Diego: Academic Press, 355–404.
- Bannikov AF. 2004a.** Eocottidae, a new family of perciform fishes (Teleostei) from the Eocene of northern Italy (Bolca). *Studi e Ricerche sui Giacimenti Terziari di Bolca* 10: 17–35.
- Bannikov AF. 2004b.** Fishes from the Eocene of Bolca, northern Italy, previously classified with the Chaetodontidae (Perciformes). *Studi e Ricerche sui Giacimenti Terziari di Bolca* 10: 55–74.
- Bannikov AF. 2006.** Fishes from the Eocene of Bolca, northern Italy, previously classified in the Sparidae, Serranidae and Haemulidae (Perciformes). *Geodiversitas* 28: 249–275.
- Bannikov AF. 2008.** Revision of the atheriniform fish genera *Rhamphognathus* Agassiz and *Mesogaster* Agassiz (Teleostei) from the Eocene of Bolca, northern Italy. *Studi e Ricerche sui Giacimenti Terziari di Bolca* 12: 77–97.
- Bannikov AF, Carnevale G. 2010.** *Bellwoodilabrus landinii*, a new genus and species of labrid fish (Teleostei: Perciformes) from the Eocene of Bolca. *Geodiversitas* 32: 201–220.
- Bedini E, Francalacci P, Landini W. 1986.** I pesci fossili del Miocene superiore di Montefiore Conca e Mondaino (Forlì). *Memorie del Museo Civico di Storia Naturale di Verona, Sezione Scienze della Terra* 3: 1–66.
- Blot J. 1969.** Les poissons fossiles du Bolca classés jusqu'ici dans les familles des Carangidae, Menidae, Ephippidae, Scatophagidae. *Studi e Ricerche sui Giacimenti Terziari di Bolca* 1: 1–525.
- Blot J. 1978.** Les apodes fossiles du Monte Bolca. *Studi e Ricerche sui Giacimenti Terziari di Bolca* 3: 1–260.
- Blot J. 1980.** La faune ichthyologique des gisements du Monte Bolca (Province de Vérone, Italie). *Bulletin du Muséum National d'Histoire Naturelle, Paris, section C* 4: 339–396.
- Blot J, Tyler JC. 1990.** New genera and species of fossil surgeon fishes and their relatives (Acanthuroidei, Teleostei) from the Eocene of Monte Bolca, Italy, with application of the Blot formula to both fossil and Recent forms. *Studi e Ricerche sui Giacimenti Terziari di Bolca* 6: 13–92.
- Bonde N. 1997.** A distinctive fish fauna in the basal Ash-Series of the Fur/Ølst Formation (U. Paleocene, Denmark). *Aarhus Geoscience* 6: 33–48.
- Bronn HG. 1856.** *Lethaea geognostica oder Abbildungen und Beschreibungen der für die Gebirgs-Formationen bezeichnendsten Versteinerungen. Dritte Auflage, 3rd edn*. Stuttgart: E. Schweizerbart, 816 pp.
- Caltran T, Zorzini R, Lazzarin R. 1998.** *Bolca ed il suo Territorio: Storia, Tradizione, Cultura e Scienza*. S. Maria di Zevio (VR): Golden Time Communication, 141 pp.
- Carnevale G. 2004.** *Tafonomia, paleoecologia e paleobiogeografia delle ittiofaune mioceniche dell'Italia centrale*. Unpublished Ph.D Thesis, Università di Pisa, 361 pp.
- Carnevale G. 2007.** Fossil fishes from the Serravallian (Middle Miocene) of Torricella Peligna, Italy. *Palaeontographia Italica* 91: 1–67.
- Carnevale G, Bannikov AF, Marramà G, Tyler JC, Zorzini R. 2014.** The Pesciara-Monte Postale Fossil-Lagerstätte: 2. Fishes and other vertebrates. In: Papazzoni CA, Giusberti L, Carnevale G, Roghi G, Bassi D, Zorzini R, eds. *The Bolca Fossil-Lagerstätte: a window into the Eocene World*. Rendiconti della Società Paleontologica Italiana 4: 37–63.
- Carnevale G, Pietsch TW. 2009.** An Eocene frogfish from Monte Bolca, Italy: the earliest skeletal record for the family. *Palaeontology* 52: 745–752.
- Carnevale G, Pietsch TW. 2010.** Eocene handfishes from Monte Bolca, with description of a new genus and species, and a phylogeny of the family Brachionichthyidae (Teleostei: Lophiiformes). *Zoological Journal of the Linnean Society* 160: 621–647.
- Carnevale G, Pietsch TW. 2011.** Batfishes from the Eocene of Bolca. *Geological Magazine* 148: 461–472.
- Carnevale G, Pietsch TW. 2012.** †*Caruso*, a new genus of anglerfishes from the Eocene of Bolca, Italy, with a comparative osteology and phylogeny of the teleost family Lophiidae. *Journal of Systematic Palaeontology* 10: 47–72.
- Clarke KR. 1993.** Non-parametric multivariate analysis of changes in community structure. *Australian Journal of Ecology* 18: 117–143.
- Collar DC, Reynaga CM, Ward AB, Mehta RS. 2013.** A revised metric for quantifying body shape in vertebrates. *Zoology* 116: 246–257.
- Constantin P. 2001.** *Holosteus finiensis* n. sp., a new fossil fish (Teleostei: Paralepididae) in the Rupelian Formation from Fieni (Eastern Carpathians, Romania). *Acta Paleontologica Romaniaae* 3: 77–86.
- Daniltshenko PG. 1960.** Bony fishes of the Maikop deposits of the Caucasus. *Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR* 78: 1–214. [in Russian]
- David LR. 1943.** Miocene fishes of Southern California. *Geological Society of America, Special Paper* 43: 1–143.
- Davis MP. 2010.** Evolutionary relationships of the Aulopiformes (Euteleostei: Cyclosquamata): a molecular and total evidence approach. In: Nelson JS, Schultze H-P, Wilson MVH, eds. *Origin and Phylogenetic Interrelationships of Teleosts*. München: Verlag Dr. Friedrich Pfeil, 431–470.

- Davis MP, Fielitz C. 2010.** Estimating divergence times of lizardfishes and their allies (Euteleostei: Aulopiformes) and the timing of deep-sea adaptations. *Molecular Phylogenetics and Evolution* **57**: 1194–1208.
- Dill LM. 1974.** The escape response of the zebra danio (*Brachydanio rerio*) I. The stimulus for escape. *Animal Behaviour* **22**: 711–722.
- Ditty JG. 2006.** Paralepididae: Barracudinas. In: Richards WJ, ed. *Early stages of Atlantic fishes: an identification guide for the Western Central North Atlantic, Vol. I*. Boca Raton, CRC Press, 385–427.
- Eastman CR. 1904.** Descriptions of Bolca fishes. *Bulletin of the Museum of Comparative Zoology* **46**: 1–40.
- Eastman CR. 1905.** Les types de poissons fossils du Monte-Bolca au Museum d'Histoire Naturelle de Paris. *Mémoires de la Société Géologique de France, Paléontologie* **34**: 1–31.
- Ege V. 1953.** Paralepididae I (*Paralepis* and *Lestidium*) – taxonomy, ontogeny, phylogeny and distribution. *Dana-Report* **40**: 1–184.
- Ege V. 1957.** Paralepididae II (*Macroparalepis*) – taxonomy, ontogeny, phylogeny and distribution. *Dana-Report* **43**: 1–101.
- Fahay MP. 2007.** *Early stages of fishes in the Western North Atlantic Ocean (Davis Strait, Southern Greenland and Flemish Cap to Cape Hatteras). Volume One: Acipenseriformes through Syngnathiformes*. Nova Scotia: Northwest Atlantic Fisheries Organization, 931 pp.
- Fierstine HL, Huddleston RW, Takeuchi GT. 2012.** Catalog of the Neogene bony fishes of California. A systematic inventory of all published accounts. *Occasional Papers of the California Academy of Sciences* **159**: 1–206.
- Fowler HW. 1936.** The marine fishes of West Africa based on the collection of the American Museum Congo Expedition, 1909–1915. *Bulletin of the American Museum of Natural History* **70**: 1–605.
- Frickhinger KA. 1991.** *Fossilien Atlas: Fische*. Melle: Mergus, 1088 pp.
- Friedman M. 2008.** The evolutionary origin of flatfish asymmetry. *Nature* **454**: 209–212.
- Friedman M. 2009.** Ecomorphological selectivity among marine teleost fishes during the end-Cretaceous extinction. *Proceedings of the National Academy of Sciences of United States of America* **106**: 5218–5223.
- Froese R, Pauly D. 2015.** *FishBase (version 07/2015)*. World Wide Web electronic publication. Available at: www.fishbase.org
- Fujita K. 1990.** *The caudal skeleton of Teleostean fishes*. Tokyo: Tokai University Press, 897 pp.
- Fukui A, Ozawa T. 2004.** *Uncisudis posteropelvis*, a new species of barracudina (Aulopiformes: Paralepididae) from the western North Pacific Ocean. *Ichthyological Research* **51**: 289–294.
- Gaudant J. 2008.** Paléobiodiversité et paléoenvironnements: l'exemple des gisements de poissons téléostéens du Messinien préévaporitique d'Oran et du bassin du Chélif (Algérie). *Geodiversitas* **30**: 141–163.
- Gill TN. 1872.** Arrangement of the families of fishes, or classes Pisces, Marsipobranchi and Leptocardii. *Smithsonian Miscellaneous Collection* **11**: 1–49.
- Goloboff PA, Farris JS, Nixon KC. 2008.** TNT, a free program for phylogenetic analysis. *Cladistics* **24**: 774–786.
- Gorbach LP. 1961.** On some pelagic fish from Carpathian Oligocene. *Paleontological Collection Lvov University* **1**: 131–136. [in Russian]
- Gozzi E. 2004.** *Analisi tassonomica e morfo-funzionale di Saurichthys e Birgeria (Osteichthyes, Actinopterygii)*. Unpublished Ph.D Thesis, Università degli Studi di Milano, 379 pp.
- Hammer Ø, Harper DAT, Ryan PD. 2001.** PAST: paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* **4**: 1–9.
- Harry RR. 1953a.** Studies on the Bathypelagic Fishes of the Family Paralepididae. 1. Survey of the Genera. *Pacific Science* **7**: 219–249.
- Harry RR. 1953b.** Studies on the Bathypelagic Fishes of the Family Paralepididae (Order Iniomi). 2. A Revision of the North Pacific Species. *Proceedings of the Academy of Natural Sciences of Philadelphia* **105**: 169–230.
- International Code of Zoological Nomenclature. 1999.** *International Commission of Zoological Nomenclature, 4th edn*. [Incorporating Declaration 44, amendment of Article 74.7.3, with effect from 31 December 1999 and the Amendment on e-publication, amendment to Articles 8, 9, 10, 21 and 78, with effect from 1 January 2012]. Available at: <http://iczn.org/iczn/index.jsp>
- Janssen J, Pankhurst NW, Harbison R. 1992.** Swimming and body orientation of *Notolepis rissoi* (Bonaparte) in relation to lateral line and visual function. *Journal of the Marine Biological Association of the United Kingdom* **72**: 877–886.
- Jordan DS. 1921.** The fish fauna of the California Tertiary. *Stanford University Publication, Biological Sciences* **1**: 235–300.
- Jordan DS. 1925.** The fossil fishes of the Miocene of Southern California. *Stanford University Publication, Biological Sciences* **4**: 1–51.
- Jordan DS, Gilbert JZ. 1919.** Fossil fishes of Southern California. *Stanford University Publications, University Series* **1**: 1–98.
- Kogan I, Pacholak S, Licht M, Schneider JW, Brücker C, Brandt S. 2015.** The invisible fish: hydrodynamic constraints for predator-prey interaction in fossil fish *Saurichthys* compared to recent actinopterygians. *Biology Open* **4**: 1715–1726.
- Kogan I, Romano C. 2016.** Redescription of *Saurichthys madagascariensis* Piveteau, 1945 (Actinopterygii, Early Triassic), with implications for the early saurichthyid morphotype. *Journal of Vertebrate Paleontology* **36**: e1151886.
- Landini W, Sorbini L. 1996.** Ecological and trophic relationships of Eocene Bolca (Pesciara) fish fauna. In: Cherchi A, ed. *Autoecology of selected fossil organisms: achievements and problems*. Bollettino della Società Paleontologica Italiana Special Volume **3**: 105–112.
- Leriche M. 1906.** Contribution à l'étude des poissons fossils du Nord de la France et des régions voisines. *Mémoires de la Société géologique du Nord* **5**: 1–430.
- Lombardo C, Tintori A. 2005.** Feeding specializations in Late Triassic fishes. *Annali dell'Università degli Studi di Ferrara volume speciale* **2005**: 25–32.

- Maddison WP, Maddison DR. 2008.** *Mesquite: a modular system for evolutionary analysis. Version 3.03.* Available at: <http://mesquiteproject.org>
- Marramà G, Bannikov AF, Tyler JC, Zorzini R, Carnevale G. 2016a.** Controlled excavations in the Pesciara and Monte Postale sites provide new insights about the paleoecology and taphonomy of the fish assemblages of the Eocene Bolca Konservat-Lagerstätte, Italy. *Palaeogeography, Palaeoclimatology, Palaeoecology* **454**: 228–245.
- Marramà G, Carnevale G. 2015a.** Eocene round herring from Monte Bolca, Italy. *Acta Palaeontologica Polonica* **60**: 701–710.
- Marramà G, Carnevale G. 2015b.** The Eocene sardine †*Bolcaichthys catopygopterus* (Woodward, 1901) from Monte Bolca, Italy: osteology, taxonomy and paleobiology. *Journal of Vertebrate Paleontology* **35**: e1014490.
- Marramà G, Carnevale G. 2016.** An Eocene anchovy from Monte Bolca, Italy: the earliest known record for the family Engraulidae. *Geological Magazine* **153**: 84–94.
- Marramà G, Garbelli C, Carnevale G. 2016b.** A morphospace for the Eocene fish assemblage of Bolca, Italy: a window into the diversification and ecological rise to dominance of modern tropical marine fishes. *Bollettino della Società Paleontologica Italiana* **55**: 11–21.
- Marramà G, Garbelli C, Carnevale G. 2016c.** A clade-level morphospace for the Eocene fishes of Bolca: patterns and relationships with modern tropical marine fish assemblages. *Bollettino della Società Paleontologica Italiana* **55**: 139–156.
- Marramà G, Villier B, Dalla Vecchia FM, Carnevale G. 2016d.** A new species of *Gladiopyenodus* (Coccoodontoidea, Pycnodontomorpha) from the Cretaceous of Lebanon provides new insights about the morphological diversification of pycnodont fishes through time. *Cretaceous Research* **61**: 34–43.
- Maxwell EE, Wilson LA. 2013.** Regionalization of the axial skeleton in the ‘ambush predator’ guild—are there developmental rules underlying body shape evolution in ray-finned fishes? *BMC Evolutionary Biology* **13**: 265.
- Menner VV. 1948.** Ikhtiofauna maikopskikh otlozhenii Kavkaza. 1. Morskije shchukoobraznye ryby. *Trudy Instituta Geologicheskikh Nauka* **98**: 51–63. [in Russian]
- Monsch K. 2006.** A revision of scombrid fishes (Scombroidei, Perciformes) from the Middle Eocene of Monte Bolca, Italy. *Palaeontology* **49**: 873–888.
- Moyle PB, Cech JJ. 2003.** *Fishes: an introduction to ichthyology, 5th edn.* London: Pearson Prentice Hall, 726 pp.
- Nelson JS, Grande TC, Wilson MVH. 2016.** *Fishes of the World, 5th edn.* Hoboken: John Wiley & Sons, 752 pp.
- Nolf D. 1988.** Les otolithes de téléostéens éocènes d’Aquitaine (sud-ouest de la France) et leur intérêt stratigraphique. *Académie Royale de Belgique, Mémoires de la Classe des Sciences* **19**: 1–147.
- Papazzoni CA, Carnevale G, Fornaciari E, Giusberti L, Trevisani E. 2014.** The Pesciara-Monte Postale Fossil-Lagerstätte: 1. Biostratigraphy, sedimentology and depositional model. In: Papazzoni CA, Giusberti L, Carnevale G, Roghi G, Bassi D, Zorzini R, eds. *The Bolca Fossil-Lagerstätte: a window into the Eocene World.* Rendiconti della Società Paleontologica Italiana **4**: 29–36.
- Papazzoni CA, Trevisani E. 2006.** Facies analysis, palaeoenvironmental reconstruction, and biostratigraphy of the ‘Pesciara di Bolca’ (Verona, northern Italy): an early Eocene Fossil-Lagerstätte. *Palaeogeography, Palaeoclimatology, Palaeoecology* **242**: 21–35.
- Patterson C. 1993.** Osteichthyes: Teleostei. In: Benton MJ, ed. *The fossil Record 2.* London: Chapman and Hall, 621–656.
- Patterson C, Johnson GD. 1995.** The intermuscular bones and ligaments of teleostean fishes. *Smithsonian Contributions to Zoology* **559**: 1–85.
- Pierce SE, Angielczyk KD, Rayfield EJ. 2009.** Morphospace occupation in thalattosuchian crocodylomorphs: skull shape variation, species delineation and temporal patterns. *Palaeontology* **52**: 1057–1097.
- Post A. 1986.** Family Paralepididae. In: Smith MM, Heemstra PC, eds. *Smiths’ Sea Fishes.* Johannesburg: Macmillan South Africa, 274–278.
- Post A. 1987.** Results of the research cruises of FRV ‘Walther Herwig’ to South America. LXVII. Revision of the subfamily Paralepidinae (Pisces, Aulopiformes, Alepisauroidei, Paralepididae). I. Taxonomy, morphology and geographical distribution. *Archiv für Fischereiwissenschaft* **38**: 75–131.
- Přikryl T, Kania I, Krzemiński W. 2016.** Synopsis of fossil fish fauna from the Hermanowa locality (Rupelian; Central Paratethys; Poland): current state of knowledge. *Swiss Journal of Geosciences* **38**: 429–443.
- Prokofiev AM. 2005.** Holosteinae, a new subfamily of paralepidids (Alepisauroidei: Paralepididae). *Journal of Ichthyology* **45**: 275–283.
- Rofen RR. 1966.** Family Paralepididae. In: Mead GW, Bigelow HB, Breder CM, Cohen DM, Merriman D, Olsen YH, Schroeder WC, Schultz LP, Tee-Van J, eds. *Fishes of the Western North Atlantic. Part 5. Iniomi and Lyomeri.* New Haven: Sears Foundation for Marine Research, Yale University, 205–461.
- Rohlf FJ. 2003.** *TpsRelw, Relative Warps Analysis, version 1.36.* Stony Brook: State University of New York.
- Rohlf FJ. 2005.** *TpsDig, digitize landmarks and outlines, version 2.05.* Stony Brook: State University of New York.
- Romano C, Kogan I, Jenks J, Jerjen I, Brinkmann W. 2012.** *Saurichthys* and other fossil fishes from the late Smithian (Early Triassic) of Bear Lake County (Idaho, USA), with a discussion of saurichthyid palaeogeography and evolution. *Bulletin of Geosciences* **87**: 543–570.
- Rosen DE. 1973.** Interrelationships of euteleostean fishes. In: Greenwood PH, Miles RS, Patterson C, eds. *Interrelationships of fishes.* London: Zoological Journal of the Linnean Society **53**(Suppl. 1): 397–513.
- Russell BC. 1999.** Bathysauridae: deepsea lizardfishes. In: Carpenter KE, Niem VH, eds. *The living marine resources of the Western Central Pacific.* FAO Species Identification Guide for Fishery Purposes **3**: 1946–1947.
- Sato T, Nakabo T. 2002.** Paraulopidae and *Paraulopus*, a new family and genus of aulopiform fishes with revised relationships within the order. *Ichthyological Research* **49**: 25–46.
- Sauvage HE. 1870.** Synopsis des poissons tertiaires de Licata en Sicile. *Annales de Sciences naturelles (Zoologie, Paléontologie)* **14**: 1–26.

- Schmid L, Sánchez-Villagra MR. 2010.** Potential genetic bases of morphological evolution in the Triassic fish *Saurichthys*. *Journal of Experimental Zoology. Part B, Molecular and Developmental Evolution* **314**: 519–526.
- Schultz ST, Kruschel C. 2010.** Frequency and success of ambush and chase predation in fish assemblages associated with seagrass and bare sediment in an Adriatic lagoon. *Hydrobiologia* **649**: 25–37.
- Sorbini L. 1988.** Biogeography and climatology of Pliocene and Messinian fossil fish of Eastern-Central Italy. *Bollettino del Museo Civico di Storia Naturale di Verona* **14**: 1–85.
- Sulak KJ. 1977.** The systematics and biology of *Bathypterois* (Pisces, Chlorophthalmidae), with a revised classification of benthic myctophiform fishes. *Galathea Report* **14**: 49–108.
- Thompson BA. 2003.** Paralepididae – Barracudinas. In: Carpenter KE, ed. *The living marine resources of the western central Atlantic*. FAO Species Identification Guide for Fishery Purposes **2**: 933–934.
- Tintori A. 1990.** The vertebral column of the Triassic fish *Saurichthys* (Actinopterygii) and its stratigraphical significance. *Rivista Italiana di Paleontologia e Stratigrafia* **96**: 93–102.
- Tintori A. 2013.** A new species of *Saurichthys* (Actinopterygii) from the Middle Triassic (Early Ladinian) of the Northern Grigna Mountain (Lombardy, Italy). *Rivista Italiana di Paleontologia e Stratigrafia* **119**: 287–302.
- Tintori A, Huang J-D, Jiang D-Y, Sun Z-Y, Motani R, Chen G. 2014.** A new *Saurichthys* (Actinopterygii) from the Spathian (Early Triassic) of Chaohu (Anhui Province, China). *Rivista Italiana di Paleontologia e Stratigrafia* **120**: 157–164.
- Tyler JC, Santini F. 2002.** Review and reconstructions of the tetraodontiform fishes from the Eocene of Monte Bolca, Italy, with comments on related Tertiary taxa. *Studi e Ricerche sui Giacimenti Terziari di Bolca* **9**: 47–119.
- Uyeno T, Matsuura K, Fuji E. 1983.** *Fishes Trawled off Suriname and French Guiana*. Tokyo: Japan Marine Fishery Resource Research Center, 519 pp.
- Volta GS. 1796.** *Ittiolitologia Veronese del Museo Bozziano ora annesso a quello del Conte Giovambattista Gazola e di altri Gabinetti Fossili Veronesi*. Verona: Stamperia Giuliani, 323 pp.
- Webb PW. 1978.** Fast-start performance and body form in seven species of teleost fish. *Journal of Experimental Biology* **74**: 211–226.
- Webb PW. 1982.** Avoidance responses of fathead minnow to strikes by four teleost predators. *Journal of Comparative Physiology* **147**: 371–378.
- Webb PW. 1984.** Body form, locomotion and foraging in aquatic vertebrates. *American Zoologist* **24**: 107–120.
- Webb PW, Hardy DH, Mehl VL. 1992.** The effect of armored skin on the swimming of longnose gar, *Lepisosteus osseus*. *Canadian Journal of Zoology* **70**: 1173–1179.
- Webb PW, Skadsen JM. 1980.** Strike tactics of *Esox*. *Canadian Journal of Zoology* **58**: 1462–1469.
- Wiley EO. 1976.** The phylogeny and biogeography of fossil and Recent gars (Actinopterygii: Lepisosteidae). *Museum of Natural History, The University of Kansas, Miscellaneous Publications* **64**: 1–111.
- Woodward AS. 1901.** *Catalogue of fossil fishes in the British Museum (Natural History), Volume 4*. London: Trustees of the British Museum, 636 pp.
- Wu FX, Sun YL, Xu GH, Hao WC, Jiang DY, Sun ZY. 2011.** New saurichthyid actinopterygian fishes from the Anisian (Middle Triassic) of southwestern China. *Acta Palaeontologica Polonica* **56**: 581–614.
- Young JW, Lansdell M, Riddoch S, Revill AT. 2006.** Feeding ecology of broadbill swordfish, *Xiphias gladius*, off eastern Australia in relation to physical and environmental variables. *Bulletin of Marine Science* **79**: 793–809.
- Zelditch ML, Swiderski DL, Sheets HD, Fink WL. 2004.** *Geometric morphometrics for biologists: a primer*. Amsterdam: Elsevier Academic Press, 478 pp.
- Zigno A De. 1874.** *Catalogo Ragionato dei Pesci Fossili del Calcare Eocene di M. Bolca e M. Postale*. Venezia: Stabilimento Tipografico Grimaldo e C., 215 pp.
- Zittel K.A von. 1932.** *Text-book of palaeontology, Vol. II*. London: Macmillan and Co., 464 pp.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Appendix. List of the morphological characters used in the phylogenetic analysis. Data are based on Davis (2010) to which we added and discussed a new state for character 84 and the new character 140.