

An Eocene scorpionfish from Monte Postale (Bolca Lagerstätte, northeastern Italy)

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ABSTRACT - A small-sized Eocene percomorph fish collected in 2003 during supervised excavations at the Monte Postale site of the Bolca Lagerstätte is described herein. Although the fossil is poorly preserved, a set of morphological characters are recognised (e.g., large head bearing prominent lachrymal, orbital, parietal, preopercular and opercular spines; six branchiostegal rays; hypurals 1+2 and 3+4 fused; about 20 vertebrae; 15 unbranched pectoral-fin rays; dorsal fin with 13 spines and 12 soft rays; anal fin with three spines and five soft rays) that allow the specimen to be referred to the *Scorpaenoidei*. This diverse group of percomorph fishes is represented today by scorpionfishes, flatheads, sea robins and stonefishes. In particular, the overall morphology of the fossil as well as certain skeletal and meristic features suggest a possible relationship with the scorpionfish families *Scorpaenidae* or *Synanceiidae*. The relevance of this fossil is primarily due to the fact that it represents the first scorpionfish from the Eocene of the Bolca Lagerstätte, and it also provides support to the hypothesis that the evolutionary origin of scorpaenoid fishes took place in warm and shallow waters.

INTRODUCTION

Scorpionfishes, flatheads, sea robins, stonefishes and allies form a group of benthic marine percomorph fishes, the *Scorpaenoidei*, which includes some of the most venomous fishes of the world (e.g., Smith & Wheeler, 2006). *Scorpaenoids* have been traditionally aligned with the cottoid lineage in the order *Scorpaeniformes* because of the shared possession of the suborbital stay, formed by the posterior extension of the third infraorbital (Allis, 1909; Regan, 1913; Greenwood et al., 1966; Johnson, 1993; Shinohara, 1994; Mooi & Johnson, 1997; Nelson, 2006). However, the monophyletic status and composition of the *Scorpaeniformes* have been the subject of considerable disagreement. In fact, recent morphological and molecular studies concur to indicate that the *Scorpaeniformes* is a polyphyletic assemblage (e.g., Imamura & Shinohara, 1998; Imamura & Yabe, 2002; Smith & Wheeler, 2004). Imamura & Yabe (2002) hypothesised that the scorpaenoid lineage is closely related to the serranid fishes sharing with them at least three synapomorphic features, including the adductor dorsalis muscle, a backwardly directed opercular spine, and a single postocular spine in larval stage. Imamura & Yabe (2002) therefore proposed a revised suborder *Scorpaenoidei* to include two superfamilies, the *Serranoidea* and *Scorpaenoidea*, with the monophyly of the latter supported by the presence of the suborbital stay, parietal sensory canal with spines, and an extrinsic swimbladder muscle derived from the obliquus superioris. A more recent total evidence analysis including 113 morphological and 5,280 molecular characters by Smith et al. (2018) tested the relationships of the *Scorpaenoidei* proposed by Imamura (2004) without recovering the monophyly of his *Scorpaenoidea* or *Serranoidea*. Smith et al. (2018) redefined the suborder *Scorpaenoidei*, uniquely diagnosed by the presence of parietal lateral-line canal with

spines, to include more than 800 species arranged in 128 genera and eight families: *Bembridae*, *Hoplichthyidae*, *Neosebastidae*, *Platycephalidae*, *Plectrogeniidae*, *Scorpaenidae*, *Synanceiidae*, and *Triglidae*.

Here we describe a small articulated scorpionfish skeleton collected in 2003 during the controlled excavations at Monte Postale, one of the main fossiliferous sites of the Bolca Lagerstätte, northeastern Italy. The specimen is housed in the Museo Civico di Storia Naturale, Verona (MCSNV), Italy, and it represents the first evidence of scorpaenoid fishes in the celebrated Bolca Lagerstätte, which further increases the overall diversity of the speciose Eocene fish assemblage. The fish assemblage of Bolca represents one of the most diverse ichthyofaunas known in the fossil record and consists of about 250 species of chondrichthyans, pycnodontiforms and teleosts that document tropical marine peri-reefal environments in the western Tethys (e.g., Bannikov, 2014; Carnevale et al., 2014, 2017; Marramà & Carnevale, 2015a, b; Marramà et al., 2016a, 2018; Cawley et al., 2018; Friedman & Carnevale, 2018). Percomorphs are by far the most diverse group within this fish assemblage, with about 160 species-level taxa and include the earliest record of many coral reef fish lineages, providing evidence of the apparent stability of the structure and composition of tropical and subtropical marine ichthyofaunas throughout the Cenozoic (Bellwood & Wainwright, 2002; Carnevale, 2006; Bannikov & Carnevale, 2010; Marramà et al., 2016b, c).

GEOLOGICAL SETTING

The specimen comes from the Monte Postale site, one of the two main fossiliferous quarries of the Bolca Lagerstätte, which is located in the Lessini Mountains

about 30 km from the city of Verona (NE Italy). The Monte Postale stratigraphic succession is remarkably thick and comprises the Cretaceous Scaglia Rossa Formation up to Ypresian fossiliferous limestone containing larger benthic foraminiferans of the genus *Alveolina* and abundant molluscs in its uppermost part (Papazzoni et al., 2014). The Ypresian fossiliferous limestone also includes layers of finely laminated micrites with fish and plant remains. Based on large benthic foraminifers and calcareous nannoplankton content, the uppermost strata of the Monte Postale have been assigned to the SBZ 11, corresponding to the late Cuisian (late Ypresian, between 50.7 and 48.9 Ma; Papazzoni et al., 2017). Solid evidence of the presence of a corallgal rim, lagoonal deposits, and a fore-reef system was detected for the Monte Postale palaeobiotope (Vescogni et al., 2016). Palaeoecological and taphonomic studies of the Monte Postale fish assemblage support this interpretation, based on the abundance of marine and terrestrial plants, invertebrates (including corals), and reef-associated fishes, which accumulated in a coral reef context close to an emerged coastal area (Marramà et al., 2016a).

MATERIAL AND METHODS

The present study is based on a single moderately preserved specimen (MCSNV IG.VR.66957), standard length: 24.6 mm. The specimen was studied using a Leica M80 stereomicroscope equipped with a camera lucida drawing arm. The specimen required matrix removal before examination in order to allow investigation of its structure in as much detail as possible; matrix removal was achieved using fine entomological needles. Measurements were taken with a dial caliper to the nearest 0.1 mm. Standard length (SL) is used throughout. Comparative data were derived mainly from the literature.

Abbreviations are as follows: ang, angular; br, branchiostegal rays; ch, ceratohyal; de, dentary; ep, epural; fr, frontal; hyp, hypural; iop, interopercle; la, lachrymal; op, opercle; pa, parietal; pecf, pectoral fin; pfs, pelvic-fin spine; ph, parhypural; pop, preopercle; pu, preural vertebra; q, quadrate; sop, subopercle; un, uroneural.

SYSTEMATIC PALAEONTOLOGY

Division PERCOMORPHACEA sensu Wiley & Johnson, 2010
Suborder SCORPAENOIDEI sensu Smith et al., 2018

Family, genus and species indet.

Material - MCSNV IG.VR.66957, a partially complete and relatively poorly preserved articulated skeleton in a single plate, 24.6 mm SL (Fig. 1).

Measurements (mm; in parentheses as percentage of SL) - Head length: 12.3 mm (49.9); head depth: 7.8 mm (31.6); preorbital length: 2.7 mm (11.1); postorbital length: 6.7 mm (27.1); orbit diameter: 2.7 mm (11.0); maximum body depth: 8.1 mm (32.9); dorsal-fin base length: 10.1 mm (40.8); anal-fin base length: 3.8 mm (15.6); caudal peduncle length: 2.6 mm (10.6); caudal peduncle depth: 1.9 mm (7.7); prepectoral distance: 10.6 mm (43.2); predorsal distance: 13.2 mm (53.6); prepelvic distance: 10.1 mm (40.8); preanal distance: 17.8 mm (72.2).

Anatomical description - The specimen represents a small-sized fish measuring about 25 mm SL (Fig. 1). The body length, coupled with a body depth reaching about one third of SL, the presence of completely developed dorsal and anal fins, ossified vertebral centra, and trace of squamation clearly indicate that the specimen is a juvenile or subadult that already overcome the postflexion stage typical of the scorpaenoid larvae (e.g., Moser et al., 1977; Washington et al., 1984b; Nagasawa & Domon, 1997). The head is large, longer than high; its length is contained about two times in SL. The mouth is relatively large and terminal. The dorsal margin of the body, from the snout to the caudal-fin origin, is convex forming a marked angle at the dorsal-fin origin. The caudal peduncle is straight, short and narrow.

The neurocranium is poorly preserved; the majority of the bones are largely fragmented and their outline is difficult to recognise (Fig. 2). However, the head spination is partially recognisable, especially the prominent spines located above and behind the orbit (postocular



Fig. 1 - (color online) Scorpaenoidei fam., gen. et sp. indet., specimen MCSNV IG.VR.66957 from the Eocene Monte Postale site of Bolca Lagerstätte, Italy. Right lateral view. Scale bar 2 mm.

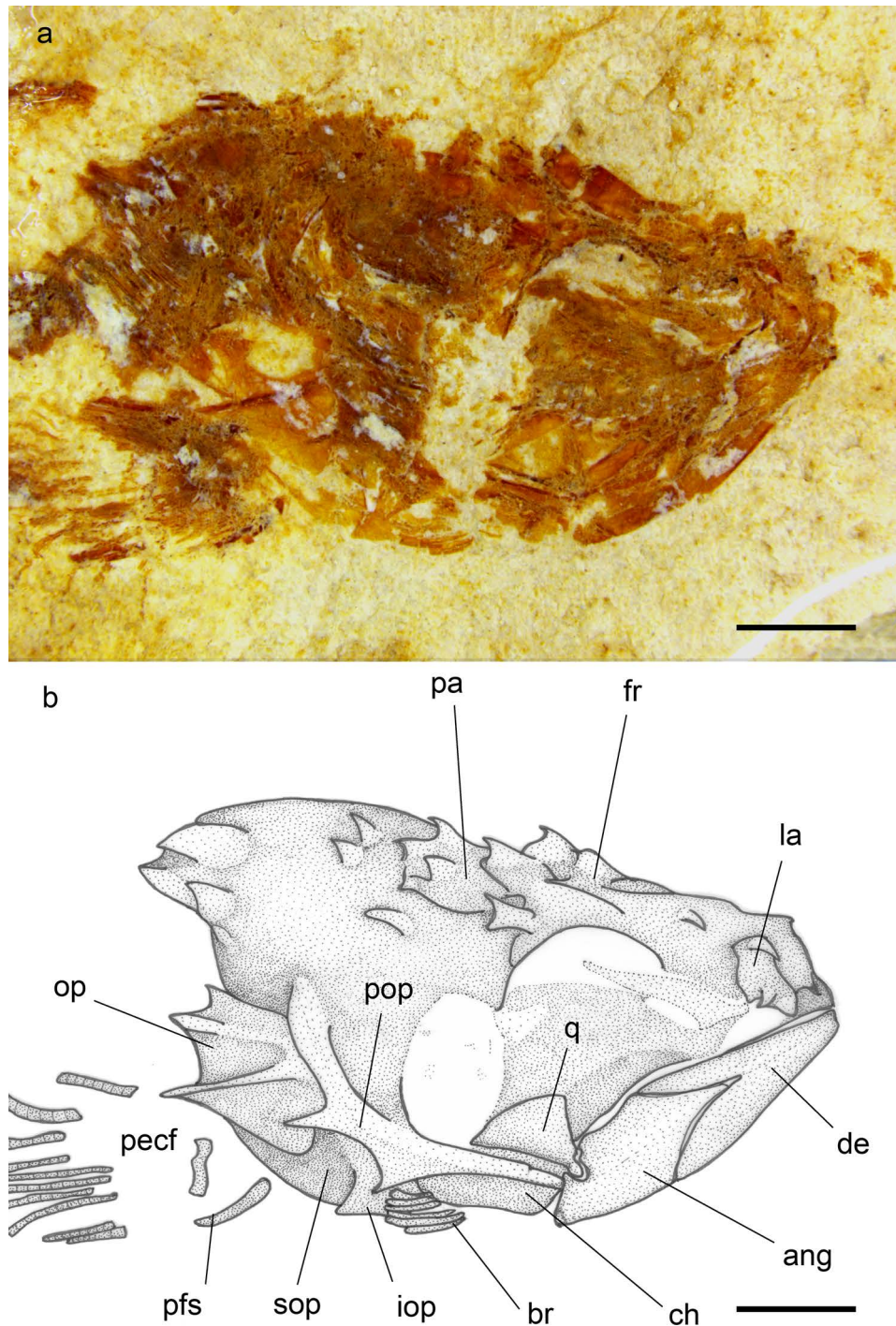


Fig. 2 - (color online) *Scorpaenoidei* fam., gen. et sp. indet., specimen MCSNV IG.VR.66957 from the Eocene Monte Postale site of Bolca Lagerstätte, Italy. a) Close up of the head in right lateral view. b) Reconstruction. Scale bars 2 mm.

and supraocular spines sensu Eschmeyer, 1969), and on the parietal, and those emerging from the lachrymal (preorbital spines sensu Eschmeyer, 1969). A backwardly directed suborbital stay on third infraorbital is not easily recognisable due to inadequate preservation of the fossil. The upper jaw is not recognisable. Of the lower jaw, the dentary and angulo-articular are clearly exposed while the teeth are not well-recognisable. The quadrate is almost triangular in shape. The majority of the suspensorium is inadequately preserved. Two large and pointed spines can be recognised along the posterior margin of the relatively

narrow preopercle. The opercle is quadrangular in outline and bears at least two spines that represent the posterior prolongation of thick and straight ridges. Interopercle and subopercle are partially exposed.

Of the hyoid bar bones the anterior ceratohyal is partially preserved. The proximal portion of six sabre-like branchiostegal rays is recognisable just below the joint between the horizontal and vertical arms of the preopercle.

The vertebral column is gently sigmoid. The anterior portion of the vertebral column is very poorly preserved, making extremely problematic to determine the original

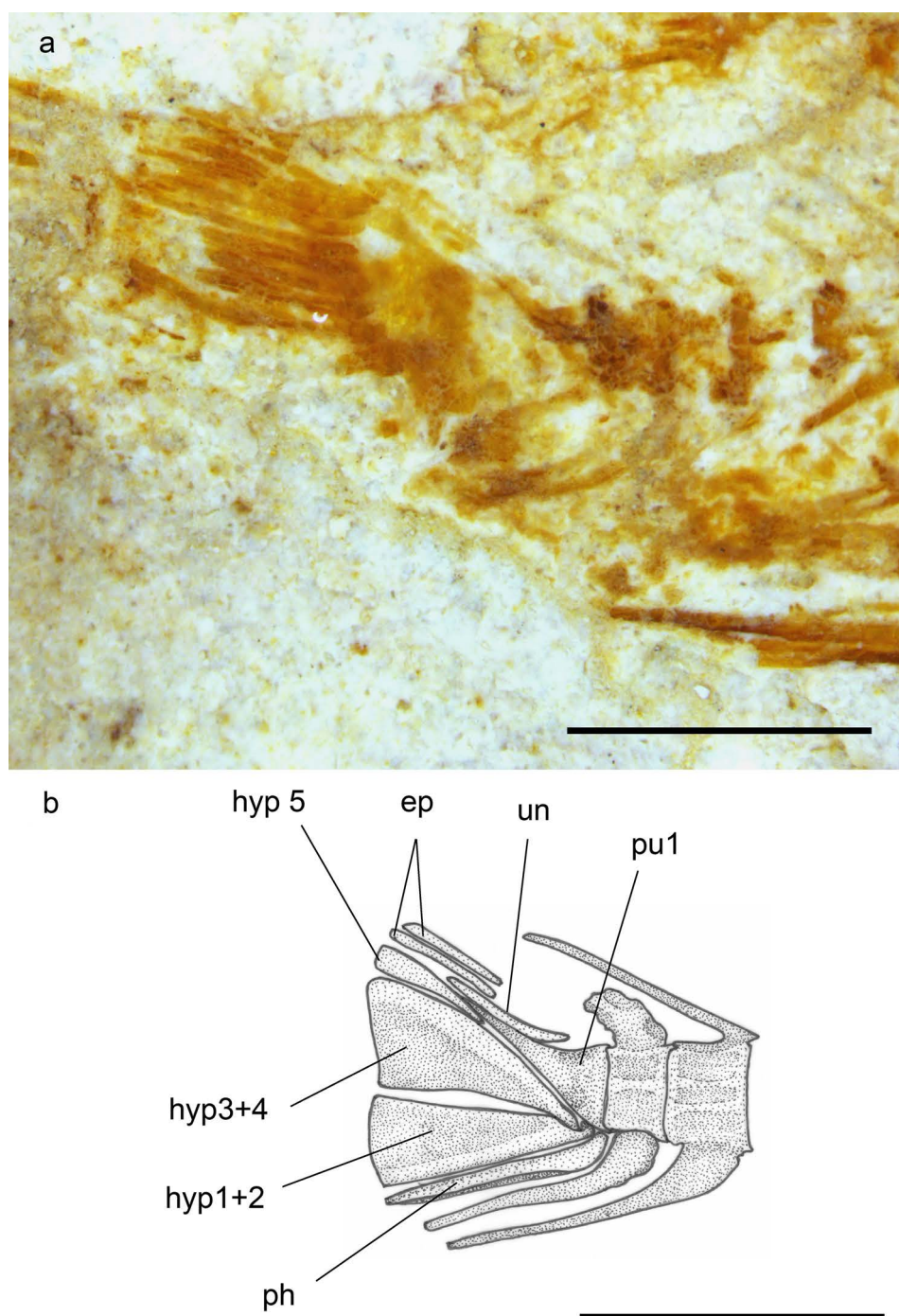


Fig. 3 - Scorpaeoidei fam., gen. et sp. indet., specimen MCSNV IG.VR.66957 from the Eocene Monte Postale site of Bolca Lagerstätte, Italy. a) Close up of the caudal skeleton. b) Reconstruction. Scale bars 2 mm.

number of abdominal vertebrae. At least six posterior abdominal and 14 caudal vertebrae, including the urostylar centrum, can be recognised. The vertebral centra are subrectangular, longer than high, and bear two large fossae separated by a strong longitudinal ridge along their lateral surface. The neural and haemal spines are rather slender and obliquely oriented. The caudal skeleton is poorly preserved but the overall structure appears consistent with that of scorpaenoid fishes (Fig. 3) (see Ishida, 1994). The urostyle appears to be separated from the hypural plates. The first and second hypurals are fused to each other, as

are the third and fourth hypurals. A delicate fifth hypural is juxtaposed along the dorsal margin of the dorsal hypural plate. The parhypural appears to be autogenous. At least a single uroneural and two epurals are present. The second preural vertebra has autogenous haemal spine and lacks a neural spine. The caudal-fin rays are only partially preserved, but at least nine unbranched rays constitute the dorsal lobe.

There is no evidence of supraneurals, although this might be a taphonomic artefact. The dorsal fin extends along the entire dorsal margin of the body and bears

13 spines and possibly 12 soft rays; the presence of a notch that separates the spinous and the soft part of the dorsal fin is difficult to determine. The anal fin is short and includes at least three spines and five soft rays. The first anal-fin pterygiophore is strong and wedge-shaped; it is exceptionally strongly inclined in relation to the body axis (perhaps being slightly displaced from its original position). Strong inclination of the first anal-fin pterygiophore is typical for the generalised scorpaenoids. The pectoral fins are large, fan shaped, and consist of about 15 unbranched rays each. The pelvic fins are scarcely preserved; the pelvic fins originate just below the pectoral fins and include at least one spine plus an indeterminate number of soft rays each.

Fragments of the scales are scattered across the body but their morphology is difficult to define.

DISCUSSION

Despite the limited quality of the preservation, there are several pieces of evidence that clearly indicate the scorpaenoid affinities of the specimen described herein. The overall body physiognomy, body proportions, meristics, and some of the recognisable skeletal features are consistent with those of extant scorpaenoid fishes (see Tab. 1). The spination of the head, in this case exemplified by lachrymal, preorbital, supraocular, postocular, parietal, preopercular, and opercular spines is especially relevant in supporting the scorpaenoid affinity of the fossil (see, e.g., Eschmeyer, 1969; Hureau & Litvinenko, 1986; Shinohara, 1994; Imamura, 1996, 2004; Imamura & Yabe, 2002; Smith et al., 2018). In particular, the presence of a parietal spine (overlying a lateral-line canal) is currently recognised as the sole unambiguous diagnostic feature

of the Scorpaenoidei (Smith et al., 2018). Because of the inadequate preservation of the cheek region, the presence of a backwardly directed suborbital stay on the third infraorbital cannot be properly recognised. In any case, despite the possession of a suborbital stay with broad distal end strongly connected with the anterior margin of the preopercle is considered as an unambiguous synapomorphy of a clade formed by scorpaenoids, cottoids and zoarcoids (Smith et al., 2018), this structure is absent in certain scorpaenoid genera (Ishida, 1994; Imamura, 2004). Moreover, the fossil exhibits a set of morphological features, including the fusion of the first and second hypurals, absence of supraneurals, strong inclination of the first anal-fin pterygiophore, and dorsal- and anal-fin formulae that strongly support its alignment with the scorpaenoids (see Washington et al., 1984a; Hureau & Litvinenko, 1986; Ishida, 1994; Smith et al., 2018).

Unfortunately, the poor preservation of the fossil makes even more problematic its accommodation at the family level. However, the attribution to the Hoplichthyidae can be ruled out because the members of this family are characterised by a fusion between parhypural and lower hypural plate (Fujita, 1990; Smith et al., 2018). Moreover, the apparent fusion of first and second hypurals rules out the possible belonging to Bembridae, Neosebastidae and Plectrojeniidae in which these bones are separated from each other (Smith et al., 2018). The alignment of the fossil with Triglidae, Platycephalidae and Hoplichthyidae seems unlikely being these families characterised by elongate bodies, a smaller head, dorsal fin with separated spinous and soft portions, thick superficial and densely ornamented cranial bones, and different meristic counts (Tab. 1) (see also Washington et al., 1984a; Imamura, 1996, 2004; Smith et al., 2018). Therefore, the overall body physiognomy and proportions (see, e.g., Eschmeyer,

	MCSNV IG.VR.66957	Scorpaenidae	Synanceiidae	Triglidae	Bembridae	Platycephalidae	Hoplichthyidae	Neosebastidae	Plectrojeniidae
Dorsal fin outline	continuous?	with notch	continuous or with notch	separated	separated	separated	separated	with notch	separated
Dorsal-fin spines	13	6-11	8-25	7-11	6-12	6-10	5-6	13	8-12
Dorsal-fin soft rays	12	8-17	4-17	10-23	8-14	11-15	14-16	7-8	6-12
Anal-fin spines	3	1-3	2-11	0-1	0-3	0-1	0	3	0-3
Anal-fin soft rays	5	3-14	4-14	11-23	5-15	10-14	16-18	5-6	5-11
Pelvic-fin spines	1	1	1	1	1	1	1	1	1
Pelvic-fin soft rays	2 or 3	2-5	3-5	5	5	5	3-5	4-5	5
Pectoral-fin rays	15	11-25	11-19	11-16+3	21-27	16-22	13-14+3-4	19-23	20-27
Vertebrae	>20	24-31	23-44	34-38	26	27	26	25-27	26

Tab. 1 - Selected morphological features used to discriminate living scorpaenoid families. Data from Washington et al. (1984a), Ishida (1994), and Nelson et al. (2016).

1969), skeletal features (structure and composition of the caudal skeleton; see Fujita, 1990), strong inclination of the first anal-fin pterygiophore, and meristic complement (number of vertebrae, dorsal- and anal-fin formulae) concur to suggest a close affinity of the fossil with the families Scorpaenidae or Synanceiidae. However, additional comparative information would be necessary to conclusively demonstrate the familial affinities of the fossil described herein and for this reason we prefer to postpone any more detailed taxonomic placement until better preserved material would be available for a detailed study.

Extant scorpaenoids are typically marine benthic fishes living in a wide range of habitats from shallow to deep water and from the poles to the tropics (Poss, 1999; Nelson, 2006; Nelson et al., 2016). Although they are not commonly regarded as typical coral-reef fishes (see Bellwood, 1996; Bellwood & Wainwright, 2002), several scorpaenoids are inshore fishes living on sandy and rocky bottoms and around coral reefs and seagrasses (Hureau & Litvinenko, 1986; Poss, 1999). From this perspective, the presence of a scorpaenoid in the Monte Postale is in agreement with the tropical shallow-water habitat associated with coral reefs as hypothesised for this palaeobiotope (Marramà et al., 2016a; Vescogni et al., 2016).

The fossil described herein represents one of the oldest scorpaenoids known based on the skeletal remains. The earliest evidence of articulated skeletal remains of scorpaenoids dates back to the basal Eocene, represented by the undescribed specimens from the Danish Mo-Clay (Bonde, 1966, 1987, 1997). Three of the eight scorpaenoid families recognised by Smith et al. (2018), Bembridae, Neosebastidae and Synanceiidae are unknown in the fossil record, and the Hoplichthyidae and Plectrogeniidae are solely represented by otoliths. While scorpaenid otoliths are known since the earliest part of the Paleocene (Danian of Denmark; Schwarzhans, 2003), genuine scorpaenid articulated skeletal remains are known since the Oligocene (e.g., Micklich, 1998; Pharissat & Micklich, 1998) becoming relatively common in the Neogene (e.g., Arambourg, 1927; Bedini et al., 1986; Bossio et al., 1986; Sorbini, 1988; Barsukov, 1989; Schultz, 1993; Yabumoto & Uyeno, 1994). The earliest otoliths referred to the family Platycephalidae date back to the early Eocene (Ypresian of New Zealand; Schwarzhans, 2019), and the oldest known skeletal remains were reported from the early Miocene of Tasmania (Corbett, 1980). Gurnards of the family Triglidae are characterised by a relatively diverse and abundant otolith record, whose earliest representatives are known from the middle Eocene (Lutetian; e.g., Schwarzhans, 2007), as well as by rare Oligocene and Neogene skeletal remains (Leriche, 1910; Arambourg, 1927; Carnevale, 2008; Carnevale & Godfrey, 2018). Finally, both the earliest records of the Hoplichthyidae and Plectrogeniidae have been reported from New Zealand from the middle (or late) Eocene (Bartonian or Priabonian; Schwarzhans, 1980) and early Miocene (Burdigalian; Schwarzhans, 2019), respectively.

Being the fossil described herein one of the earliest occurrences of scorpaenoids, it might provide support to the hypothesis that scorpaenoids originated in shallow and warm waters and transitioned later in deeper and colder habitats (Smith et al., 2018).

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