A RUPELIAN CORAL REEF FISH ASSEMBLAGE FROM THE VENETIAN SOUTHERN ALPS (BERICI HILLS, NE ITALY)

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Abstract. We describe here a new bony fish assemblage collected from a fossiliferous outcrop located in Perarolo, Berici Hills, Venetian Southern Alps. The fossiliferous deposits pertain to the Rupelian (lower Oligocene) Castelgomberto Calcarenite and are indicative of a tropical marine shallow water setting associated with coral reefs. The assemblage is characterized by diminutive putative cryptobenthic fishes, including a single goby (family Gobiidae) and several cardinalfishes of the subfamily Pseudamiinae (family Apogonidae). Furthermore, a new apogonine of the extinct tribe †Eoapogonini, a new butterflyfish (family Chaetodontidae), and an indeterminate viviparous brotula belonging to the ophidiiform family Dinematichthyidae, are also present, and likely represented part of the epibenthic community. Some of the taxa described herein are among the first occurrences within their respective lineages in the fossil record. The Perarolo taxa document the first Oligocene coral reef fish assemblage known to date. Four taxa are described as new: †*Arconiapogon deangelii* gen. et sp. n., †*Chaetodon* (*Blumchaetodon*) *wattsi* subgen. et sp. n., †*Oligopseudamia iancurtisi* gen. et sp. n., and †*Oniketia akihitoi* gen. et sp. n.

INTRODUCTION

The Oligocene was a period of dramatic climatic and biotic changes. The Eocene-Oligocene transition (c. 34 Ma) marked the passage from a warmhouse to a cooler and seasonal climate, driven by declining atmospheric CO_2 content, long-term deep-sea cooling, and establishment of large Antarctic ice sheets, resulting in one of the most profound climatic shifts of the entire Cenozoic (e.g., Coxall et al. 2005; Pagani et al. 2005; Lear et al. 2008; Zachos et al. 2008; Pusz et al. 2011). These climate changes, which persisted into the early Oligocene, caused biotic turnovers in both marine and terrestrial environments (e.g., Kvaček & Walther 2001; Prothero et al. 2003; Pearson et al. 2008; Kaminski & Ortiz 2014).

Although the general patterns of Palaeogene abiotic disruptions have been documented extensively, the impact of the global changes on tropical marine shallow water fish communities,

particularly those associated with coral reefs, is poorly known. This is mostly because most of the Palaeogene marine deposits from the Tethyan realm are usually not associated with coral reefs. The only exception to this pattern are the Bolca Lagerstätten, which include a series of Ypresian sites yielding fossil remains of bony and cartilaginous fishes that lived in heterogeneous palaeobiotopes undoubtedly associated with coral reefs (e.g., Carnevale et al. 2014; Friedman & Carnevale 2018; Marramà et al. 2016, 2021a), which are crucial to properly understand the origin and evolution of fishes on coral reefs.

The fossil record shows that the earliest records of most of the modern reef fish families occur in the Eocene of the western Tethys (Patterson 1993; Bellwood 1996; Carnevale et al. 2014; Bellwood et al. 2015; Friedman & Carnevale 2018), a tropical shallow sea in the area that was a hotspot of biodiversity for tropical marine life, comparable to the current Indo-Australian Archipelago (see Renema et al. 2008). The early Palaeogene rise of modern tropical reefs built primarily by scleractinian corals (e.g., Wallace & Rosen 2006), associated with the appearance of other important coastal biomes like seagrasses, promoted the exploitation of new ecological resources by reef fishes, as highlighted by the development and expansion of piscine herbivory, high-precision feeding, nocturnal feeding, and ambush predation (e.g., Bellwood 2003; Goatley et al. 2010; Schmitz & Wainwright 2011; Bellwood et al. 2014; Marramà & Carnevale 2017; Floeter et al. 2018). Although the Bolca Lagerstätten mark the earliest record for several reef families (e.g., Acanthuridae, Apogonidae, Holocentridae, Labridae, Pomacentridae, Siganidae, Zanclidae), other lineages closely associated with modern coral reefs, like the Gobiidae, Chaetodontidae, and parrotfishes are absent in these Ypresian sites (Bellwood 1996; Carnevale et al. 2014; Bellwood et al. 2017) possibly because of their very low abundance or their late origin (e.g., Fessler & Westneat 2007; Cowman & Bellwood 2011).

In this paper, we describe a new western Tethyan bony fish assemblage collected from a Rupelian outcrop in Perarolo in the Berici Hills (Vicenza Province, NE Italy), representing the only Oligocene coral reef fish assemblage known to date, and therefore crucial to our understanding of the origin and early evolution of coral reef fishes.

GEOLOGICAL SETTING

The geology of Berici Hills

The fossils come from a locality of the north-central sector of Berici Hills (Fig. 1A), one of the classical regions for stratigraphical and palaeontological investigations of the Italian Palaeogene since the middle of the XIX century (Bassi et al. 2000). The Berici Hills, located in the southern Vicenza plain (Veneto region), extend for about 200 km^2 and are considered the south-western extension of the Lessini Mountains (Fig. 1A). The local stratigraphical succession, investigated in detail for the first time by Fabiani (1911), is mainly represented by carbonates and volcanic rocks whose age ranges from Late Cretaceous to early Miocene (see Mietto 1988; Cornale 1994; Bassi et al. 2000, 2008; Fig. 2A). The oldest lithostratigraphic unit cropping out in the Berici Hills is the Scaglia Rossa (Turonian-Maastrichtian), resulting from pelagic sedimentation in a structural high, the Trento Plateau, derived from the drowning of the previous Early Jurassic Trento Platform (e.g., Winterer & Bosellini 1981; Bosellini 1989). The transition from the Cretaceous to the Palaeogene is demarcated by a hard-ground, marking a stratigraphic gap spanning the entire Palaeocene (Mietto 1988). In the Palaeogene, the *mise en place* of the Alpone-Chiampo graben (or semigraben) in the Southern Alpine area of northeastern Italy, a tectonic structure bounded toward the west by the Castelvero fault (Barbieri et al. 1991; Zampieri 1995; Fig. 1A), deeply infuenced the sedimentation and facies distribution in the western Berici Hills and eastern Lessini Mountains. Within this graben, during the Palaeocene to the middle Eocene, basaltic volcanites intercalated in a succession that records the transition from pelagic to neritic sedimentation, due to the uplift and segmentation of the former Trento Plateau. Such a dismembered structural high, also punctuated by several volcanic piles, became a centre of carbonate deposition, giving rise to the "Lessini Shelf", a sort of Palaeogene "resurrected" Trento Platform, scattered with reefs, lagoons, islands, and volcanoes (Bosellini 1989). Lower Eocene pelagic sedimentation in the "Scaglia Rossa" facies is recorded in the south-eastern portion of the Berici Hills (Bassi et al. 2000). The Scaglia Rossa is overlain by a Middle Eocene carbonate-marly arenaceous complex, including the "Marne Euganee", representing tuffs and tuffaceous marls passing up-

Fig. 1 - A) Simplified geologic map of the study area with location of the Perarolo site in the Berici Hills (modified after Mattioli et al. 2016); B) Reconstruction of the Rupelian Castelgomberto Calcarenite depositional system with indication of localities cited in the text (modified from Bosellini et al. 2020).
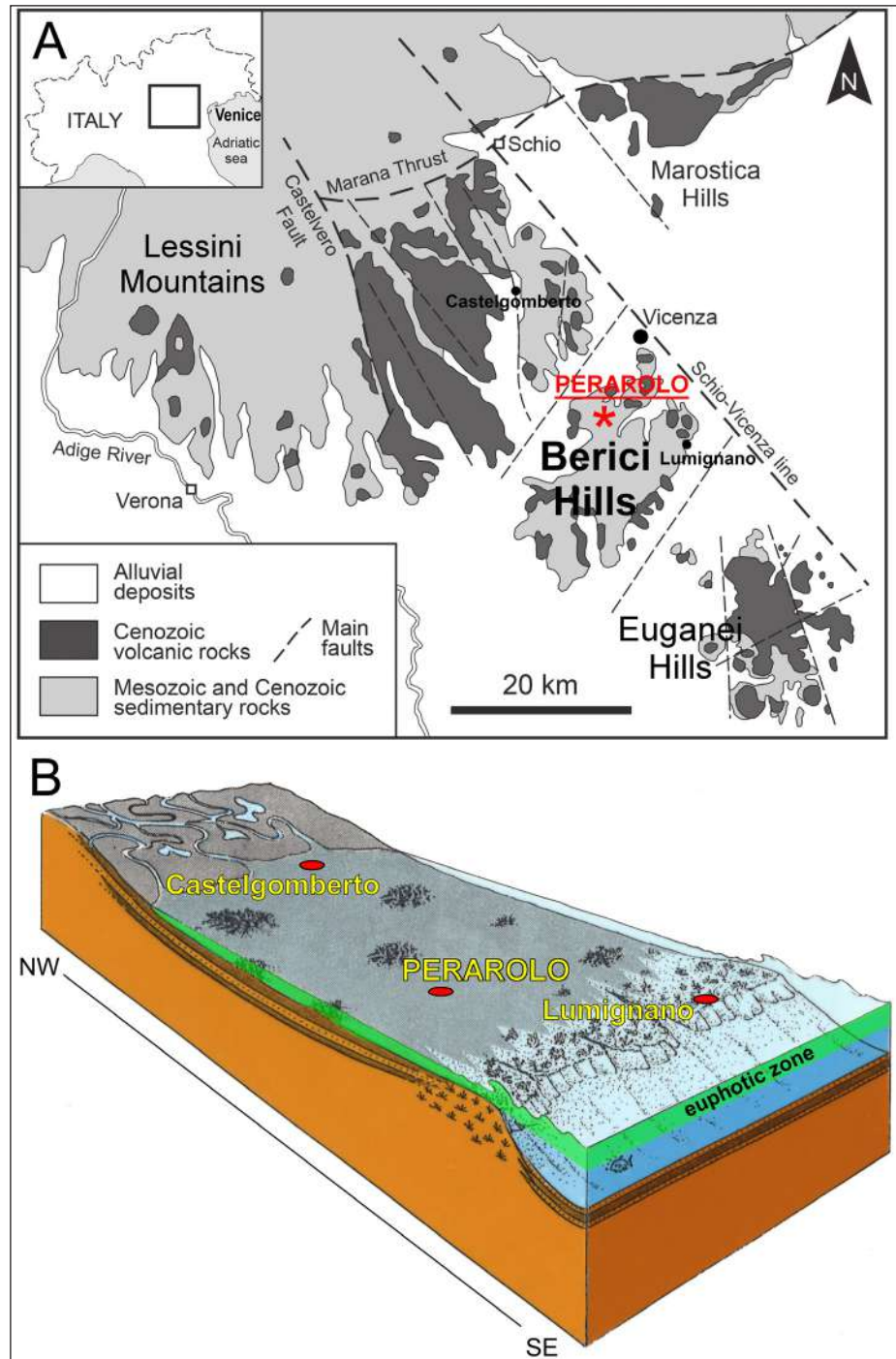
ward into marly calcarenites locally known as "Pietra di Nanto", actively quarried as building stone (Fabiani 1915; Cornale 1994; Bassi et al. 2000, 2008; Fig. 2A). This unit grades upward into "Calcari Nummulitici" (nummulitic limestones) that in the eastern Berici Hills extend up to the Bartonian-Priabonian transition (Fig. 2A). In the western Berici Hills, the sector belonging to the Alpone-Chiampo graben, the deposition of nummulitic limestones was interrupted by huge extrusion of basalts that lead to the emersion of this area at the end of mid-

dle Eocene, in the context of a general regressive phase (Fig. 2A). Such a regression also caused the emersion and the establishment of brackish conditions in some areas of the eastern Berici Hills (Bassi et al. 2000, 2008). The Late Eocene transgression, recorded by the deposition of the *Cerithium diaboli* horizon (Fabiani 1915; Mietto 1988) over the altered Bartonian basalts in the western sector, led to widespread deposition of the marly-calcareous complex of the Priabona Formation in the Berici Hills, in a context of total interruption of volcanic activity
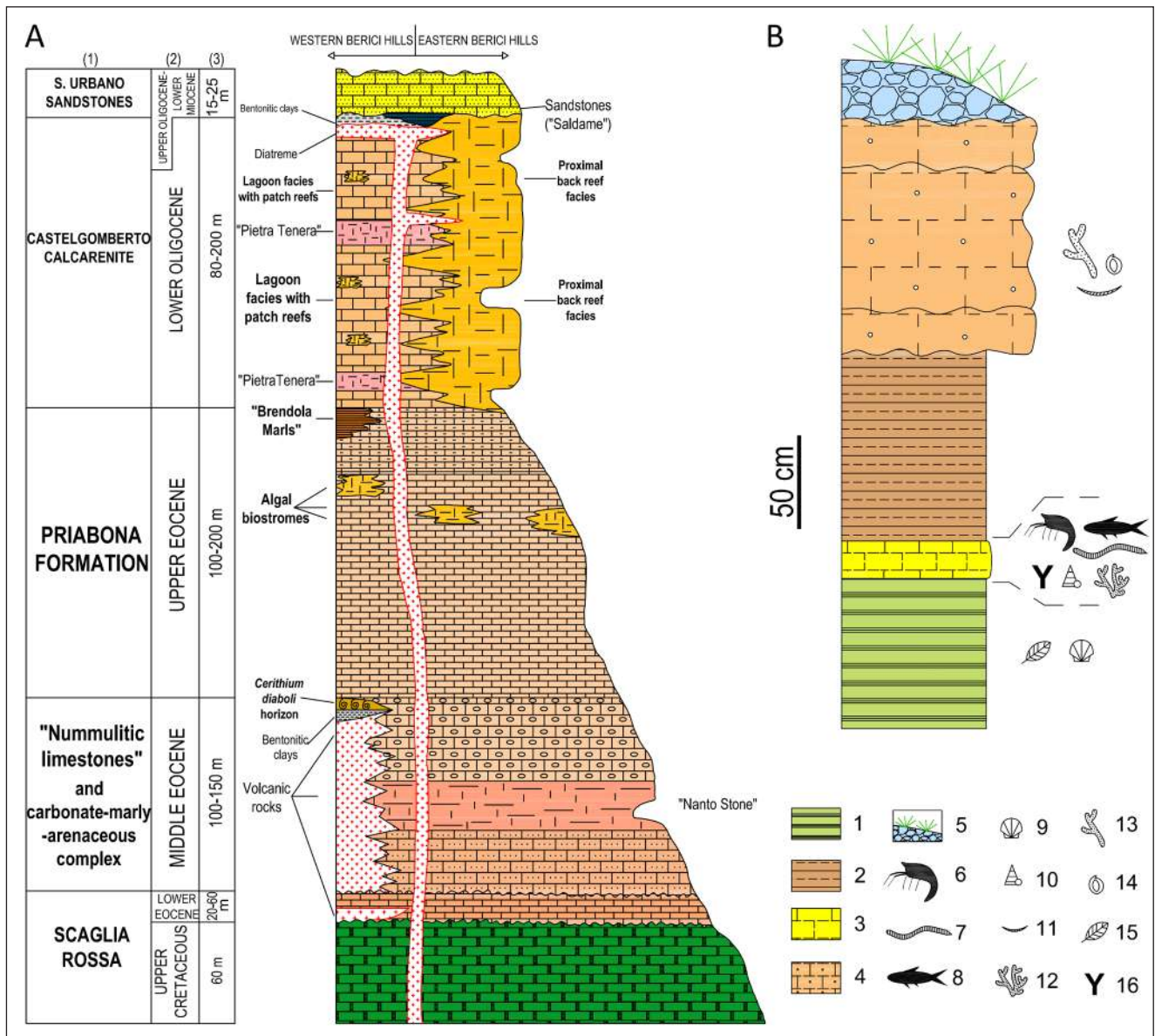
Fig. 2 - A) The stratigraphic succession of the Berici Hills, Veneto region, northeastern Italy (redrawn after Girardi & Mezzalira 1991 and Cornale 1994): 1) Lithostratigraphic units; 2) Chronostratigraphy; 3) Thickness. B) Reconstruction of the outcrop of Perarolo (Berici Hills) based on De Angeli & Messina (1992), personal communications of A. De Angeli and field observations. Legend: 1) basal marly complex with alternations of indurate and soft marls; 2) unfossiliferous marls; 3) yellow fine-grained fossiliferous limestones; 4) calcarenites with corals; 5) rocky debris, soil and vegetation; 6) crustaceans; 7) annelids; 8) fish; 9) mollusk molds; 10) gastropods; 11) fragments of mollusks; 12) corals; 13) fragments of corals (molds and imprints); 14) miliolids; 15) vegetal remains; 16) burrows.

over the Lessini Shelf area. This lithostratigraphic unit, whose maximum thickness attains around 200 metres (Fig. 2A), testifies to sedimentation in a warm shallow sea influenced by a significant terrigenous input coming from northern emerged lands likely located in the Recoaro-Valdagno areas (Mietto 1988; Cornale 1994). In some sectors of the Priabonian platform, populated by a variety of organisms such as larger foraminifera, mollusks, brachiopods, crustaceans, bryozoans, corals and echinoids, the terrigenous input was limited or absent and algal

biostromes developed (Ungaro & Bosellini 1965; Fig. 2A). This macrofauna has been investigated by Fabiani (1908, 1911). Some intervals of the Priabona Formation have been quarried in the Berici Hills as building stones and are considered a variety of "Pietra di Nanto" ("Nanto Stone"; Cornale 1994). The top of this formation is locally represented by a terrigenous unit known as "Brendola marls" or "bryozoan marls" (Mietto 1988; Fig. 2A). The Priabona Formation grades upward into the 200 m thick Rupelian "Castelgomberto Calcarenite" (larg-

er foraminiferal Shallow Benthic Zones 21-22a), represented by a variety of richly fossiliferous lithologies exposed in the southeastern Lessini Mountains and Berici Hills (calcarenites, calcirudites, coral boundstones, marly limestones and clay horizons; Frost 1981; Bassi et al. 2000, 2007, 2008; Bosellini et al. 2020; Fig. 2A–B). According to classical models (see Frost 1981), these rocks testify to a barrier reef mainly constructed by massive to columnar colonial corals located in the southeastern Berici Hills (e.g., Lumignano), with a wide shallow euphotic lagoon protected from the action of waves and currents and extending for about 30 km northwestward into the Lessini Mountains (Fig. 1B). A recent study (Bosellini et al. 2020) substantiate this model rejecting the interpretation of a low angle ramp system with scattered coral colonisations limited to the meso-oligophotic zone proposed by Nebelsick et al. (2013) and Pomar et al. (2017). The facies exposed in the southeastern Berici Hills (e.g., Lumignano; Fig. 1A–B), according to Geister & Ungaro (1977) and Bosellini et al. (2020), represent the proximal back reef of the proper barrier reef that likely was destroyed by tectonic activity and/or erosion. Massive to columnar coral colonies built thickets and small patch reefs in the protected lagoon, whereas the most proximal areas that received episodic terrigenous inputs were characterized by thicket-like structures formed by ramose coral assemblages (Bosellini et al. 2020). A rejuvenation of the volcanic activity in the Oligocene is recorded in the Berici Hills by several volcanic necks or diatremes. Temporary emersion of volcanic islands interrupted the Castelgomberto lagoon sedimentation, documented by lignite fossiliferous deposits; among them is the site of Monteviale (Lessini Mountains), renowned for its extraordinary vertebrate fauna (Mietto 2006; Bassi et al. 2008; Ghezzo & Giusberti 2016; Pandolfi et al. 2017). Calcarenitic beds rich in fragments of calcareous algae deposited in back reef channels are quarried as building stone under the name "Pietra Tenera" or "Vicenza Stone" (Mietto 1988; Cornale 1994; Fig. 2A). In the Late Oligocene the Castelgomberto Calcarenite was subaerially exposed, as documented by palaeokarst formation and deposition of clays produced by alteration of volcanic products present at the top of the unit (Bassi et al. 2008). Such materials are overlain by siliciclastic sands locally known as "saldame", which grades into Chattian-lowermost Miocene sandstones and calcareous sandstones rich in larger foraminifera ascribed to the "S. Urbano Sandstones", representing the most recent stratigraphical unit preserved in the Berici Hills area (Mietto 1988; Fig. 2A).

The Perarolo site and its fauna

The fossiliferous site, no longer exposed, was discovered in the mid-1980s during basement excavation of a house located about 100 meters northwest of the San Bernardino church in the Perarolo district (Arcugnano, Vicenza province; De Angeli & Messina 1992). The outcrop, belonging to the Castelgomberto Calcarenite, is represented, from bottom to top, by a complex of unknown thickness of greyish soft marls alternating with indurate yellow-greyish marls containing mollusk molds and plant remains (De Angeli & Messina 1992; Fig. 2B) and capped by an indurate yellow micritic limestone 15-20 cm-thick containing the fossil fauna (De Angeli & Messina 1992; Antonio De Angeli, com. pers.; Fig. 2B). The marly complex ends with about one meter of strongly weathered and barren marls overlaid by "madreporic limestone" (De Angeli & Messina 1992). A recent survey conducted by one of us (LG) at Perarolo resulted in the observation, in the garden of a house just in front of the original site, solely of the top of the "madreporic limestone", consisting of a yellowish calcarenite containing abundant moulds and impressions of fragmented corals, small fragments of mollusks and porcelaneous small benthic foraminiferans.

The fossiliferous bed of Perarolo was excavated by several private collectors (among them the late Mr. Antonio Rossi and Mr. Vincenzo Messina) and by the palaeocarcinologist Antonio De Angeli and yielded an abundant crustacean fauna associated with fish, annelids, sparse gastropods, and corals (Fig. 2B; Figs 3–4). The most important collections of fossils from this site are presently housed in the Museo Civico "G. Zannato" of Montecchio Maggiore (Vicenza; MCGZ), Museo di Geologia e Paleontologia dell'Università degli Studi di Padova (MGP-PD) and Museo Naturalistico Archeologico of Vicenza.

The eight taxa of crustaceans reported thus far from Perarolo include six new species and are represented by stomatopods, a single mysid, an isopod and decapods (see De Angeli & Messina 1992; De Angeli & Rossi 2006; Messina 2012). In terms of abundance, the most common taxon is the mud
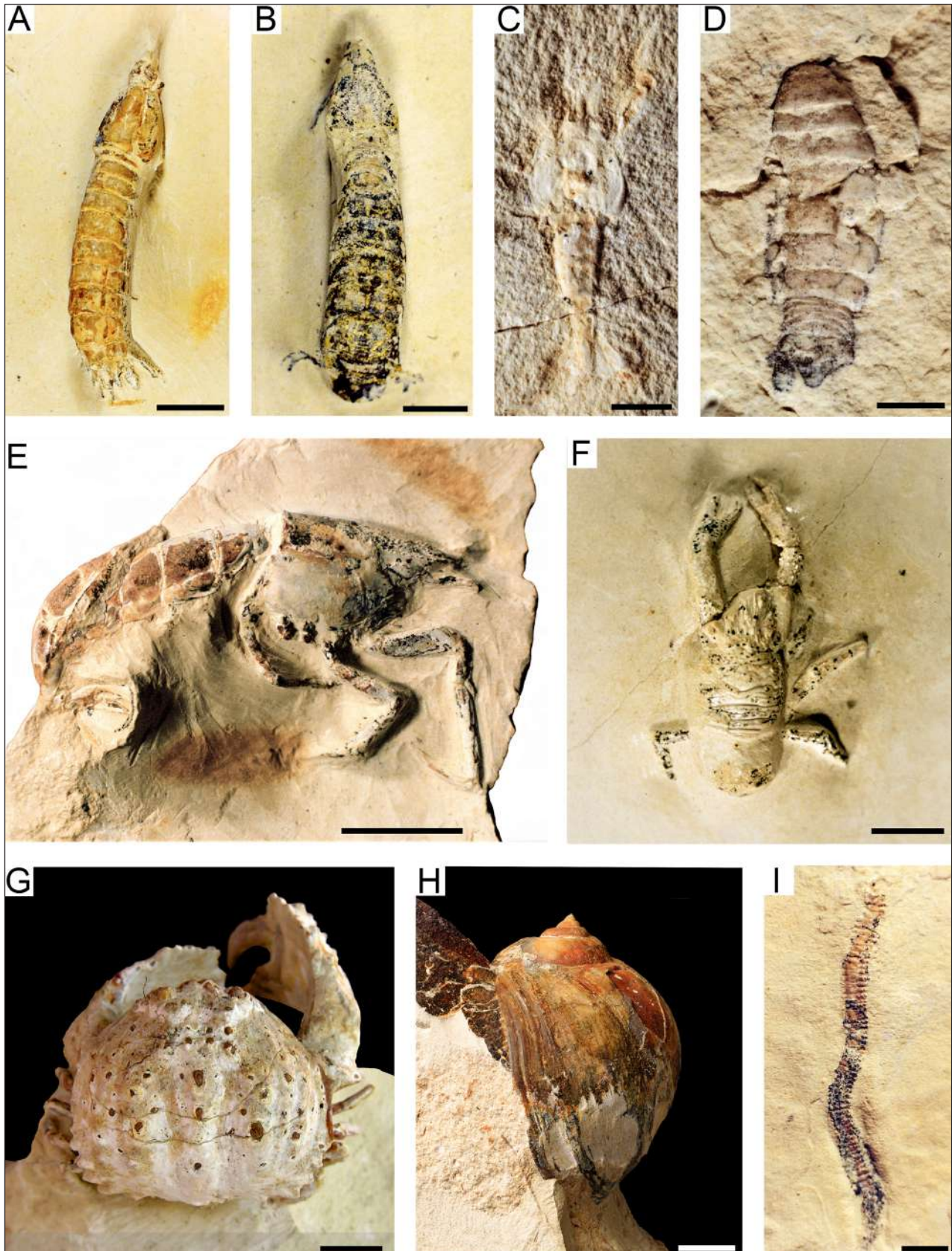
Fig. 3 - Invertebrates associated with fossil fishes at Perarolò, Berici Hills (northeastern Italy) - A) *Pseudosquilla berica* De Angeli & Messina, 1996 (holotype MCGZ 1547). B) *Lysiosquilla messinae* De Angeli, 1997 (holotype MCGZ 1546). C) *Mysidopsis oligocenica* De Angeli & Rossi, 2006 (holotype MCGZ 2415). D) *Cirolana fabianii* De Angeli & Rossi, 2006 (holotype MCGZ 2418). E) *Upogebia perarolensis* De Angeli & Messina, 1992 (holotype MCGZ 1363). F) *Galathea valmaranensis* De Angeli & Garassino, 2002 (MCGZ 1550). G) *Calappilia vicetina* Fabiani, 1910 (MCGZ 3494). H) Ampullinid gastropod (MGP-PD 32417). I) Acephalous polychaete annelid worm (MCGZ 1527). Scale bars: A, E, H = 10 mm; B, F, G, I = 5 mm; C, D = 2.5 mm.
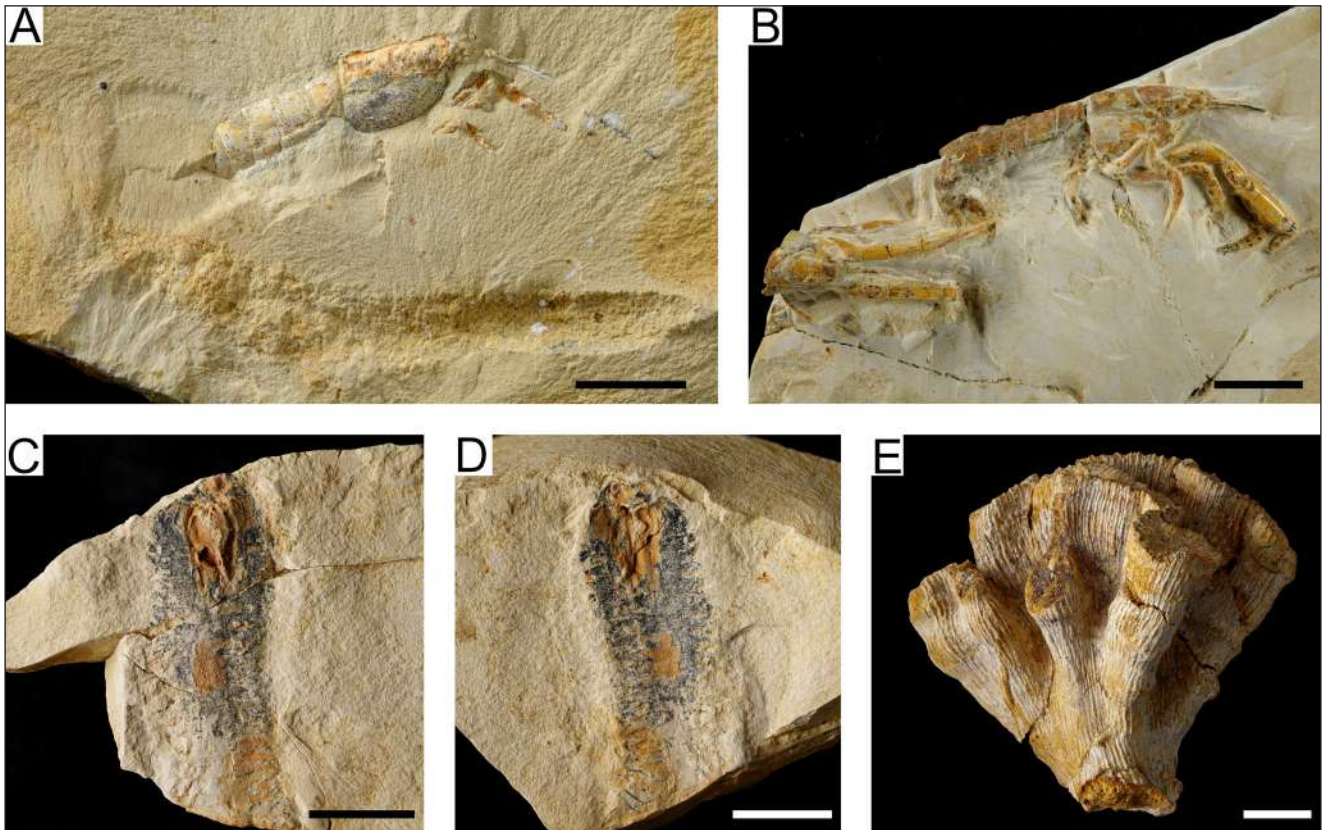
Fig. 4 - Invertebrates associated with fossil fishes at Perarolo, Berici Hills (northeastern Italy) - A) The mud shrimp *Upogebia perarolensis* preserved with its burrow (specimen MGP-PD R467). B) Detail of a small cluster of *Upogebia perarolensis* (specimen MGP-PD R258). C) and D) part and counterpart of an incomplete annelid preserving the head (specimen MGP-PD R254). E) Colonial coral (specimen MGP-PD R255). Scale bars 10 mm.

shrimp *Upogebia perarolensis* (Fig. 3E; Fig. 4A–B) that represents at least 60-70 % of the entire assemblage (estimation based on about 100 fossils from Perarolo housed in the collections of Museo di Geologia e Paleontologia dell'Università degli Studi di Padova). Some individuals are associated with their burrows and sometimes they are clustered (De Angeli & Messina 1992; Fig. 4A–B). The high abundance of these thalassinids is not surprising considering that upogebiid shrimps constitute the dominant decapod crustacean group in modern shallow water marine environments (e.g., tidal flats) and may occur in extremely high densities, up to 200 individuals per square meter (e.g., Dworschak 1987). The preservation of crustaceans from Perarolo is exceptional; the specimens are usually three-dimensional with all the appendages perfectly articulated and even the most delicate structures preserved, including the impressions of the setae of the telson and uropods of the upogebiids. According to previous studies (see De Angeli & Messina 1997; De Angeli & Ros-

si 2006), the exquisitely preserved crustaceans, sometimes fossilized in "life position", as well as the presence of remains of soft bodied organisms like the polychaete annelids (Fig. 3I; Fig. 4C–D) indicate a rapid in situ burial of the Perarolo fauna in an extremely fine-grained sediment (calcareous mud). The absence of lamination and presence of crustacean burrows in the fossiliferous bed likely rule out anoxia as the main controlling factor in the preservation of these fossils.

The crustacean assemblage of Perarolo indicates deposition of the fossiliferous bed in a warm shallow sea in close proximity to a reefal environment (Fig. 1B), as indicated by finds of colonial corals and a galatheid, a decapod typically inhabiting the coralligenous "complexes" of the Oligocene of the Berici Hills (see De Angeli & Messina 1997; De Angeli & Rossi 2006). Such coralligenous buildups likely correspond to the thicket-like structures and small patch reefs widely documented by several authors in the very shallow-water lagoonal succession of the Castelgomberto Calcarenite in

the central-NW Berici Hills (see Geister & Ungaro 1977; Ungaro 1978; Frost 1981; Bosellini et al. 2020; Fig. 1B). Interestingly, Ungaro (1978) reported the presence of facies with colonial corals and calcareous algae at Perarolo-San Gottardo.

To establish the precise stratigraphic position of the Perarolo site within the Castelgomberto Calcarenite succession is difficult, considering that preliminary micropalaeontological investigations of the matrix embedding the fossils and the top samples of the "madreporic limestone" did not yield any stratigraphically significant microfossil. Unfortunately, during the excavations carried out about 35 years ago, no samples of the marls embedding the fossiliferous horizon were collected, thereby preventing any detailed micropalaeontological investigation. Pending further geological and stratigraphical research in the area, it must be emphasised that some authors proposed to locate the fossiliferous bed of Perarolo in the upper portion of the Castelgomberto Calcarenite (upper Rupelian), deposited when the lagoon progressively filled and sedimentation of fine-grained laminated limestones took place associated with fine grained terrigenous deposits (see Mietto 1988, 2003; De Angeli & Rossi 2006).

MATERIAL AND METHODS

This study is based on 11 fish specimens, all housed in the collections of the Museo di Geologia e Paleontologia dell'Università degli Studi di Padova. Seven specimens were originally collected by the late Mr. Antonio Rossi, while the remaining four were collected by Mr. Antonio De Angeli. Besides fishes, the collection of the Università degli Studi di Padova includes several crustaceans (especially the mud shrimp *Upogebia perarolensis*), annelids, a single gastropod and corals. The fossils are preserved in micritic limestone, with limited compression. The specimens were studied using a Leica M80 stereomicroscope equipped with camera lucida drawing arms. Some of them required matrix removal that was achieved using entomological needles to allow investigation of their anatomical details. Osteological terminology and comparative morphological data were derived from the literature (e.g., Fraser 1972; Miller 1973; Springer 1983; Birdsong et al. 1988; Blum 1988; Howes 1992; Nielsen et al. 1999; Mabuchi et al. 2014; Carnevale & Johnson 2015; Bannikov & Carnevale 2016). Extinct taxa are marked with a dagger (†) preceding their name.

Morphometric abbreviations (in the text). AFB, anal-fin base; CPD, caudal peduncle depth; CPL, caudal peduncle length; DFB, dorsal-fin base; MBD, maximum body depth; HD, head depth; HL, head length; OD, orbit diameter; PAD, preanal distance; PDD, predorsal distance; PPD, prepelvic distance; SL, standard length; TL, total length.

SYSTEMATIC PALAEONTOLOGY

Subdivision **PERCOMORPHACEAE** *sensu*
Betancur-R. et al., 2017
Order **Ophidiiformes** Berg, 1937
Suborder **Bythitoidei** Cohen & Nielsen, 1978
Family Dinematichthyidae *sensu* Møller et al., 2016
gen. and sp. indet.
Figs 5, 6

Material: MGP-PD R661, incomplete articulated skeleton, in part and counterpart; measurable length 46.5 mm (Fig. 5).

Description. MGP-PD R661 is represented by an incomplete articulated skeleton, lacking the posterior portion of the body and with partially displaced cranial elements (Fig. 5). The head is exposed in dorsal view. The cranial bones are badly damaged and displaced from their original position, making it difficult to interpret their morphology. The paired frontals and parietals are the only bones still in anatomical connection. The paired frontals are antero-posteriorly elongated and subquadrangular in shape, with smooth outer margins. The two contralateral parietals suture to each other along their medial margins, showing a condition similar to that of *Dinematichthys*, whereas in other cusk-eels they are usually separated by the supraoccipital (Howes 1992). Of the other cranial bones, only fragments of the jaws, preopercle and the opercle are partially recognizable, the latter being roughly triangular in shape, with at least one horizontal spine projecting posteriorly.

The preserved vertebral column consists of 11 abdominal and 22 (23) caudal vertebrae. However, this count is affected by the incomplete preservation of the caudal region. The structure of the anteriormost part of the vertebral column, especially the morphology and configuration of the epineurals and parapophyses (Fig. 6), is clearly consistent with that of ophidiiform fishes (e.g., Howes 1992; Carnevale & Johnson 2015; Parmentier et al. 2018; Přikryl & Carnevale 2018). The five anterior vertebrae possess modified epineurals that articulate with the vertebral centra. The first epineural, consistent with the 'wing-like process' as reported by Fine et al. (2007), occurs on the first vertebra; it is narrow proximally and expanded distally into a plate-like structure; it was probably originally horizontally oriented with its main axis able to rotate
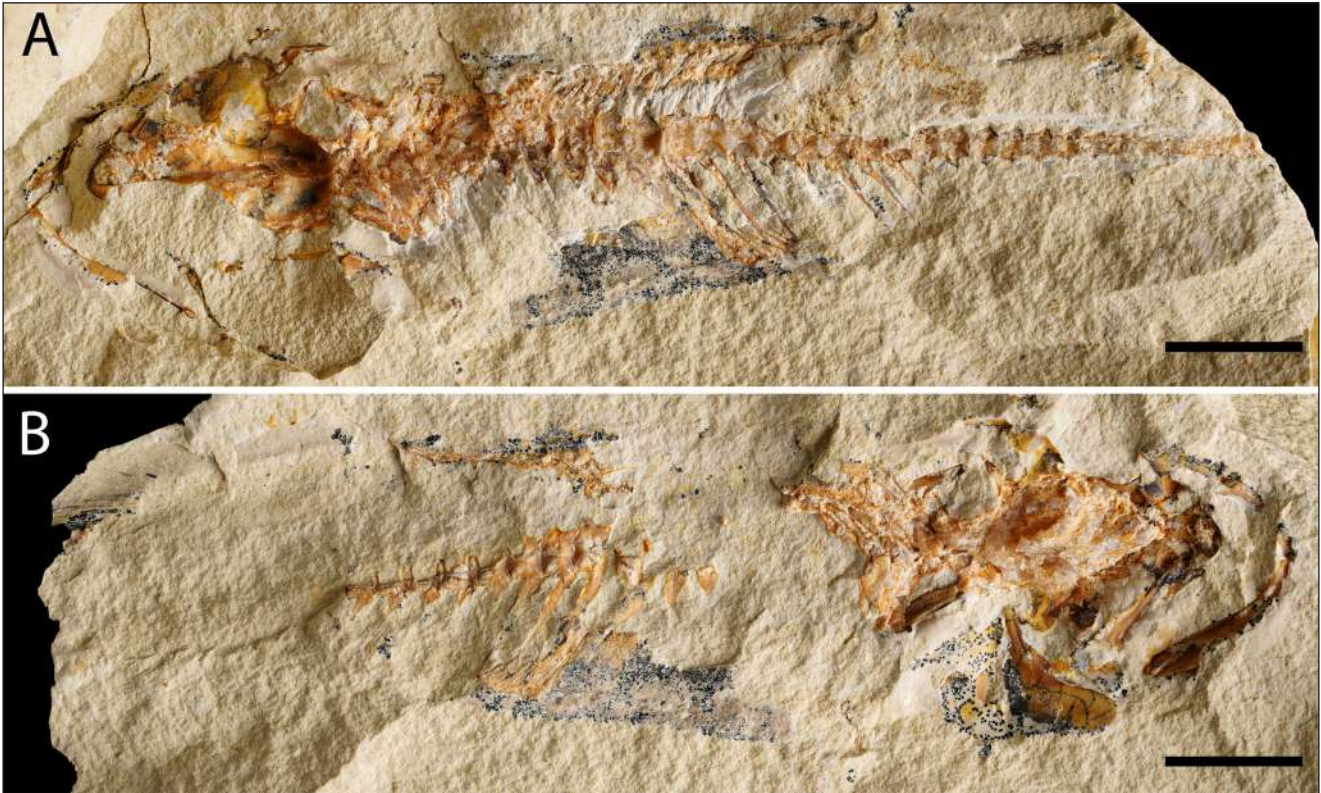
Fig. 5 - Dinematichthyidae indet., MGP-PD R661 in A) part and B) counterpart. Scale bars 5 mm.

posteriorly. The second to fourth epineurals are also plate-like but, contrary to the first one, these seem to be less free to rotate. The second epineural shows a rounded tip. It is interesting to note that a rounded tip on the second epineural is the only skeletal feature of the sound-producing apparatus that separates male from female individuals of *Neobythites* (Parmentier et al. 2018). The fifth epineural is proximally wider and tapers distally into a rod. The subsequent six abdominal vertebrae (from 6th to 11th) bear robust, lateral parapophyses with distally pointed tips, which become gradually longer and wider posteriorly. Some rib fragments are scattered in the abdominal cavity, displaced from their original position. The vertebral centra are almost subrectangular in shape, with the abdominal ones gradually increasing their size posteriorly. The anteriormost neural spine is shorter than those following, a condition that is characteristic of bythitoid taxa (Howes 1992; Nielsen 1999). The preserved 22 or 23 caudal vertebrae bear equally long neural and haemal spines, which are all fused to their respective centra and decrease gradually in length posteriorly.

Supraneurals appear to be absent although we cannot determine whether this represents a tapho-
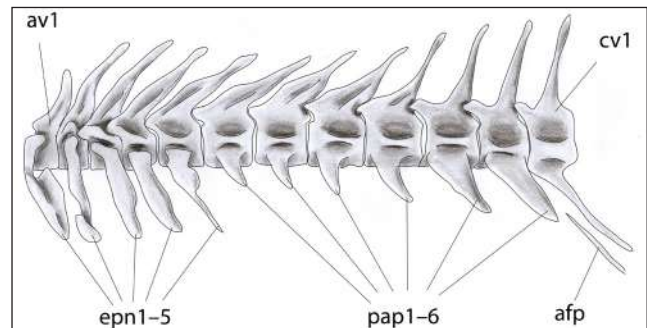
Fig. 6 - Dinematichthyidae indet., reconstruction of the anteriormost portion of the vertebral column of MGP-PD R661. Abbreviations: afp, first anal-fin pterygiophore; av1, first abdominal vertebra; cv1, first caudal vertebra; epn, epineurals; pap, parapophyses.

nomic artifact or a genuine morphological feature, as supraneurals can be either absent or cartilaginous (never ossified) in ophidiiforms (Rosen & Patterson 1989). Despite the dorsal and anal fins being poorly preserved and the number of rays and supports difficult to determine, their general outline and insertion can be partially recognized in the examined material. Both the dorsal and anal fins are long-based. The dorsal- and anal-fin rays are roughly equal in length and gradually decrease in size posteriorly. The dorsal- and anal-fin pterygiophores are more

numerous than adjacent vertebrae, as two dorsal pterygiophores usually insert on each interneural space (ratio 2:1), whereas three anal pterygiophores insert on each interhaemal space (ratio 3:1). The dorsal fin seems to originate at the level of the 5th or 6th vertebra, whereas the anal-fin origin is located more posteriorly, in the interneural space between the first and second caudal vertebrae, respectively. The first eight anal-fin pterygiophores are clearly recognizable. The anteriormost one is extremely elongated, being about twice the length of the succeeding ones, reaches the tip of the last abdominal parapophysis, and overtaking the tip of the first haemal spine. This condition is unique among bythitoids and has been used to diagnose the family Dinematichthyidae (Schwarzhans & Møller 2005, 2007; Møller & Schwarzhans 2006, 2008; Møller et al. 2016).

A single spine-like ray lying at the level of the opercle is interpreted here as the single pelvic-fin ray that characterizes several bythidoits, especially the dinematichthyids (Møller et al. 2016). The caudal skeleton is not preserved. Body scales are apparently absent but, even in this case, we cannot determine whether this represents a genuine morphological character or a taphonomic artifact, as scales can be either absent or present in dinematichthyids and other ophidiiforms (e.g., Nielsen et al. 1999).

Remarks. Fishes of the order Ophidiiformes, also known as cusk-eels, are a diverse group of acanthomorph fishes that includes about 120 genera and 550 species mostly inhabiting the deep sea and the oceanic environment, although some taxa live in shallow continental shelves, tropical coral reefs, and brackish waters, including some inland caves (Nielsen 1977; Nielsen et al. 1999, 2009; Møller et al. 2006; Nelson et al. 2016; Fricke et al. 2021; Froese & Pauly 2021). Cusk-eels have been traditionally arranged into two suborders, Ophidioidei and Bythitoidei, each represented by two oviparous (Carapidae and Ophidiidae) and two viviparous (Aphyonidae and Bythitidae) families, respectively, with the subordinal classification primarily based on their reproductive biology, position of the anterior nostrils and pelvic-fin origin, and caudal fin connection with dorsal and anal fins (Cohen & Nielsen 1978; Nielsen et al. 1999; Carnevale & Johnson 2015; Betancur R et al. 2013). More recently, based on molecular, morphological and fossil evidence, Møller et al. (2016) proposed a new classification of

the suborder Bythitoidei, elevating the bythitid tribe Dinematichthyini at familial level and placing the Aphyonidae as a derived, paedomorphic member of the Bythitidae. Moreover, Campbell et al. (2017) recognized another family of unclear taxonomic affinity, the Parabrotulidae, as phylogenetically nested within Bythitidae. Therefore, the Ophidiiformes currently comprises four families: Carapidae, Bythithidae, Dinematichthyidae, and Ophidiidae (Møller et al. 2016; Fricke et al. 2021).

Ophidiiforms are characterized by elongate and tapering eel-like bodies with long dorsal and anal fins that are usually confluent with the caudal fin, and mental or jugular pelvic fins (e.g., Howes 1992; Nielsen et al. 1999, 2009). According to Carnevale & Johnson (2015) the exclusion of the supraoccipital from the posterior margin of the neurocranium can be considered as the only putative ophidiiform synapomorphy (see also Howes 1992). Although this character cannot be unambiguously checked in the fossil under study, the assignment of MGP-PD R661 to the order Ophidiiformes is justified by the general physiognomy of the body, which is elongate, with long-based dorsal and anal fins, dorsal- and anal-fin pterygiophores more numerous than adjacent vertebrae (dorsal ratio about 2:1), pelvic fin inserted at the level of the opercular apparatus, supraneurals absent (or cartilaginous in origin), and the peculiar anatomy of the anterior portion of the vertebral column (see e.g., Howes 1992; Nielsen et al. 1999; Carnevale & Johnson 2015; Nelson et al. 2016; Parmentier et al. 2018; Přikryl & Carnevale 2018).

MGP-PD R661 exhibits a combination of features that support its placement in the suborder Bythitoidei (see Cohen & Nielsen 1978; Howes 1992; Nielsen et al. 1999; Carnevale & Johnson 2015; Nelson et al. 2016; Přikryl & Carnevale 2018), including a small number of abdominal vertebrae (11), anterior abdominal vertebrae with expanded epineurals and parapophyes, anterior neural spine shorter than those following, a single spine-like pelvic-fin ray inserted at the level of the opercle, strong opercular spine, and anal-fin rays almost equal in length to the opposite dorsal ones. We can exclude the alignment of MGP-PD R661 with the Ophidioidei, because their pelvic fins, when present, originate at least at the level of the preopercle, and the anal-fin rays are usually longer than opposing dorsal-fin rays (Nielsen et al. 1999; Nelson et al. 2016).

The development of expanded anterior epineurals, as well as the other skeletal structures associated with the swimbladder (e.g., rocker bone, swimbladder plate, etc.) have been regarded as a derived condition emerging simultaneously in several bythitoid and ophidioid taxa characterized by an anteriorly situated swimbladder, intimately associated with expanded first to third epipleurals, the first of which occurs on the first centrum ('Group 1' of Howes 1992). Conversely, ophidiiform taxa characterized by a posteriorly situated swimbladder (secondarily lost in bythitids of the traditional 'Aphyonidae' clade) lack the expanded epineurals associated with the anterior vertebrae ('Group 2' of Howes 1992). In this context, the presence of expanded epipleurals on the first five vertebrae in MGP-PD R661, suggest that an anteriorly positioned swimbladder was probably characteristic of this Oligocene ophidiiform. Although the possession of expanded epineurals and parapophyses, united with the presence of 11 abdominal vertebrae is characteristic of many ophidioid and bythitoid genera (see Carnevale & Johnson 2015; Møller et al. 2016), the hypertrophy of the vertebral structures associated with the first centra and the number of abdominal vertebrae is exclusive of the Dinematichthyidae and those members of the family Bythitidae possessing a swimbladder (Cohen & Nielsen 1978; Nielsen et al. 1999; Nelson et al. 2016).

The two bythitoid families Bythitidae and Dinematichthyidae were diagnosed by Møller et al. (2016) based on the number of copulatory organs, a caudal fin that can be separated or fused with the dorsal and anal fins, different meristic ranges, and length of the first anal-fin pterygiophore that can be equal to the succeeding ones (Bythitidae), or slightly to strongly elongated (Dinematichthyidae) (see also Schwarzhans & Møller 2005, 2007; Møller & Schwarzhans 2006, 2008). Although the morphology of some of these features cannot be determined in MGP-PD R661 (e.g., copulatory organs, caudal-fin pattern, number of median-fin rays and caudal vertebrae), and 11 abdominal vertebrae are not indicative of the familial affinity (10-50 in Bythitidae; 10-25 in Dinematichthyidae), the presence of a first anal-fin pterygiophore that is twice as long as the following ones and parietals that meet mesially along their midline (see Howes 1992; Møller et al. 2016) clearly support the placement of MGP-PD R661 as a dinematichthyid cusk-eel. Unfortunately, due to its incompleteness a more detailed taxonomic interpretation is not possible.

Order **Gobiiformes** *sensu* Thacker, 2014
Suborder **Apogonoidei** *sensu* Thacker, 2014
Family Apogonidae Günther, 1859
Subfamily Pseudamiinae Smith, 1954
Genus †*Oligopseudamia* gen. n.
urn:lsid:zoobank.org:act:1F73FA6F-D6E1-4EB3-A21A-05AC5175D725

Origin of the name: The genus name is a combination of Oligocene and the extant genus name *Pseudamia*, hence a pseudamiine cardinalfish from the Oligocene.

Diagnosis: A pseudamiine that differs from *Pseudamia* in having an anal fin with a single spine plus seven rays (vs. II, 8–10), supraneurals absent (vs. 1–2), and no scales on the opercle (vs. opercle scaled). Moreover, †*Oligopseudamia* gen. n. is also defined by the following combination of characters: very large orbit contained about two times in the length of the head; dorsal-fin pterygiophore pattern -/-/1/2/1/1/0/1/2/1/3/1/1; anal-fin pterygiophore pattern 2/3/1/1; spinous and soft dorsal fins well separated; dorsal fin VI+I,8; a single supernumerary spine on the first dorsal-fin pterygiophore; first segmented anal ray branched; pelvic fin I,5; 24 (10+14) vertebrae; eight rod-like rib pairs on 3rd to 10th vertebra; canine teeth on the anterior border of the premaxilla and dentary; supramaxilla absent; preopercle with smooth posterior and ventral margins; deep notch on the dorsal side of the anterior ceratohyal; hypurals 1+2 and 3+4 fused, forming two separate and autogenous large triangular plates; fifth hypural present and splint-like; parhypural autogenous and not fused to the hypaxial hypural plate; a single pair of uroneurals; two epurals; haemal spines of PU2 and PU3 fused to their respective centra; seven horizontal rows of thin cycloid scales; no scales on cheek, urohyal, opercular and gular regions, or caudal fin base.

Type species: †*Oligopseudamia iancurtisi* sp. n.
Included species: Type species only.

†*Oligopseudamia iancurtisi* sp. n.

Figs 7–10

Origin of the name: Species named after the late British musician and composer Ian Curtis in honour of his music, which was an excellent companion during long hours at the microscope while analysing the fossil specimens.

Holotype: MGP-PD R662, well-preserved articulated skeleton, 21.5 mm SL (Fig. 7).

Paratypes: MGP-PD 31968, nearly complete, articulated skeleton, in part and counterpart, 22.2 mm SL (Fig. 8A); MGP-PD R665, nearly complete, articulated skeleton, in part and counterpart, 17.1 mm SL (Fig. 8B–C); MGP-PD 31964, nearly complete, articulated skeleton, in part and counterpart, 24.8 mm SL; MGP-PD R656, incomplete skeleton lacking the anterior part of the body, in part and counterpart; MGP-PD 31965, incomplete skeleton lacking the anterior part of the body.

Type horizon: Rupelian, lower Oligocene (see Bassi et al. 2007; Bosellini et al. 2020).

Type locality: Perarolo district, Arcugnano town, Berici Hills (Vicenza Province; NE Italy).

Fig. 7 - †*Oligopseudamia iancurtisi* gen. et sp. n., MGP-PD R662, holotype. Scale bars 5 mm.

Diagnosis: As for the genus.

Measurements as % SL: TL 125.8–128.4; HL 26.1–36.3; HD 24.7–29.2; MBD 25.0–31.6; OD 12.5–14.0; DFB 31.5–33.0; AFB 10.9–11.6; CPL 27.0–32.7; CPD 12.9–17.0; PDD 40.0–41.1; PPD 39.5; PAD 61.7–63.3.

Description. The general body physiognomy of †*Oligopseudamia iancurtisi* gen. et sp. n. (Figs 7–8) is consistent with that of the living genus *Pseudamia* (see e.g., Randall et al. 1985), being relatively elongate, deeper in the anterior portion (MBD contained 3.2–4.0 in SL) and tapering posteriorly (CPD 5.9–7.8 in SL). The caudal peduncle is straight, long and slender (CPL 3.1–3.7 in SL). There are two well-separated dorsal fins and a large caudal fin. The head is large and contained about three times in SL. The mouth is terminal. The orbit is very large, contained about two times in head length.

The neurocranium is moderately deep (Fig. 9). The frontals are the largest bones of the skull roof. The parietals contact the frontals anteriorly but are separated medially by the supraoccipital, whose crest appears to be poorly developed. The ethmoidal, otic and occipital regions are inadequately preserved and their bones difficult to describe in all specimens, except for the lateral ethmoid which is narrow, columnar and forms the anteriormost border of the orbit, whereas the prootic and sphenotic contribute to the formation of the posterior border of the orbit.

There are six infraorbitals, the first of which (lachrymal) is the largest of the series and shows a smooth ventral edge; the second and third infraorbitals are smaller and have smooth upper edges; the fourth to sixth are small, thin, and surround the posterior border of the orbit.

The premaxilla is elongate with a tiny and straight posterior end; the ascending and articular processes of the premaxillae are equally developed, whereas a quadrangular postmaxillary process emerges at its midlength. Small villiform teeth are distributed along the entire alveolar margin of the premaxilla, whereas enlarged canine-like teeth can be observed at its anteriormost extremity. The edentulous maxilla is narrow and elongate, without a downwardly projected spine at its posterior corner. There are no supramaxillae. The lower jaw is large and relatively low. The dentary is elongate and nearly triangular in outline, with numerous small villiform teeth and enlarged caniniform teeth at its anterior extremity. The angulo-articular is well developed, its articulatory facet for the condyle of the quadrate is situated below the posterior border of the orbit.

The quadrate is large and triangular. The ectopterygoid is thin, with the anterior horizontal arm longer than the vertical one, and the two arms forming an angle of about 114 degrees. The metapterygoid is well developed and quadrangular in outline. The other bones of the suspensorium are inadequately preserved in all specimens examined.

The opercular series and hyoid apparatus are better preserved in the holotype and MGP-PD R665
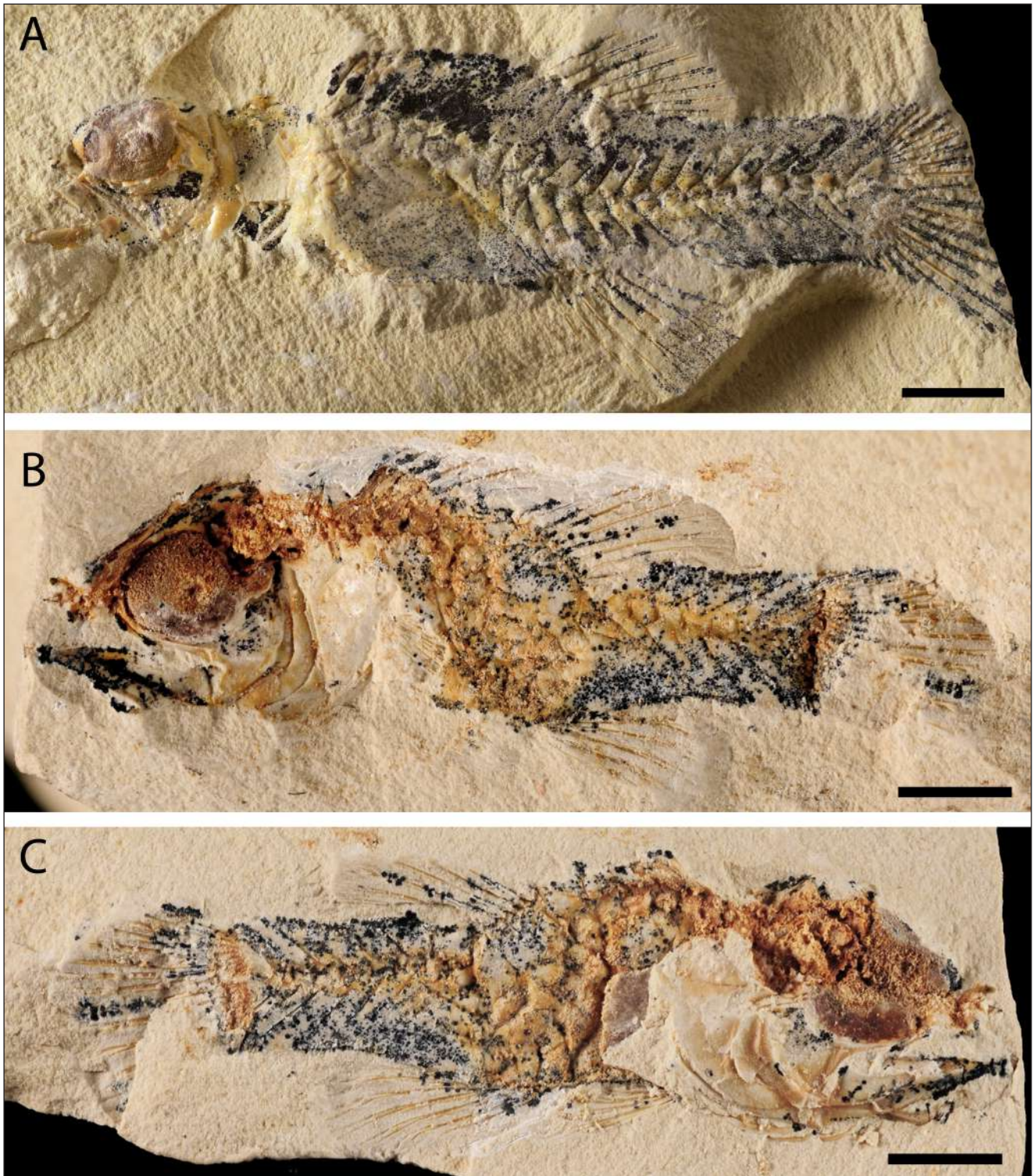
Fig. 8 - †*Oligopseudamia iancurtisi* gen. et sp. n., selected paratypes. A) MGP-PD 31968, B) MGP-PD R665b, C) MGP-PD R665a. Scale bars 2 mm.

(Figs 7–9). The preopercle is crescent shaped, with equally developed dorsal and ventral arms forming a right angle. The interopercle is rather large. The opercle is relatively large, almost quadrangular. The subopercle is small and elongate. There are no spines or serrations on any bone of the opercular series.

The hyoid arch is consistent with that of apogonids (see Mabuchi et al. 2014), bearing seven branchiostegal rays, the three anterior ones lying on the anterior portion of the anterior ceratohyal,

Fig. 9 - †*Oligopseudamia iancurtisi* gen. et sp. n., reconstruction of the head mainly based on the holotype MGP-PD R662 and the paratype MGP-PD R665. Abbreviations: aa, angulo-articular; 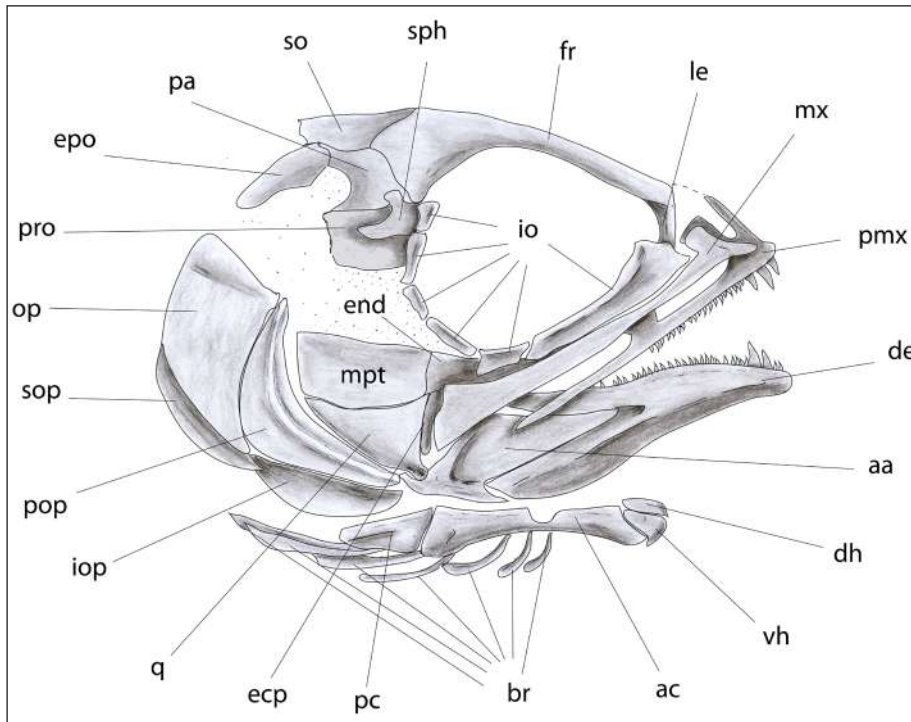ac, anterior ceratohyal; br, branchiostegal rays; de, dentary; dh, dorsal hypohyal; ecp, ectopterygoid; enp, endopterygoid; epo, epioccipital; fr, frontal; io, infra-orbitals; iop, interopercle; le, lateral ethmoid; mtp, metapterygoid; mx, maxilla; op, opercle; pa, parietal; pc, posterior ceratohyal; pmx, premaxilla; pop, preopercle; pro, prootic; q, quadrate; so, supraoccipital; sop, subopercle; sph, sphenotic; vh, ventral hypohyal.
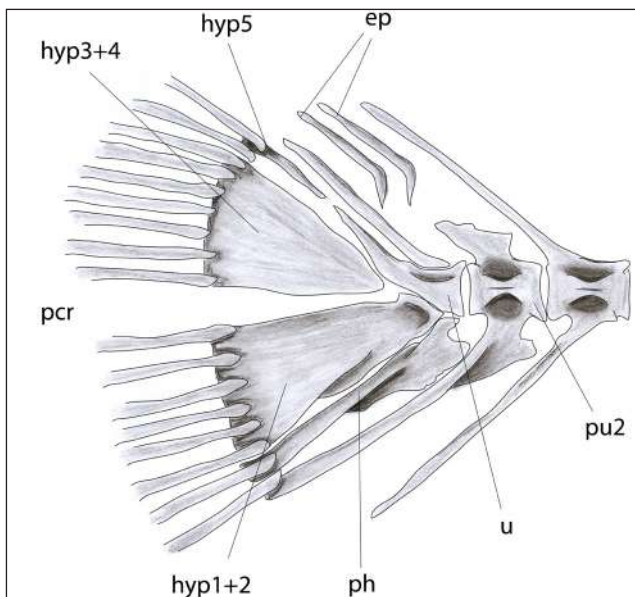

Fig. 10 - † *Oligopseudamia iancurtisi* gen. et sp. n., reconstruction of the caudal skeleton mainly based on the holotype MGP-PD R662 and paratype MGP-PD 31964. Abbreviations: ep, epurals; hyp, hypurals; pcr, principal caudal-fin rays; ph, parhypural; pu, preural centrum; u, urostyle.

followed by two branchiostegals articulating on its posterior sector; the posteriormost two branchiostegal rays articulate with the posterior ceratohyal. Furthermore, the anterior ceratohyal is characterized by a deep notch in its dorsal margin at about midlength, resembling the condition in *Pseudamia* (see Randall et al. 1985) and some apogonine species like *Taeniamia* (see Fraser 2013). Dorsal and

ventral hypohyals are barely recognizable.

The vertebral column is moderately curved and comprises 24 vertebrae (including the urostyle), of which ten are abdominal and 14 are caudal. The centra are hourglass-shaped. There are eight relatively slender, rod-like rib pairs from the 3rd to the 10th vertebrae. The epineurals are difficult to recognize.

The morphology of the caudal skeleton (Fig. 10) is consistent with that of *Pseudamia* and some apogonines (see e.g., Fraser 1972, pls. 5–6; Mabuchi et al. 2014). There are two autogenous hypural plates formed by the fusion of hypurals 1+2 and 3+4, with the latter plate separated from the urostyle. The fifth hypural is small and splint-like. The parhypural is long and autogenous. There is a single uroneural pair and two epurals. The haemal spines of the second and third preural vertebrae are fused to the centrum; the second preural vertebra bears a short neural crest. The caudal fin is broad, with a convex posterior margin, and comprises 17 (9+8) principal rays plus six dorsal and five ventral procurrent rays.

There are no supraneurals (Figs 7–8). The spinous dorsal fin is well separated from the soft dorsal fin. In the most complete specimens, the spinous dorsal fin has six spines, the first of which is supernumerary on the first dorsal-fin pterygiophore, and originates at the level of the third

abdominal vertebra. The second dorsal fin possesses a single spine and eight soft rays (dorsal-fin formula VI+I,8) and the following pterygiophore pattern (*sensu* Springer & Smith-Vaniz 2008): -/-/1/2/1/1/0/1/2/1/3/1/1. The anal fin is nearly opposite to the second dorsal fin, possesses a rounded distal margin, and consists of a single spine in supernumerary association and seven soft rays (I,7). The anteriormost anal-fin pterygiophore has a straight proximal-middle portion. The anal-fin pterygiophore pattern is 2/3/1/1.

The pectoral girdle is partially exposed in the holotype only (Fig. 7). The posttemporal is poorly preserved. The supracleithrum is thin and rod-like. The cleithrum is elongate with a dorsally directed projection at its antero-dorsal corner and a postero-dorsal fan-shaped plate; the cleithrum narrows ventrally where it sutures with the anterior margins of the coracoid and the scapula, this latter bearing a posterior facet for articulation with the pectoral-fin rays, which are at least ten in MGP-PD R665. Dorsal and ventral postcleithra are possibly fused into a single rod-like bone (see Fraser 1972, pl. 13). The pelvic fins are thoracic in position and originate anterior to the spinous dorsal fin insertion. Each pelvic fin bears a single spine and five soft rays (I,5). The outline of the basipterygia is difficult to determine.

The squamation is recognizable only in the anterior part of the body of MGP-PD R665 (Fig. 8B–C) and consists of at least seven horizontal rows of thin cycloid scales. The lateral line is difficult to see. Minute spots of dark pigments cover the entire body, head and fins in most specimens.

Remarks. Several morphological and molecular analyses concur to suggest that a large group of percomorph fishes including cardinalfishes (suborder Apogonoidei), gobies (suborder Gobioidei), nurseryfishes (suborder Kurtoidei), and possibly ponyfishes (family Leiognathidae) and sanddivers (genus *Trachinotus*) are closely related (e.g., Miller 1973; Winterbottom 1993; Near et al. 2012, 2013; Betancur-R et al. 2013; Thacker 2014; Thacker et al. 2015), leading Thacker (2014) to include all of them in the order Gobiiformes.

The suborder Apogonoidei has been reliably resolved as the sister group of the Gobioidei by Thacker (2014). Cardinalfishes of the family Apogonidae include about 380 species arranged in about 40 genera that are distributed in all oceans, with a few of them living in brackish of fresh waters

(Mabuchi et al. 2014; Nelson et al. 2016; Fricke et al. 2021). Despite several studies (e.g., Fraser 1972, 2013; Baldwin & Johnson 1999) suggesting putative morphological synapomorphies to diagnose the family, its taxonomic composition and intrarelationships are still debated. Mabuchi et al. (2014), in their revision of cardinalfish systematics based on morphological and molecular data, recognized four possible apogonid synapomorphies: 1) a single supernumerary anal spine with the following spine or ray in serial association with the first anal-fin pterygiophore; 2) mouth brooding of fertilized eggs; 3) simple filaments around the micropyle of the egg; 4) swimbladder with a dorsal or anterodorsal oval and ventral gas glands, with no anterior projections to the skull or posterior connections with the first anal pterygiophore. Although most of these characters are impossible to detect in fossils, Fraser (1972, 2013), Johnson (1984), Baldwin & Johnson (1999), and Mabuchi et al. (2014) indicated a combination of key morphological and meristic features, easily recognizable in fossils, which make it possible to distinguish the apogonids from other percomorphs. In this perspective, Mabuchi et al. (2014) proposed a new classification of the family that includes, along with the traditional Apogoninae (34 genera) and Pseudamiinae (one genus, *Pseudamia*), two new subfamilies: the Amioidinae, with the genera *Amioides* and *Holapogon*, and the monotypic Paxtoninae, including the peculiar genus *Paxton* only. Mabuchi et al. (2014) regarded *Pseudamia* as sister to all the other extant apogonids. This genus was assigned to a separate family by Thacker & Roje (2009) and Cowman & Bellwood (2011).

†*Oligopseudamia* gen. n. can be assigned to the Apogonidae based on the presence of parietals separated by the supraoccipital; six infraorbitals including a lachrymal with a smooth lower margin; seven branchiostegals, of which the anteriormost three lie in the middle part of the anterior ceratohyal, followed by two on the distal corner of anterior ceratohyal, and two on the posterior ceratohyal; a single anal-fin spine in supernumerary association; first anal-fin ray branched; two completely separated dorsal-fin lobes; 10+14 vertebrae; second preural vertebra bearing a neural crest (see Fraser 1972; Johnson 1984; Mabuchi et al. 2014).

The combination of meristic and osteological features easily allows us to detect the subfamilial affinities of †*Oligopseudamia iancurtisi* gen. et sp.

	†*Oligopseudamia*	Pseudamiinae	Apogoninae	Amiodinae	Paxtoninae
Posterior edge of preopercle	smooth	smooth/serrate	smooth/serrate	serrate	single spine
Prootic included in orbit margin	yes	yes	yes	?	no
Supramaxilla	absent	absent	absent/present	present	absent
Enlarged caniniform teeth	present	present	present/absent	absent	absent
Anterior ceratohyal	notched	notched	notched/unnotched	perforated	unnotched
Supraneurals	0	1-2	0-3	3	0
Dorsal-fin lobes	separate	separate	separate	separate	continuous
Dorsal-fin	VI+I,8	VI+I,8-10	VI-VIII+I,9-13	VII-VIII+I,9-10	VI,19
Supernumerary dorsal spines	1	1	1-2	2	1
Some dorsal pterygiophores	equidistant	equidistant	equidistant	closely associated	closely associated
Anal-fin	I,7	II,8-10	II,8-18	II,7-8	I,15-16
First anal pterygiophore	straight	straight	straight	straight	curved
Caudal-fin shape	rounded to rhomboid	rounded to rhomboid	forked, truncate, or slightly rounded	forked	truncate or slightly rounded
Caudal-fin rays	17	17	17	15	17
Hypurals 1-4	1+2, 3+4	1+2, 3+4	1+2, 3+4; 1+2, 3 and 4 unfused; 1+2+3+4; all unfused	unfused	1+2, 3+4+U
Hypural 5	present	present	present	present	absent
Uroneural pairs	1	0-1	0-1	2	0
Epurals	2	2	0-3	3	2
Parhypural	autogenous	autogenous	fused to hyp1+2 or autogenous	autogenous	fused to hyp1+2
PU2 haemal spine	fused to centrum	fused to centrum	autogenous/fused	autogenous	?
PU3 haemal spine	fused to centrum	fused to centrum	autogenous/fused	autogenous	fused to centrum
Scales	cycloid	cycloid	cycloid/ctenoid/spinoid/absent	ctenoid	absent
Head scales	absent	absent	present	?	absent

Tab. 1 - Selected morphological and meristic features used to discriminate the apogonid subfamilies. Grey cells indicate those characters of †*Oligopseudamia iancurtisi* gen. et sp. n. that fall within the range of the subfamilies. Data from Smith (1954), Fraser (1972), Randall et al. (1985), Allen (1999), Baldwin & Johnson (1999), and Mabuchi et al. (2014).

n. (Tab. 1). Alignment with the Amioidinae can be ruled out because of the absence of a supramaxilla (vs. large supramaxilla in amioidines), presence of 17 branched caudal-fin rays (vs. 15), fused hypurals 1+2 and 3+4 (vs. unfused), haemal spines of the second and third preural vertebrae fused to the centra (vs. autogenous), two epurals (vs. three), dorsal-fin formula VI+I,8 (vs. VII or VII-II+I,9–10), anal-fin formula I,7 (vs. II,7–8), a single supernumerary dorsal-fin spine (vs. two), supraneurals absent (vs. three), dorsal-fin pterygiophores not closely associated (vs. closely associated), and preopercle edge smooth (vs. serrate). †*Oligopseudamia* gen. n. differs from the monotypic paxtonine *Paxton* in the presence of a dorsal fin with two well separated lobes (vs. single continuous), dorsal fin VI+I,8 (vs. VI,19), no spines on the preopercle (vs. a single spine), prootic included in the inner orbit margin (vs. excluded), anal fin I,7 (vs. I,15–16), first anal-fin pterygiophore straight (vs. strongly curved), uroneurals present (vs. absent), parhypural autogenous (vs. fused to hypurals 1+2),

and fifth hypural present (vs. absent). Conversely, the combined osteological features and meristic counts of †*Oligopseudamia* gen. n. are more consistent with features that occur in some genera of the subfamily Apogoninae and the monotypic pseudamiine genus *Pseudamia* in having a prootic included as part of the inner orbit margin; supramaxillae absent; internal support of dorsal spines by serial proximal-middle radials not in close association; straight first anal-fin pterygiophore; a single supernumerary dorsal-fin spine; smooth preopercle; and the caudal skeleton configuration (see Mabuchi et al. 2014). However, †*Oligopseudamia* gen. n. clearly shares more traits with the monotypic pseudamiine genus *Pseudamia*, being also characterized by a similar body physiognomy, dorsal-fin formula (VI+I,8), deep notch on the dorsal margin of anterior ceratohyal, a large caudal fin, enlarged canine-like teeth on premaxilla and dentary, and scales absent on cheek, urohyal, gular regions, and caudal-fin base (Smith 1954; Randall et al. 1985; Mabuchi et al. 2014). The presence of large caniniform teeth on

the premaxilla and dentary was formerly regarded as a synapomorphy of the genera *Gymnapogon* and *Pseudamiops*, which were traditionally included in the Pseudamiinae (e.g., Smith 1954, 1961; Fraser 1972; Allen 1999). In any case, contrary to †*Oligopseudamia* gen. n., *Pseudamiops* possesses a rear corner of the maxilla with a tiny, downward projecting spine, whereas *Gymnapogon* has a distinct posteriorly directed spine at the angle of the preopercle, scales absent, and a forked caudal fin (Smith 1954, 1961; Allen 1999; Mabuchi et al. 2014). Another apogonine, *Cheilodipterus*, has enlarged canine-like teeth but it also possesses strong transforming ctenoid scales (*sensu* Roberts 1993) and a deeply forked caudal fin (Allen 1999). Although the absence of supraneurals also has been observed in some apogonine species, the condition of †*O. iancurtisi* gen. et sp. n. can be considered as a distinctive trait with respect to the condition of *Pseudamia* (1–2 supraneurals) and most of the apogonines (1–3). In conclusion, the overall physiognomic similarity with *Pseudamia* and the presence of several shared skeletal and meritistic features (Tab. 1; Smith 1954; Fraser 1982; Randall et al. 1985; Mabuchi et al. 2014) support the assignment of †*Oligopseudamia* gen. n. as a putative member of the apogonid subfamily Pseudamiinae.

Subfamily Apogoninae Günther, 1859
Tribe †Eoapogonini Bannikov, 2005
Genus †*Arconiapogon* gen. n.
urn:lsid:zoobank.org:act:D0E774B3-0B18-4371-AA27-
66693CEB967C

Origin of the name: Genus name derived from '*Arconianum*', referring to the Latin name of the Arcugnano town, and the extant cardinalfish genus *Apogon*.

Diagnosis: †Eoapogonine cardinalfish unique in having dorsal-fin formula VI+I,9. Moreover, †*Arconiapogon* shows the following combination of characters: head length and depth less than body depth; prootic included as part of the inner orbit margin; supramaxilla small; no canine-like teeth on premaxilla or dentary; preopercle with fine serrations along posterior border; posttemporal without posteroventrally directed spines; dorsal fin with two well-separated lobes; anal fin with two spines and six rays; posterior edge of caudal fin rounded; large cycloid scales on body; small cycloid scales on the cheek, urohyal, gular regions, and base of caudal fin; single lateral-line series formed by 23 or 24 grooved and pored scales.

Type species: †*Arconiapogon deangelii* sp. n.
Included species: Type species only.

†*Arconiapogon deangelii* sp. n.
Figs 11, 12

Origin of the name: The species is named after Mr. Anto-

nio De Angeli who collected and made available some of the specimens described in this paper.

Holotype: MGP-PD 31963, well-preserved, nearly complete articulated skeleton, in part and counterpart, 118.8 mm SL (holotype by monotypy; Fig. 11).

Type horizon: Rupelian, lower Oligocene (see Bassi et al. 2007; Bosellini et al. 2020).

Type locality: Perarolo district, Arcugnano town, Berici Hills (Vicenza Province; NE Italy).

Diagnosis: As for the genus.

Measurements as % SL: TL 126.3; HL 37.3; HD 30.5; MBD 41.3; OD 9.9; DFB 41.5; AFB 16.0; CPL 21.9; CPD 17.6; PDD 37.7; PPD 45.5; PAD 64.2.

Description. †*Arconiapogon deangelii* gen. et sp. n. is represented by a fish measuring 118.8 mm SL and about 150 mm TL (Fig. 11). The body is relatively deep and its maximum depth is contained 2.4 times in SL. The head is large, slightly longer than high with its length contained 2.7 times in SL. The dorsal and ventral profiles of the body are almost equally convex. The orbit is rounded and large, its diameter contained about ten times in SL. The mouth is terminal with a relatively small and oblique gape. The dorsal fin is formed by clearly separated spiny and soft lobes. The caudal peduncle is straight, relatively long (4.6 times in SL) and deep (5.7 times in SL).

The neurocranium is relatively robust and deep (Fig. 12). The outer margin of the nasal-frontal profile is nearly straight, with the frontals representing the largest bones of the skull roof. The moderately developed supraoccipital crest extends on the rear part of the skull. The parasphenoid is poorly preserved and appears straight for most of its length. The prootic is included as part of the inner margin of the orbit, suggesting that it probably separated the parasphenoid from the pterosphenoid as, for example, in *Taeniamia macroptera* (see Fraser 2013, fig. 15). There are six infraorbitals closely associated to each other. The lachrymal is the largest of the series and shows a smooth lower margin. All the other infraorbitals gradually decrease in size posteriorly in the series and have smooth dorsal and ventral margins. The last two infraorbitals are preserved as thin sheets of bone just below the sphenotic. A subrectangular bone apparently contacting the frontal is interpreted herein as a nasal.

The premaxilla is sigmoid in shape and well developed, extending for the entire oral margin and possibly excluding the maxilla from it. The ascending and articular processes of the premaxilla are rather small and roughly equal in size. Small pre-
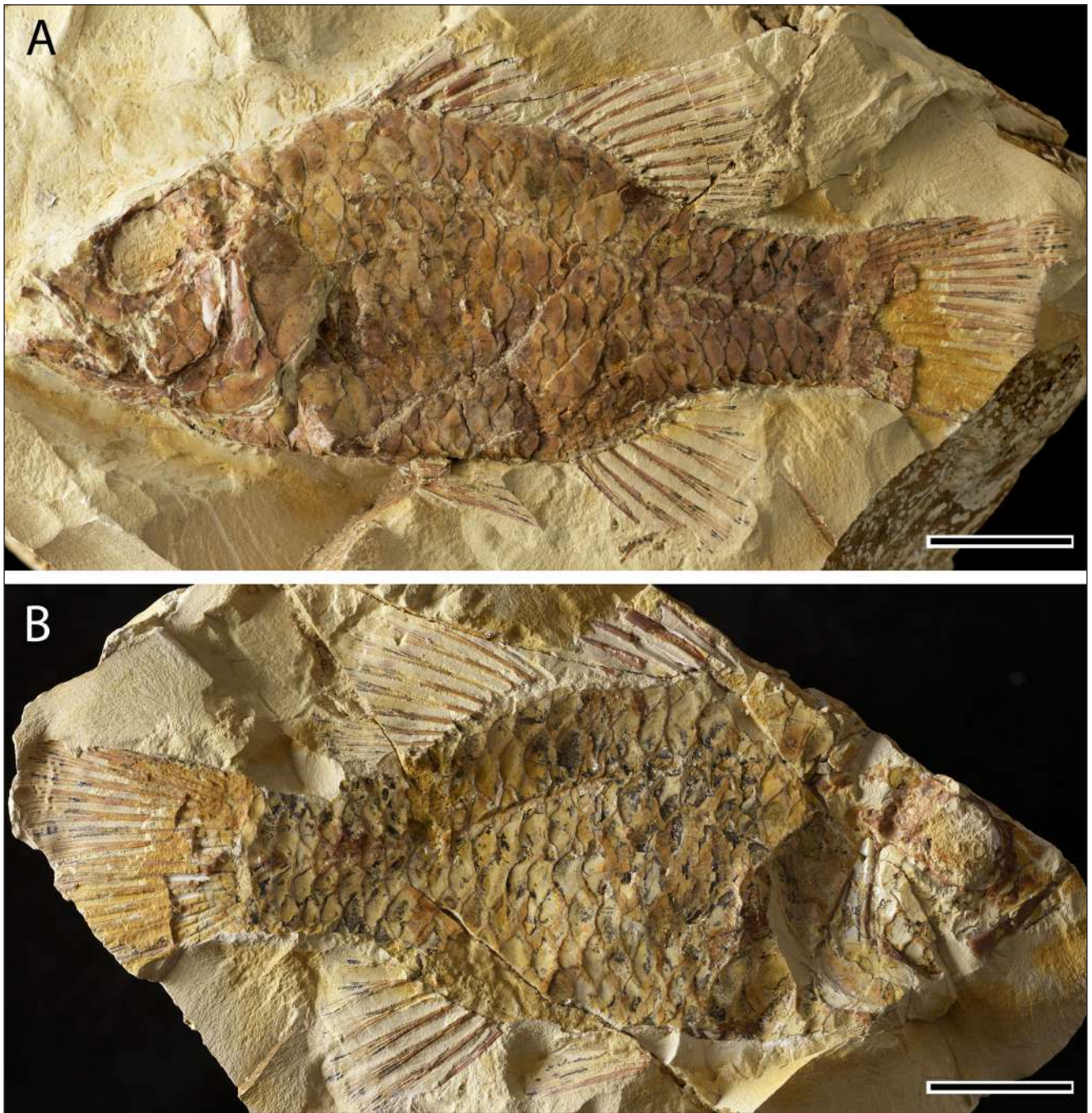
Fig. 11 - †*Arconiapogon deangelii* gen. et sp. n., MGP-PD MGP-PD 31963, holotype in A) part and B) counterpart. Scale bars 20 mm.

maxillary teeth are visible along the alveolar process. The maxilla has an elongated and very narrow anterior shaft and an expanded posterior edge. The maxilla is not sheathed by the lachrymal. There is a single, small supramaxilla. The dentary is moderately deep, steep at the symphysis, showing almost equally elongate coronoid and ventral processes. Dentary teeth are small and numerous along the entire alveolar surface but no symphyseal canine-like teeth are present. The anguloarticular and most of the bones of the suspensorium are hidden by the infraorbitals as well as by the scales on cheek.

The preopercle is L-shaped, with dorsal and ventral arms of almost the same length. The posterior edge of the preopercle is ornamented with fine serrations, whereas the ventral margin appears to be smooth. The interopercle is slightly larger than the subopercle and borders the ventral margin of the preopercle. The opercle is large, about twice as deep as it is broad and trapezoidal in shape. The surface

Fig. 12 - †*Arconiapogon deangelii* gen. et sp. n., reconstruction of the head of the holotype MGP-PD 31963. Abbreviations: ac, anterior ceratohyal; de, dentary; epo, epioccipital; fr, frontal; io, infraorbitals; iop, interopercle; le, lateral ethmoid; mx, maxilla; na, nasal; op, opercle; pa, parietal; pmx, premaxilla; pop, preopercle; pro, prootic; psp, parasphenoid; sc, scales; smx, supramaxilla; so, supraoccipital; sop, subopercle.
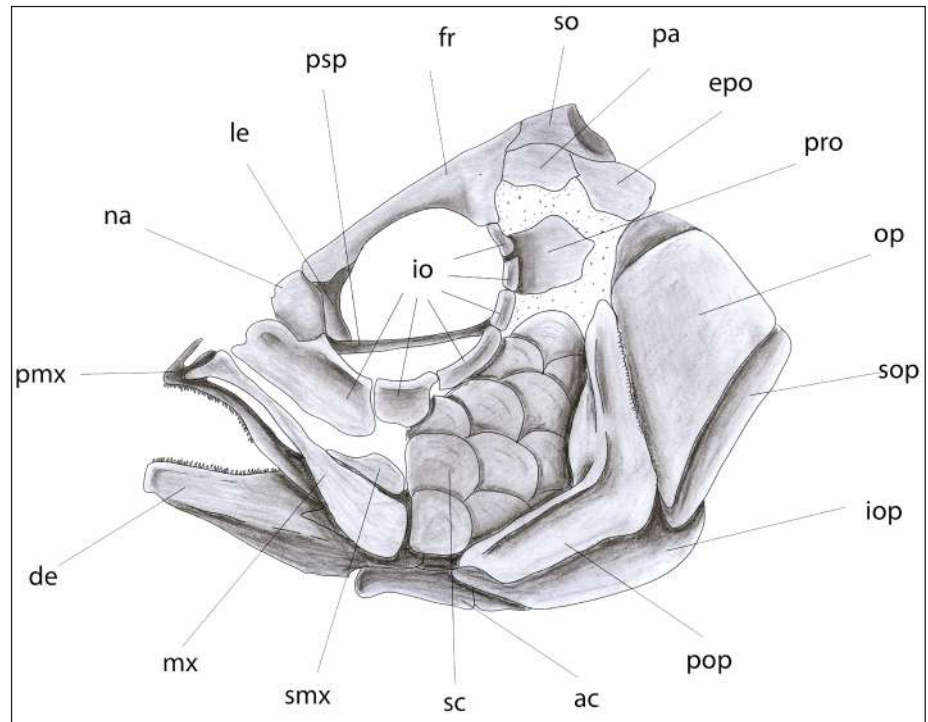
of the opercle is smooth and there are no scales on it. The subopercle is small and contacts the postero-ventral margin of the opercle.

There are two or three branchiostegals that articulate with the anterior and posterior ceratohyal; however, their original number and configuration cannot be determined.

Because the body is covered by thick scales, the number of supraneurals and supernumerary dorsal-fin spines cannot be observed. There are two dorsal-fin lobes completely separated from each other, the first one containing six spines and the second one consisting of a spine plus nine branched rays (dorsal-fin formula: VI+I,9). The penultimate dorsal-fin spine (the last one of the spiny dorsal fin) is the shortest, like in all apogonids. The anal fin is composed of two spines and six branched rays (anal-fin formula: II,6). Although the first spine is recognizable as an impression in the matrix only, it is clearly the smallest one and supernumerary on the first anal-fin pterygiophore. The first anal-fin ray following the last spine is branched. The caudal fin is large, with a rounded posterior margin, and possesses 17 (9+8) principal fin-rays. The number of dorsal and ventral procurrent rays is difficult to determine.

The dorsal limb of the posttemporal is long, whereas the ventral one is not preserved. The supracleithrum is small and characterized by a gently rounded posterior profile. Neither the posttemporal nor the supracleithrum appear to be serrated or ornamented with spines. The other bones of the pectoral girdle are not exposed in the fossil. The pelvic fins contain a single spine plus five rays each.

The body is completely covered by 11(12) horizontal and 24(25) vertical rows of large cycloid scales. Smaller scales are also present in the cheek, urohyal and gular regions, as well as on the caudal-fin base. Four predorsal scales appear to be present. The lateral-line series is formed by 24 or 25 grooved and pored scales.

Remarks. The peculiar combination of morphological features observed in MGP-PD 31963 supports the assignment of †*Arconiapogon* gen. n. to the Apogonidae, based on the presence of two anal-fin spines, the first of which small and in supernumerary association; first anal-fin ray following the last spine segmented and branched; two completely separated dorsal-fin lobes; dorsal-fin formula VI+I,9; 17 (9+8) principal caudal-fin rays; pelvic-fin formula I,5; six infraorbitals including a lachrymal with smooth lower margin; scales also on cheek, urohyal, gular region, and caudal-fin base, and maxilla incompletely sheathed by the lachrymal (see Mabuchi et al. 2014).

The alignment of †*Arconiapogon* gen. n. with the Amioidinae can be ruled out because of the presence of 17 branched caudal-fin rays (vs. 15 in

	Tribe †Eoapogonini				Tribe indet.	
	†Arconiapogon	*†Eoapogon*	*†Bolcapogon*	*†Apogoniscus*	*†Leptolumamia*	*†Eosphaeramia*
Dorsal fin lobes	separated	connected at base	separated	separated	connected at base	connected at base
Dorsal fin	VI+I,9	VIII+I,9	VII+I,9	VI+I,8	VII+I,10	VII+I,9
Anal fin	II,6	II,6	II,7	II,6	II,9	II,9
Supramaxilla	present	absent	?	absent	present	absent
Supramaxilla shape	small	-	?	-	thin	
Pelvic fin length	short	short	short	short	short	long
Caudal fin margin	rounded	rounded	rounded	forked	forked	forked
Posttemporal spines	absent	?	2	2	?	?
Posterior edge of preopercle	serrate	serrate	serrate	smooth	smooth	smooth
Scales	cycloid	ctenoid	cycloid	cycloid	ctenoid	cycloid

Tab. 2 - Selected morphological and meristic features used to discriminate †*Arconiapogon deangelii* gen. et sp. n. from the other genera of the apogonine tribe †Eoapogonini and the indeterminate apogonines from Bolca. Grey cells indicate those characters of †*Arconiapogon* that fall within the range of the other genera. Data from Bannikov (2005, 2008) and Bannikov & Fraser (2016).

amioidines) and of a small supramaxilla (vs. large). †*Arconiapogon* gen. n. differs from the Paxtoninae by having a supramaxilla (vs. absent), bilobed dorsal fin (vs. single and continuous), two anal-fin spines (vs. one), no preopercular spines (vs. a single spine), prootic included in the inner orbit margin (vs. prootic excluded). Finally, compared to Pseudamiinae, †*Arconiapogon* gen. n. possesses a single supramaxilla (vs. none), single lateral-line series (vs. two), and a very different body physiognomy. On the other hand, the combination of skeletal and meristic features of †*Arconiapogon* gen. n. is consistent with that of the Apogoninae in having dorsal-, pelvic-, and caudal-fin formulae within the range of this subfamily, prootic included as part of the inner part of the orbit, cycloid scales, single lateral-line series formed by grooved and pored scales (see Mabuchi et al. 2014). However, the possession of six anal-fin rays in the anal fin (vs. 7–18 in all extant apogonids; Fraser 2013; Mabuchi et al. 2014) is exclusive to the Eocene apogonid genera †*Apogoniscus*, †*Bolcapogon* and †*Eoapogon* from Bolca, which were placed by Bannikov (2005) in a separate tribe within the subfamily Apogoninae, the †Eoapogonini. In this perspective, †*Arconiapogon deangelii* gen. et sp. n. can be considered as the fourth and youngest representative of the †Eoapogonini, and can be distinguished from the other three members by its unique dorsal-fin formula VI+I,9, and by a combination of other osteological and meristic features (Tab. 2). Contrary to †*Arconiapogon* gen. n., †*Apogo-*

niscus is smaller in size (up to 30 vs. 120 mm SL) and shows a preopercle with a smooth (vs. serrated) posterior margin, head length exceeding body depth (vs. head shorter than body depth), posttemporal with two posteroventrally directed spines (vs. no spines), forked caudal fin margin (vs. rounded), and no supramaxillae (vs. present). †*Eoapogon* has connected dorsal-fin lobes (vs. separated), no supramaxilla (vs. present), and fleebly ctenoid scales (vs. cycloid). †*Bolcapogon* has two posttemporal spines (vs. no spines), and an anal fin with seven rays (vs. 6) (the presence of seven soft rays in †*Bolcapogon* is considered a reversal; Bannikov 2005). Two further apogonine genera from Bolca, †*Eosphaeramia* and †*Leptolumamia*, whose affinities remain uncertain (Bannikov 2008; Bannikov & Fraser 2016), can be easily distinguished from †*Arconiapogon* gen. n. †*Eosphaeramia* has preopercle posteriorly smooth (vs. serrated), no supramaxillae (vs. present), dorsal-fin lobes connected at base, with the anterior one very high and triangular in shape (vs. separated lobes and first lobe low), dorsal-fin formula VII+I,9 (vs. VI+I,9), anal-fin formula II,9 (vs. II,6), exceptionally elongate pelvic fins (vs. relatively short), and forked caudal-fin margin (vs. rounded). Finally, †*Leptolumamia* has a preopercle with posterior margin smooth (vs. serrated), dorsal-fin formula VII+I,10 (vs. VI+I,9), anal fin with nine rays (vs. 6), rays of the upper and lower caudal-fin lobes mostly unbranched (vs. branched), forked caudal fin (vs. rounded), and ctenoid scales (vs. cycloid).

Fig. 13 - Apogonidae indet., MGP-PD R658. Scale bars 10 mm.

Apogonidae indet.

Material. MGP-PD R658, a largely complete articulated skeleton lacking the ventral and posterior part of the body (Fig. 13).

Description. The general physiognomy of the preserved portion of this specimen, measuring about 44 mm, is consistent with that of some apogonid fishes. The body is relatively deep with a convex dorsal profile. The head is large, with a rounded and large orbit, whose diameter is contained slightly less than two times in the head length. The skeletal anatomy of the skull is only partially recognizable. The nasal-frontal profile is nearly straight, with the frontals representing the largest bones of the skull roof, whereas the supraoccipital extends on posterior part of the skull. The parasphenoid is straight. The lachrymal has a smooth lower margin, while the other infraorbitals are poorly preserved and difficult to recognize. The otic region of the neurocranium, suspensorium, opercular series, hyoid apparatus and gill arches are inadequately preserved.

The spiny lobe of the dorsal fin contains five spines. However, this number is likely taphonomically biased, since apogonids are characterized by six to nine spines on the spiny lobe of the dorsal fin (e.g., Mabuchi et al. 2014). The first three dorsal pterygiophores are recognizable, showing the presence of a single supernumerary spine on the first dorsal-fin pterygiophore. Supraneurals appear to be absent.

Remarks. Although the specimen is incomplete, a combination of features (general body physiognomy, a single supernumerary dorsal-fin spine; large lachrymal with smooth lower margin; no supraneurals) tentatively support its attribution to the Apogonidae (see Fraser 1972, 2013; Baldwin & Johnson 1999; Mabuchi et al. 2014). Any more detailed taxonomic interpretation is prevented by the inadequate preservation of the specimen.

Suborder **Gobioidei** *sensu* Thacker, 2014
Family Gobiidae Cuvier, 1816
†*Oniketia* gen. n.
urn:lsid:zoobank.org:act:10BAD31D-CA6C-4C66-B458-4900DC30F9F3

Type species: †*Oniketia akihitoi* sp. n.

Origin of the name: The genus name is after the Greek word *Oniketia*, the possible origin for the Veneto Region name and literally meaning 'land of the Venetians'; hence, in a broad sense, a goby from Veneto.

Diagnosis: A diminutive gobiid fish, unique in having the dorsal pterygiophore formula of 2-3210. Moreover, it shows the following combination of characters: relatively elongate and low body tapering posteriorly; low coronoid process; quadrate-anguloarticular joint below the anterior border of the orbit; endopterygoid absent;
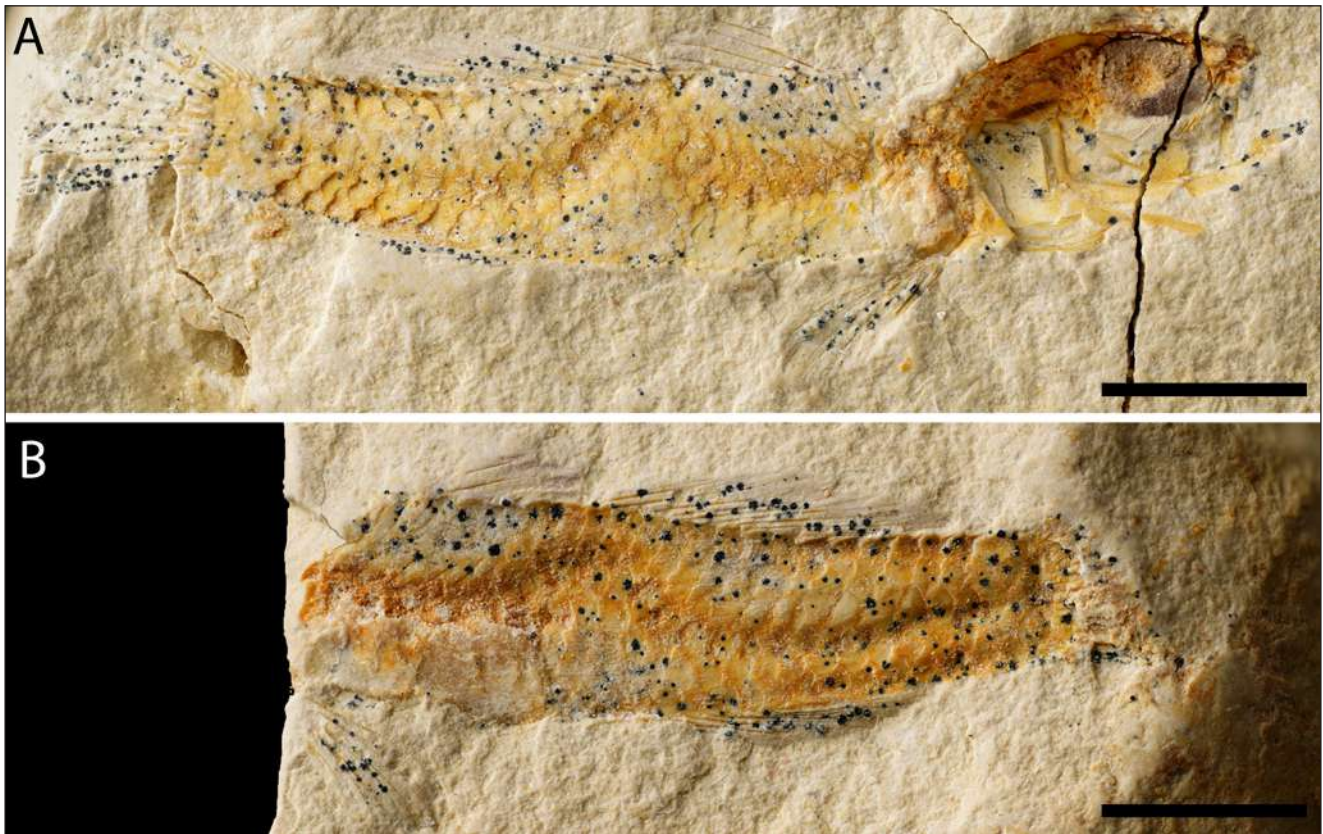
Fig. 14 - †*Oniketia akihitoi* gen. et sp. n., MGP-PD R657, holotype in A) part and B) counterpart. Scale bars 4 mm.

palatine T-shaped; five branchiostegal rays; penultimate branchiostegal articulates with the anterior ceratohyal just anterior to the articulation with the posterior ceratohyal; preopercular canal passes only on the vertical branch of the preopercle; 25 (10+15) vertebrae; small villiform teeth and no enlarged caniniform teeth; supraneurals absent; dorsal-fin lobes separated; dorsal fin VI+I,10; anteriormost dorsal pterygiophore enters the second interneural space; interneural gap between last spiny and first soft dorsal pterygiophores; dorsal postcleithrum absent; pelvic fin I,5; pelvic fins separated; 13 (7+6) principal caudal-fin rays; peripheral ctenoid scales.

Included species: Type species only.

†*Oniketia akihitoi* sp. n.
Figs 14, 15

Origin of the name: The species name honours Akihito, Emperor Emeritus of Japan and renowned ichthyologist, for his remarkable contributions to the study of extant gobies.

Holotype: MGP-PD R657, partially complete articulated skeleton, in part and counterpart, 17.0 mm SL (Fig. 14).

Type horizon: Rupelian, lower Oligocene (see Bassi et al. 2007; Bosellini et al. 2020).

**Type locality:** Perarolo district, Arcugnano town, Berici Hills (Vicenza Province; NE Italy).

Diagnosis: As for the genus.

Measurements as % SL: TL 119.1; HL 29.9; HD 19.6; MBD 18.8; OD 8.2; DFB 36.5; CPD 12.2; PDD 38.2; PPD 34.9; PAD 74.3 (CPD and PAD are estimated, due to the poor preservation of the anal fin).

Description. The general body physiognomy and size of †*Oniketia akihitoi* gen. et sp. n. (17 mm SL, about 20 mm TL) are consistent with those of gobioid fishes, and particularly with the diminutive cryptobenthic extant gobiids like *Eviota*, being small, relatively elongate, and with a low body that gradually tapers posteriorly (Fig. 14). The head is rather large, pointed anteriorly, its length contained 3.3 times in SL, whereas the snout is rather short. A well-marked thin, organic film reveals the presence of a large eyeball. The mouth is small and terminal. The maximum body depth is reached at the level of the occiput. The caudal peduncle appears to be rather short and low. The dorsal fin has a long base (2.7 times in SL) and is formed by two well-separated lobes. The caudal fin was likely rounded in origin. Despite its diminutive size, the specimen likely represents an adult or subadult individual, as most of the bones appear well ossified.

The neurocranium is moderately elongate, longer than deep (Fig. 15). The frontals are the largest bones of the skull roof and there is no evidence for the presence of parietals, as is typical in gobioid fishes. Of the ethmoidal region, only the lateral ethmoid is preserved, which is columnar, projecting

Fig. 15 - †*Oniketia akihitoi* gen. et sp. n., MGP-PD R657, holotype; A) close up of the head; B) reconstruction. Scale bar 2 mm. Abbreviations: aa, angulo-articular; ac, anterior ceratohyal; br, branchiostegal rays; cl, cleithrum; de, dentary; dh, dorsal hypohyal; ecp, ectopterygoid; epo, epioccipital; fr, frontal; hyo, hyomandibula; io, infraorbital; iop, interopercle; le, lateral ethmoid; mtp, metapterygoid; mx, maxilla; op, opercle; pc, posterior ceratohyal; pl, palatine; pmx, premaxilla; pop, preopercle; psp, parasphenoid; pto, pterotic; ptt, posttemporal; q, quadrate; so, supraoccipital; sop, subopercle; sph, sphenotic; sym, symplectic; vh, ventral hypohyal; vplc, ventral postcleithrum.
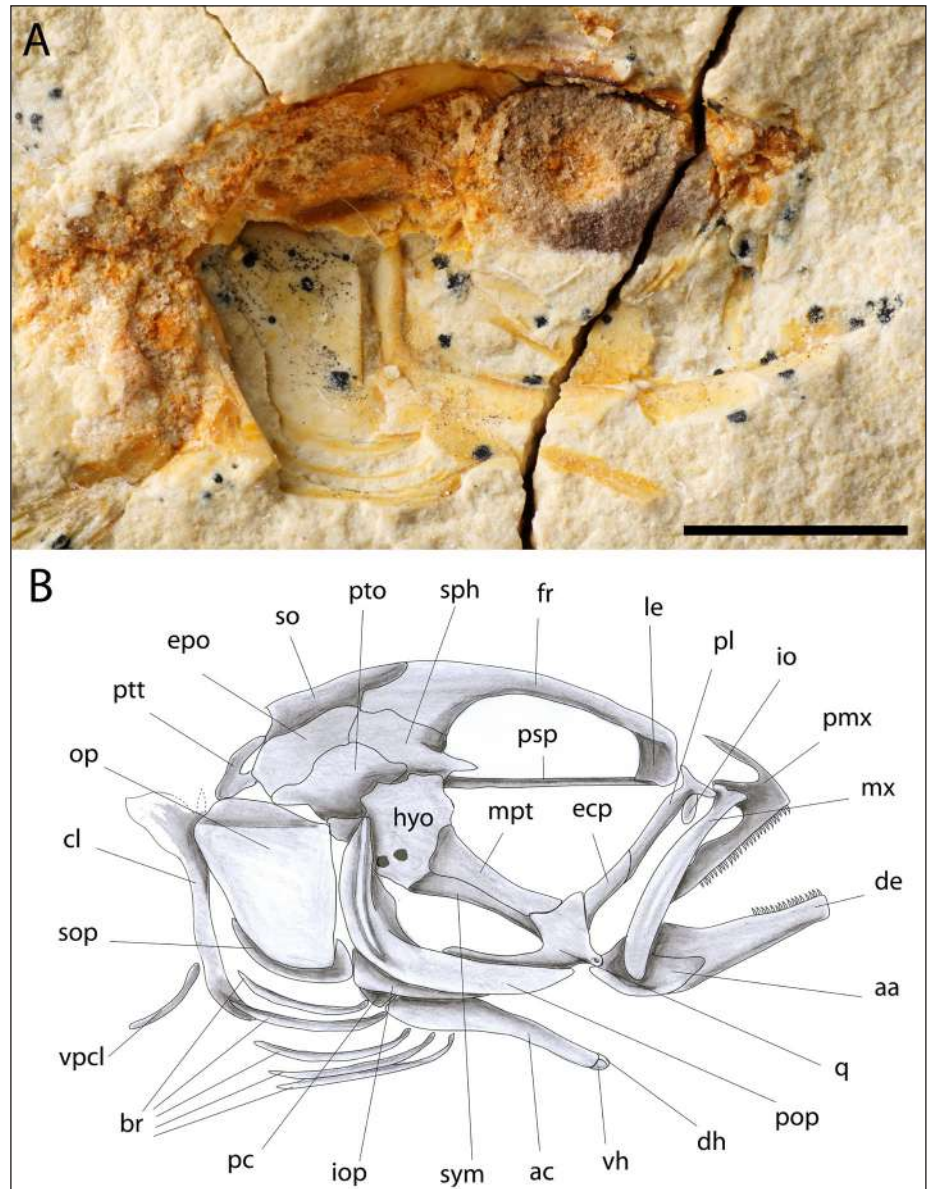
from the antero-ventral margin of the frontals and forming the anteriormost border of the orbit. Conversely, the otic and occipital regions are moderately preserved. The supraoccipital is large and bears a rather low supraoccipital crest. The pterotic is well ossified and lenticular in shape; it sutures with the sphenotic antero-dorsally, and the epioccipital postero-dorsally. The two contralateral epioccipitals are clearly separated from each other by the supraoccipital. The prootic is not exposed, hidden below the hyomandibula.

As in all gobioids, the infraorbitals are represented by the lachrymal only, which is small and placed on the antero-ventral border of the orbit.

The premaxilla is large, with separated ascending and articular processes and a poorly developed postmaxillary process. The maxilla is rather long and slightly bent. The supramaxilla is absent. The dentary is elongate and relatively low. The angulo-articular possesses a rather low coronoid process and its articulation with the quadrate is situated below the anterior border of the orbit. Small and sharp villiform teeth appear to be arranged into a single row on both the premaxilla and dentary; there are no enlarged caniniform teeth.

The overall configuration of the bones of the suspensorium (Fig. 15) resembles that of gobioid fishes with the presence of a moderately developed suspensorial interspace, an open space between the enlarged symplectic and preopercle (Regan 1911; Miller 1973; Springer 1983; Harrison 1989; Johnson & Brothers 1993; Herler et al. 2006; Wiley & Johnson 2010; Bannikov & Carnevale 2016). The suspensorium is particularly reminiscent of that

of the Gobiidae, being stout and short with an ectopterygoid presenting a flat articulation with the quadrate (see Tacker 2013). The hyomandibula is a large plate, irregular in outline; two or three foramina for the passage of the hyomandibular trunk of the facial nerve and the anterior lateral line nerve are visible in its ventral portion (see Kindermann et al. 2007). There are two articular heads for articulation with pterotic and sphenotic. The quadrate is subtriangular in shape with a distinct articular head for articulation with mandibular condyle and a long posterior process for articulation with the preopercle. Dorsally, the quadrate is firmly attached to the robust and elongate metapterygoid, and anteriorly with the posterior margin of the ectopterygoid through a flat surface. The endopterygoid is clearly absent as in other gobiids, thalasseleotrids, some gobionellids, and †*Eleogobius* (Regan 1911; Springer 1983; Gill & Mooi 2012; Gierl & Reichenbacher 2015). The symplectic is relatively robust and elongate, with an enlarged head for articulation with the hyomandibula and a tapered distal portion that articulates with the posterior margin of the quadrate through the *fossa quadrati*. The palatine is robust, relatively straight, short and T-shaped, as it possesses long ethmoid and maxillary processes, resembling the condition of Gobiidae, Gobionellidae and †*Eleogobius* (e.g., Regan 1911; Hoese 1984; Gierl & Reichenbacher 2015; Reichenbacher et al. 2020). The T-shaped palatine articulates anteriorly with the maxilla with its rostral branch and with the ectopterygoid posteriorly.

The preopercle is crescent shaped, with a ventral arm that is slightly longer than the dorsal arm, and the two forming an angle of about 90 degrees. A tiny flange is present at the angle formed by the vertical and horizontal branches. The preopercular canal appears confined to the vertical branch of the preopercle (*sensu* Hoese & Gill 1993). The opercle is relatively large, roughly subtrapezoidal in shape. The subopercle is small and crescent shaped. The interopercle is elongate. There is no trace of spines or serrations on the opercular series.

The hyoid arch is consistent with that of gobioid fishes, particularly the most derived gobiids and gobionellids, in possessing five branchiostegal rays (see Hoese & Gill 1993; Gill & Mooi 2012). The anteriormost four articulate with the anterior ceratobranchial; the fourth branchiostegal lies anterior to the gap between the anterior and posterior

ceratohyals, whereas the last ray articulates with the posterior ceratohyal.

Although partially covered by scales, we counted 25 (10+15) vertebrae on the vertebral column of †*Oniketia* gen. n. (Fig. 14). The vertebral column is strongly deformed and broken exactly at the transition between abdominal and caudal vertebrae. Like in most gobioids (e.g., Johnson & Brothers 1993) the first vertebral centrum appears to be equal in length to the succeeding centra, which are all subrectangular in shape and longer than high. The neural spines are slightly curved in the abdominal vertebrae, becoming gradually straight toward the caudal region. Ribs, intermusculars and the caudal skeleton are poorly preserved or hidden by scale covering and, therefore, cannot be described.

There are no supraneurals. The dorsal fin is moderately elongate, with clearly separated spiny and soft lobes. It comprises six slender and flexible spines in the anterior lobe, and a single spine plus ten rays in the posterior lobe (dorsal formula: VI+I,10). Interestingly, the anteriormost dorsal-fin pterygiophore enters the second interneural space, a condition that has been observed only in some gobiids like *Gunnellichthys*, *Paragunnellichthys*, and the Eocene gobioid †*Carlomonnius* (Birdsong et al. 1988; Bannikov & Carnevale 2016). The dorsal pterygiophore formula of †*Oniketia* gen. n. is 2-3210, which is unique among gobioids and therefore represents a unique feature of this Oligocene genus (see Birdsong et al. 1988). The relationships of the pterygiophores of the soft dorsal-fin lobe with the underlying vertebrae are unclear due to the taphonomic displacement of the vertebral column in this region, but they likely had a one-to-one relationship. An interneural gap separates the last spiny and the first soft pterygiophores, like in most derived gobioids (Hoese & Gill 1993; Reichenbacher et al. 2020). The anal fin is poorly preserved and only a few remains of rays and pterygiophores can be seen. However, it possibly originates under the sixth caudal vertebra and terminates under the level of the 11th caudal vertebra. The caudal fin is relatively large and comprises 13 (7+6) principal rays plus four (or five) dorsal procurrent rays (ventral ones are not preserved).

The pectoral girdle is partially preserved. Of the posttemporal only the dorsal branch is recognizable, whereas the supracleithrum and part of the cleithrum are not clearly exposed. The cleithrum is

dorso-ventrally elongate and clearly enlarged in its upper part. There is a single postcleithrum, which is rod-like, slightly bent and projected postero-ventrally, like in the Gobiidae, Thalasseleotrididae, †Pirskeniidae, †*Carlomonnius,* and certain eleotrid and gobionellid species (Hoese 1984; Gill & Mooi 2012; Bannikov & Carnevale 2016; Reichenbacher et al. 2020). The pelvic fins are thoracic in position, lying close to the pectoral girdle level, and originating just anterior to the the dorsal-fin insertion. Each pelvic fin bears a single spine and five bifurcated rays (I,5). There are no multibranched pelvic-fin rays. Contrary to most gobiids, the pelvic fins appear separated. The anterior portion of the basipterygia almost reaches the posterior margin of the cleithrum to which was likely connected originally.

The body squamation consists of ctenoid scales having tiny spines in a single row at the posterior margin only, corresponding to the peripheral ctenoid type *sensu* Roberts (1993). There is no evidence of lateral-line scales. There are no scales on the head, nape, or pectoral-fin base. Minute spots of dark pigment cover the whole body, including the head and fins.

Remarks. Based on morphological and molecular traits, the Gobioidei are currently separated into eight extant families, including Rhyacichthyidae, Odontobutidae, Milyeringidae, Eleotridae, Butidae, Thalasseleotrididae, Gobiidae, and Gobionellidae (= Oxudercidae of some authors) (e.g., Agorreta et al. 2013; Nelson et al. 2016). According to the most recent phylogenetic analyses (Thacker 2009; Betancur et al. 2017) the Rhyacichthyidae + Odontobutidae clade is sister to all other gobioid families, whereas the Gobionellidae + Gobiidae clade represents the most derived one, because of the presence of derived traits like five branchiostegal rays (vs. six in the other groups), T-shaped palatine (vs. L-shaped), and united pelvic fins (e.g., Akihito 1969; Hoese & Gill 1993; Thacker & Roje 2011; Gill & Mooi 2012). The Gobiidae represents by far the largest gobioid family, including more than 1900 benthic and cryptobenthic species in 258 genera (Nelson et al. 2016; Fricke et al. 2021). Based on fossil material from the lower Oligocene of the Czech Republic, Reichenbacher et al. (2020) suggested that the extinct gobioid family †Pirskeniidae represents the sister taxon to the Thalasseleotrididae + (Gobionellidae + Gobiidae) clade.

Conversely, the familial affinities of two extinct genera, †*Eleogobius* from lower-middle Miocene of Germany and †*Carlomonnius* from the lower Eocene of Bolca, are uncertain, leading Gierl & Reichenbacher (2015) and Bannikov & Carnevale (2016) to classify them as Gobioidei *incertae sedis.*

†*Oniketia* gen. n. exhibits a suite of features that unquestionably support its alignment with the Gobioidei, including the absence of parietals, infraorbital series represented by the lachrymal only, presence of the suspensorial interspace, slender and flexible dorsal spines, absence of supraneurals, and pelvic fins placed below the pectorals (Regan 1911; Miller 1973; Springer 1983; Harrison 1989; Birdsong et al. 1988; Johnson & Brothers 1993; Wiley & Johnson 2010; Bannikov & Carnevale 2016; Nelson et al. 2016).

Within gobioid fishes, †*Oniketia* gen. n. exhibits a unique suite of features that support its placement within the family Gobiidae (Tab. 3), including the presence of well-separated spinous and soft dorsal fins, five branchiostegal rays, the fourth at the anterior ceratohyal and clearly anterior to the gap to the posterior ceratohyal, absence of endopterygoid, dorsal postcleithrum and lateral-line scales, other than being within the meristic ranges of gobiids for vertebral and fin ray counts (see Springer 1983; Hoese 1984; Ruple 1984; Hoese & Gill 1993; Gill & Mooi 2012; Thacker 2013; Nelson et al. 2016).

The presence of five branchiostegal rays, a T-shaped palatine, first dorsal pterygiophore inserting on the second interneural space, and the absence of the endopterygoid and dorsal postcleithrum exclude †*Oniketia* gen. n. from the basalmost gobioid families Rhyacichthyidae, Odontobutidae, Milyeringidae, Eleotrididae and Butidae, which possess the endopterygoid and dorsal postcleithrum, an L-shaped palatine, six or seven branchiostegals and a first dorsal pterygiophore inserting on the third to fifth interneural space (Tab. 3). Although the Thalasseleotrididae have no endopterygoid and dorsal postcleithrum, their alignment with our Oligocene genus can be ruled out because thalasseleotrids have an L-shape palatine, six branchiostegals, and the first dorsal pterygiophore inserting in the third interneural space. Despite †*Oniketia* gen. n. sharing more characters with the Gobiidae and Gobionellidae, its alignment with the latter family can be rejected because gobionellids generally exhibit

	†*Oniketia*	Gobiidae	Gobionellidae	Thalasseleotrididae	Butidae	Eleotrididae
Endopterygoid	absent	absent	absent	absent	present	present
First dorsal pterygiophore on interneural space n.	2	2 to 3	3 to 6	3	3	3 to 5
Palatine	T-shaped	T-shaped	T-shaped	L-shaped	L-shaped	L-shaped
Dorsal interneural gap	present	present	present	present	absent/ present	absent/ present
Branchiostegal rays	5	5	5	6	6	6
Penultimate branchiostegal position	at anterior ceratohyal and clearly anterior to gap to posterior ceratohyal	at anterior ceratohyal and clearly anterior to gap to posterior ceratohyal	at anterior ceratohyal and clearly anterior to gap to posterior ceratohyal	at anterior ceratohyal and clearly anterior to gap to posterior ceratohyal	at anterior ceratohyal and clearly anterior to gap to posterior ceratohyal	at anterior ceratohyal and clearly anterior to gap to posterior ceratohyal
Preopercular canal	on vertical branch only	on vertical branch only	on vertical branch only	on vertical branch	usually complete	on vertical branch only
Scales	peripheral ctenoid	peripheral ctenoid/cycloid	peripheral ctenoid/cycloid	peripheral ctenoid	peripheral ctenoid	peripheral ctenoid/cycloid
Dorsal postcleithrum	absent	absent	present (rarely absent)	absent	present	present (rarely absent)
Pelvic fin	I,5	I,5	I,4-5	?	?	I,4-5
Dorsal fin	VI+I,10	V-X+I,5-37	IV-XVII+9-31	VI-VII+I,8-10	V-VIII+I,7-15	VI-X+I,6-15
Anal fin	?	I,11-18	I,8-30	I,7-9	I,6-12	I,6-12
Dorsal fins	separated	continous/ separated	continous/ separated	separated	separated	separated

Tab. 3a - Selected morphological and meristic features used to discriminate the gobioid families. Grey cells indicate those characters of †*Oniketia akihitoi* gen. et sp. n. that fall within the range of the families. Data from Springer (1983, 1988), Hoese (1984), Birdsong et al. (1988), Roberts (1993), Larson & Murdy (2001), Murdy & Hoese (2003), Gill & Mooi (2012), Gierl & Reichenbacher (2015, 2017), Reichenbacher et al. (2018, 2020), and Froese & Pauly (2021). The gobiid subfamilies Kraemeriinae and Microdesminae were not considered here because of their peculiar body physiognomy and meristics.

a dorsal postcleithrum, a first dorsal pterygiophore inserting in the third to sixth interneural space, and a suspensorium that is overall more elongated and gracile than that of gobiids (see also Tacker 2013; Nelson et al. 2016). Other features that support the gobiid affinity of †*Oniketia* gen. n. are the stout and short suspensorium with an ectopterygoid presenting a flat articulation with the quadrate (gobionellids generally exhibit a suspensorium that is more elongated and gracile than that of gobiids; Tacker 2013) and the insertion of the first dorsal-fin pterygiophore in the second interneural space. This pterygiophore usually enters the third interneural space, and sometimes even more posterior positions, in most gobioids, whereas the peculiar condition of †*Oniketia* gen. n. has been observed only in †*Carlomonnius* and the gobiids *Gunnellichthys* and

Paragunnellichthys (Birdsong et al. 1988; Bannikov & Carnevale 2016).

Interestingly, the general body physiognomy of †*Oniketia akihitoi* gen. et sp. n. associated with its diminutive size and meristic counts, closely resembles that of the dwarfgoby *Eviota*, a tropical, cryptobenthic marine Indo-Pacific genus that includes about 120 species, most of them being under 20 mm SL (Lachner & Kamella 1978, 1980; Tornabene et al. 2013; Greenfield 2016). These gobies are well known for their rapid lifecycle, high turnover, and overall abundance, making them an important component of tropic food web in coral reef settings (Depczynski & Bellwood 2003, 2005, 2006). Among the features that support the possible affinity of †*Oniketia* gen. n. with *Eviota* is the presence of separated pelvic fins, periph-

	Milyeringidae	Odontobutidae	Rhyacichthyidae	†Pirskeniidae	†*Carlomonnius*	†*Eleogobius*
Endopterygoid	present	present	present	present	present	absent
First dorsal pterygiophore on interneural space n.	?	3	3	3	2	3
Palatine	L-shaped	L-shaped	L-shaped	L-shaped	?	T-shaped
Dorsal interneural gap	absent	absent	absent	present	absent	present
Branchiostegal rays	6	6-7	6	7	5	6
Penultimate branchiostegal position	at anterior ceratohyal and clearly anterior to gap to posterior ceratohyal	at gap or just before gap to posterior ceratohyal	at posterior ceratohyal / at gap or just before gap to posterior ceratohyal	at gap or just before gap to posterior ceratohyal	at gap or just before gap to posterior ceratohyal	?
Preopercular canal	complete	complete	complete	on vertical or on horizontal branch	?	?
Scales	peripheral ctenoid	transforming ctenoid	transforming ctenoid	peripheral ctenoid	cycloid	peripheral ctenoid
Dorsal postcleithrum	present	present	present	absent	absent	?
Pelvic fin	I,3-5	?	I,5	I,5	I,4	I,5-6
Dorsal fin	0 or IV-V+I,7-13	V-IX+I,7-12	VIII-IX+8-9	VI-VII+I,9-10	VII+11	VI+I,10-11
Anal fin	0-I,6-9	0-III,7-10	I,8-9	I,9-10	I,7	I,8-11
Dorsal fins	separated	separated	separated	separated	continuous	separated

Tab. 3b - Selected morphological and meristic features used to discriminate the gobioid families. Grey cells indicate those characters of †*Oniketia akihitoi* gen. et sp. n. that fall within the range of the families. Data from Springer (1983, 1988), Hoese (1984), Birdsong et al. (1988), Roberts (1993), Larson & Murdy (2001), Murdy & Hoese (2003), Gill & Mooi (2012), Gierl & Reichenbacher (2015, 2017), Reichenbacher et al. (2018, 2020), and Froese & Pauly (2021). The gobiid subfamilies Kraemeriinae and Microdesminae were not considered here because of their peculiar body physiognomy and meristics.

eral ctenoid scales on the body but absent on the head, nape, and pectoral-fin base, and the possession of 25 (10+15) vertebrae (see Birdsong et al. 1988; Greenfield 2016). As far as this last feature is concerned, while the number of vertebrae in extant and fossil gobioids ranges between 24 and 64 (Birdsong et al. 1988; Gierl & Reichenbacher 2015; Bannikov & Carnevale 2016; Reichenbacher et al. 2020), within the family Gobiidae 10+15 vertebrae have been reported only in some *Eviota* species (Lachner & Kamella 1980; Akihito et al. 1984; Birdsong et al. 1988). In any case, the separate taxonomic placement of †*Oniketia* gen. n. is supported by the absence of enlarged teeth anteriorly in both jaws (vs. present in *Eviota*), bifurcated fourth pelvic-fin ray (vs. multibranched, the lateral branching often fringelike), and spots of pigments scattered throughout the whole body (vs. trunk usually with dark, vertical bars) (e.g., Lachner & Kamella 1980).

Order **Chaetodontiformes** *sensu* Betancur et al., 2017
Family Chaetodontidae Bonaparte, 1832
Genus *Chaetodon* Linnaeus, 1758
Subgenus †*Blumchaetodon* subgen. n.
urn:lsid:zoobank.org:act:09422C76-E925-421C-BF25-89218FED-CB93

Origin of the name: The new subgenus name honours the American ichthyologist Stanley D. Blum for his remarkable contributions to the study of extant butterflyfishes.

Diagnosis: A *Chaetodon* subgenus unique in having body deep, ovoid, slightly antero-posteriorly elongated; six infraorbitals, the second small and excluded from the margin of the orbit; second and third infraorbitals without expanded, ventrally directed lamina; ascending process of premaxilla longer than alveolar process; angle formed by ascending and alveolar processes of about 90 degrees; setiform teeth protruded anteriorly from premaxilla and dentary, at about 30 degrees from the horizontal; premaxillary teeth restricted to anterior part of alveolar process of premaxilla; ectopterygoid broad, antero-posteriorly expanded; two separated supraneurals; heads of supraneurals roughly of the same size and shape; dorsal fin continuous; ten dorsal-fin spines.

Fig. 16 - †*Chaetodon* (*Blumchaetodon*) *wattsi* subgen. et sp. n., MGP-PD R664, holotype. Scale bar 10 mm.

Type species: †*Chaetodon* (*Blumchaetodon*) *wattsi* sp. n.

Remarks. †*Blumchaetodon* subgen. n. can be distinguished from subgenera *Chaetodon* (*s.s.*), *Rabdophorus*, *Megaprotodon*, *Gonochaetodon*, *Tetrachaetodon*, *Discochaetodon*, *Corallochaetodon*, and *Citharoedus*, in having the head of supraneurals (=heads of predorsal bones of Blum 1988) roughly of the same size and shape (vs. head of the first supraneural longer and flatter). It differs from subgenera *Roaops*, *Exornator, and Lepidochaetodon*, in having two supraneurals (vs. only one, or supraneurals fused forming a single bone), and particularly with *Lepidochaetodon* in having a single type of teeth (vs. two kinds, the most labial teeth are significantly larger and stouter than the more lingual ones). †*Blumchaetodon* subgen. n. differs from *Tetrachaetodon* in having teeth only on the anterior part of the alveolar process (vs. teeth along the entire oral border), and differs from *Discochaethodon,* in having an ovoid and slightly elongated body (vs.

disc-shaped). It differs from *Megaprotodon, Gonochaetodon, Discochaetodon, Corallochaetodon* and *Citharoedus*, in having teeth on the alveolar process of the premaxilla (vs. alveolar process edentulous). †*Blumchaetodon* subgen. n. can be further distinguished from *Corallochaetodon* and *Citharoedus* in having the angle formed by the ascending and alveolar processes of the premaxilla measuring about 90 degrees (vs. 120), a broad ectopterygoid, which is antero-posteriorly expanded (vs. rod-like), and a second circumorbital (vs. absent in *Citharoedus*). It also differs from *Megaprotodon* in having ten dorsal-fin spines (vs. 13–15).

Included species: Type species only.

†*Chaetodon* (*Blumchaetodon*) *wattsi* sp. n.
Figs 16, 17

Origin of the name. Species named after the British musician Charles Robert Watts, drummer of the Rolling Stones, who sadly passed away during the preparation of this paper.

Fig. 17 - †*Chaetodon* (*Blumchaetodon*) *wattsi* subgen. et sp. n., reconstruction of the head of MGP-PD R664, holotype. Abbreviations: aa, angulo-articular; de, dentary; ecp, ectopterygoid; enp, endopterygoid; epo, epioccipital; fr, frontal; io, infraorbitals; iop, interopercle; le, lateral ethmoid; mtp, metapterygoid; mx, maxilla; na, nasal; op, opercle; pa, parietal; pl, palatine; pmx, premaxilla; pop, preopercle; pto, pterotic; q, quadrate; so, supraoccipital; sop, subopercle.
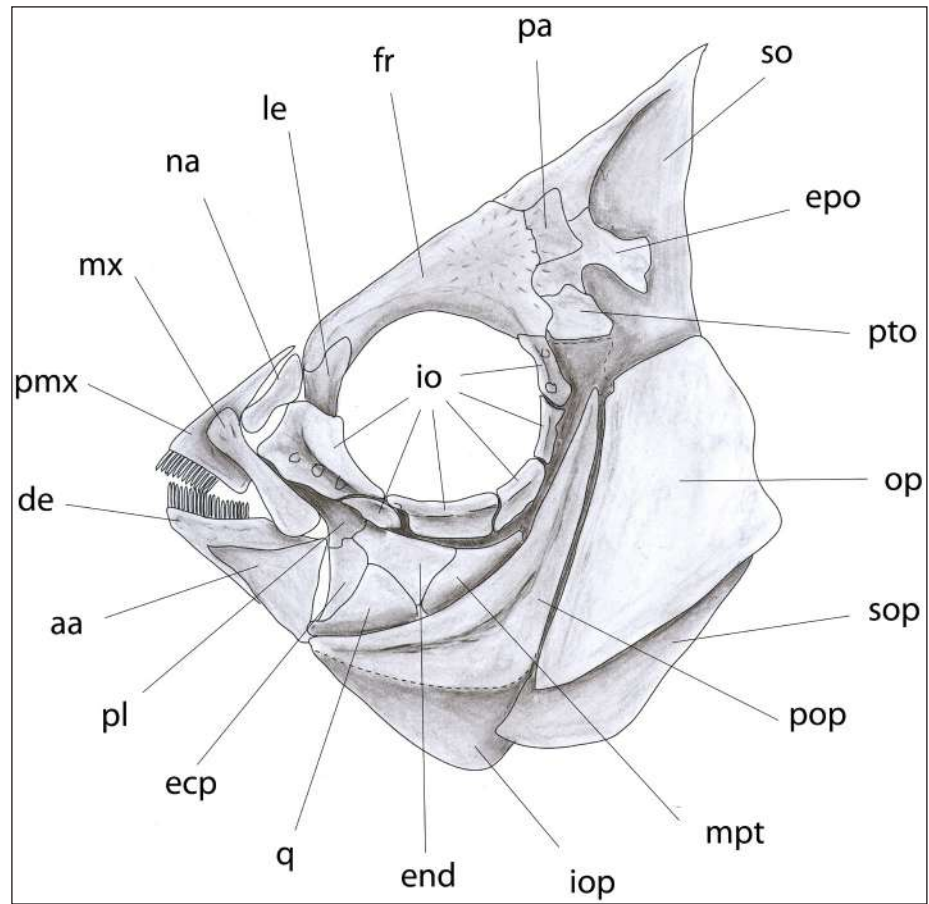
Holotype: MGP-PD R664, articulated skeleton lacking most of the caudal region (measurable length of the specimen 55.2 mm) (Fig. 16).

Type horizon: Rupelian, lower Oligocene (see Bassi et al. 2007; Bosellini et al. 2020).

Type locality: Perarolo district, Arcugnano town, Berici Hills (Vicenza Province; NE Italy).

Diagnosis: As for the subgenus.

Measurements (in mm): HL 21.8; HD 25.9; MBD 37.8; OD 7.6; DFB 24.7 (only spiny lobe); PDD 27.4; PPD 35.4.

Description. The body is deep, ovoid, slightly elongate antero-posteriorly, and laterally compressed (Fig. 16). The head is deeper than long. The snout is relatively pronounced, with its length contained about 3.5 times in HL. The structure and mutual relationships of the premaxilla and dentary suggest that this subgenus probably had a prognathous terminal mouth. The orbit is large, contained about three times in HL. The dorsal fin is continuous. The pelvic fin originates slightly posterior to the vertical at the dorsal-fin origin.

The overall head anatomy of †*C. wattsi* sp. n. (Fig. 17) resembles that of the other *Chaetodon* species (e.g., Motta 1982, figs 2–4; Blum 1988, figs 29–36; Ferry-Graham et al. 2001, fig. 2.6A). The frontals are the largest bones of the skull roof, closely followed in size by the supraoccipital, which possesses a large, high supraoccipital crest ending posterodorsally as a spine articulating with the shaft of the first supraneural. Posteriorly, the frontal sutures with the pterotic, epioccipital, parietal and supraoccipital. The parietal is small and sutures with the supraoccipital dorsally; it is separated from the pterotic by the epioccipital. The mesethmoid and vomer are hidden by other cranial bones. The lateral ethmoids are roughly subrectangular in shape and form the anterior wall of the orbit. The postero-ventral portion of the neurocranium is difficult to interpret.

There are six infraorbitals. The lachrymal is the largest of the series and subtrapezoid in outline. The second infraorbital bone is small and excluded from the margin of the orbit. The sixth infraorbital borders the postero-dorsal margin of the orbit. There is no expanded, ventrally directed lamina on the second and third infraorbitals. The nasals are slender, hourglass shaped, and laterally compressed.

†*Chaetodon* (*Blumchaetodon*) *wattsi* sp. n. shows the primitive dental and jaw morphology of chaetodontids (*sensu* Blum 1988). The premaxilla is L-shaped. Its ascending process is about 1.5 times

longer than the alveolar process, and together they form a right angle. The articular process of the premaxilla is straight, almost parallel to the ascending process. The teeth protrude from the jaws; they are setiform, with spatulate and unicuspid tooth caps. The size and shape of the premaxillary teeth are consistent throughout the alveolar process, except for its posterior extremity, where they are absent. The maxilla is relatively short, characterized by a robust cranial condyle and a slightly expanded posterior portion. The dentary is elongate, subtriangular in shape, and has a posterior deep notch housing the anterior process of the anguloarticular.

Although the suspensorium is partially hidden by the preopercle, its structure closely resembles that of most *Chaetodon* species (e.g., Motta 1982, figs 2–4; Blum 1988, figs 29–33). Of the quadrate, only its anterior portion can be seen but it is evident it bears a thick articular facet for articulation with the anguloarticular. The quadrate sutures anteriorly with a robust ectopterygoid. The endopterygoid and metapterygoid are clearly recognizable. The anterior portion of the palatine is difficult to define in being partially covered by the maxilla and infraorbitals, while the symplectic and the hyomandibula are almost completely hidden by the preopercle.

The preopercle is large, deep, and crescent shaped, with a vertical limb roughly 1.5 times as long as the horizontal limb. Its antero-dorsal margin almost reaches the posterior edge of the orbit. The preopercular sensory canal runs within a tube throughout the length of this bone. The preopercle is partially broken at ventral margin, exposing large part of interopercle. The opercle is large, deep and trapezoidal in shape, with an almost straight and vertical anterior margin. The subopercle is deep, long and slender posteriorly. All the bones of the opercular series are characterized by smooth margins, with no spines or serrations. No bones of the hyoid or gill arches are preserved.

The analysis of the vertebral column and associated structures is hindered by diagenetic alteration of the bones and overlapping body scales. There seems to be 11 abdominal vertebrae. Neural arches, epineurals, and pleural ribs are only preserved in their proximal part and, therefore, their entire morphology and organization are difficult to interpret. There are possibly eight pairs of ribs articulating with abdominal vertebrae three to ten. Only nine caudal vertebrae can be recognized, due

to the missing caudal portion of the body; butterflyfishes commonly possess 13 caudal vertebrae, thereby suggesting that at least two vertebrae are missing in the fossil (e.g., Pyle 2001; Burgess 2003; Nelson et al. 2016).

There are two separated supraneurals. The sequential articulation between the supraoccipital crest, the supraneurals, and the first dorsal pterygiophore that characterize all chaetodontids is clearly recognizable (Blum 1988). The head of the first supraneural overlaps the supraoccipital, that of the second supraneural overlaps the first, and the first pterygiophore overlaps the second supraneural. The distal end of both supraneurals is bent anteriorly and expanded into a thickened head. The head of both supraneurals shows a similar size and shape. The dorsal fin of †*Blumchaetodon* subgen. n. originates above the second or third abdominal vertebra; it contains ten spines, increasing in length up to the fifth and then decreasing to the last, and seven distally segmented soft rays, although their original number was probably higher.

Almost all the bones of the pectoral girdle are either extensively fragmented, not preserved, or hidden by other bones. The dorsal arm of the cleithrum is partially exposed. The number of pectoral-fin rays cannot be discerned. The pelvic fins are thoracic in position and originate slightly behind the vertical at the dorsal-fin origin, at the level of the 6th or 7th vertebra. A single short and robust pelvic-fin spine plus four or five soft rays are preserved. The basipterygium is barely recognizable.

The gular and abdominal regions of the body are partially covered with rounded ctenoid scales arranged in ascending rows. The lateral-line scales are not preserved.

Remarks. Butterflyfishes of the family Chaetodontidae are small to medium-sized (up to 30 cm) diurnal, reef-associated fishes usually occurring in tropical and warm-temperate marine shallow waters at depths less than 20 m in the Atlantic, Indian, and Pacific Oceans (Burgess 1978, 2003; Pyle 2001; Rajan 2010; Nelson et al. 2016; Froese & Pauly 2021). Several studies consistently resolved this family as sister to the Leiognathidae, leading Betancur et al. (2017) to resurrect the order Chaetodontiformes Jordan, 1923 to include ponyfishes and butterflyfishes. According to Blum (1988) the family Chaetodontidae includes 11 genera: *Amphichaetodon*, *Chelmon*, *Chelmonops*, *Coradion*, *Forcipiger*, *Hemitaurichthys*,

Heniochus, Johnrandallia, Prognathodes, Roa, and *Chaetodon s.l.* The genus *Chaetodon* comprises 12 subgenera, including *Chaetodon s.s., Citharoedus, Corallochaetodon, Discochaetodon, Exornator, Gonochaetodon, Lepidochaetodon, Megaprotodon, Paracheatodon, Rabdophorus, Roaops,* and *Tetrachaetodon.* More recently, Fessler & Westneat (2007) found the subgenera *Chaetodon s.s.* and *Exornator* to be polyphyletic, and elevated *Parachaetodon* to the genus level. The family is therefore thus far composed of over 130 species in 12 genera (see also Nelson et al. 2016; Fricke et al. 2021).

Blum (1988) provided the first cladistic evidence for the monophyletic status of the Chaetodontidae based on osteological features, describing six characters that unambiguously diagnose the family: (1) sequential articulation between the supraoccipital crest, supraneurals, and the first dorsal pterygiophore; (2) pleural rib laminae that extend forward from the medial edges of the descending shafts; (3) pleural ribs elongated, extending almost to reach the ventral margin of the body; (4) a ligament that connects the anterior edge of the second postcleithrum to the basipterygium, just anterior to the origin of the pelvic spine; (5) the first or first two anterior branchiostegals do not make contact with the ceratohyal; (6) specialized larval stage known to as tholichthys. Although most of these features cannot be detected in the fossil described herein, the recognition of the first character clearly supports its placement within the family Chaetodontidae. Other features that support its inclusion within the chaetodontids and, in particular, within the genus *Chaetodon,* include the general body physiognomy, high supraoccipital crest, parietal reduced dorsoventrally remaining in contact with the supraoccipital dorsally but losing its ventral contact with the pterotic, frontals sutured with the epioccipitals, second infraorbital small and excluded from the orbit, and 11 abdominal vertebrae (Regan 1913; Johnson 1984; Blum 1988; Ferry-Graham et al. 2001; Smith et al. 2003; Carnevale 2006). Following the detailed analysis of Blum (1988), attribution to the chaetodontid genera *Chelmon, Chelmonops, Coradion, Amphichaetodon* and *Forcipiger* can be excluded because these taxa are peculiar in having hypertrophically elongated jaws, with teeth reduced in size (vestigial in *Coradion*) or produced from jaws almost vertically (in *Chelmon, Chelmonops, Coradion*). Assignement to *Heniochus* and *Hemitaurichthys* can be ruled out because their oral teeth are shorter and straighter compared to all the other chaetodontids. Furthermore, *Heniochus* is unique also in having a considerably elongate fourth dorsal spine, a condition absent in the fosssil. Its alignment with the genus *Parachaetodon* (subgenus for Blum 1988) can be excluded because this is unique in having only six dorsal-fin spines, (vs. 9 to 16 in other butterflyfishes). Its alignment with *Prognathodes* and *Johnrandallia* can also be ruled out because these genera show expanded, ventrally directed laminae on the second and third infraorbitals, which are absent in the fossil. Moreover, the fossil can be also distinguished from *Amphichaetodon* and *Forcipiger* by having a different number of dorsal-fin spines (10 vs. 12–13 and 11–13, respectively; Froese & Pauly 2021). Finally, although Blum (1988) did not find osteological features that unambiguously diagnose *Roa,* the alignment with this genus can be excluded because the fossil has ten dorsal-fin spines (vs. 11 in all *Roa* species; Kuiter 2004; Rocha et al. 2017; Froese & Pauly 2021).

†*Blumchaetodon* subgen. n. can be distinguished from subgenera *Chaetodon s.s., Rabdophorus, Megaprotodon, Gonochaetodon, Tetrachaetodon, Discochaetodon, Corallochaetodon,* and *Citharoedus,* in having the head of both supraneurals roughly of the same size and shape (vs. head of the first supraneural longer and much flattened). The fossil described herein cannot be aligned with the subgenera *Roaops, Exornator,* and *Lepidochaetodon,* since their two supraneurals are consolidated into a single bone, and especially with *Lepidochaetodon* whose oral jaws contain two different types of teeth (labial teeth are significantly larger and stouter than lingual ones; Motta 1985, 1987; Blum 1988). *Tetrachaetodon* can be distinguished from all the other subgenera, including †*Blumchaetodon* subgen. n., in retaining teeth on the entire oral border of the alveolar process of the premaxilla. Also, the lateral profile of the body can be used to exclude the alignment of MGP-PD R664 with *Discochaethodon,* as this latter is characterized by a peculiar disc-shaped silhouette and has different median-fin spine proportions. Furthermore, contrary to the condition of †*Blumchaetodon* subgen. n., the alveolar process of the premaxilla is edentulous in *Megaprotodon, Gonochaetodon, Discochaetodon, Corallochaetodon* and *Citharoedus.* Affinities with *Corallochaetodon,* and *Citharoedus* can be furtherly excluded because in these subgenera the angle formed by the ascending and alveolar processes of premaxilla is about 120 degrees, the ectopterygoid is rod-like, and the sec-

ond circumorbital is absent in *Citharoedus*, whereas teeth are clearly present in †*Blumchaetodon* subgen. n., the premaxillary angle is about 90 degrees, and the second infraorbital is clearly present. Finally, *Megaprotodon* differs from †*Blumchaetodon* subgen. n., in having 13–15 dorsal-fin spines (vs. 10).

Although the unique combination of features clearly supports the creation of a new *Chaetodon* subgenus, the preservation of the fossil makes it difficult to resolve the phylogenetic relationships of †*Blumchaetodon* subgen. n. within the *Chaetodon* group complex.

DISCUSSION

Implications for the fossil record

Despite their exceptional abundance and diversity in modern tropical and subtropical seas of the world, viviparous brotulas, cardinalfishes, gobies, and butterflyfishes are poorly or only moderately represented in the fossil record, at least that consisting of skeletal remains.

The fossil record of the Ophidiiformes has been examined in detail by Carnevale & Johnson (2015), whereas Přikryl & Carnevale (2018) mostly focused on the Oligocene-Miocene taxa. In summary, the oldest ophidiiform, †*Pastorius methenyi*, is represented by a single articulated specimen from the Upper Cretaceous, collected from the uppermost Campanian-lower Maastrichtian (c. 69 Ma) laminated limestone of the Liburnica Formation, near the village of Trebiciano, NE Italy (Carnevale & Johnson 2015). The anatomy of †*Pastorius methenyi* shows that the modern body plan of the group was already in existence at that time (Carnevale & Johnson 2015). Based on the presence of a free caudal fin and overall meristics similar to many dinematichthyids and certain bythitids, †*Pastorius* was regarded as a stem bythitoid, sister to all extant taxa of the suborder (Møller et al. 2016). The oldest Cenozoic cusk-eel records based on articulated skeletal remains come from the Palaeocene-Eocene boundary of Turkmenistan with the ophidioid †*Eolamprogrammus senectus* (Daniltshenko 1968; Patterson & Rosen 1989), the lower Eocene of Italy and England with the incertae sedis †'*Ophidium*' *voltianum* (Carnevale et al. 2014), the ophidioid †*Ampheristus tolipiacus* (Schwarzhans et al. 2018), and the middle-upper Eocene fossiliferous strata of the Pabdeh Forma-

tion in Iran (see Afsari et al. 2014) with the bythitoid †*Propteridium douvillei* (Arambourg 1967). Oligocene and Miocene skeletal records of Ophidiiformes are known from the Carpathians (see Přikryl & Carnevale 2018, for a detailed analysis), Argentina (Riva Rossi et al. 2000), Japan (Sato 1962), Italy (e.g., Leonardi 1959), and Maryland (Carnevale & Godfrey 2018). Ophidiiform otoliths are by far more abundant than skeletal remains. They are known at least from the Upper Cretaceous and show that, from the early Eocene onwards, cusk-eels became highly diversified and extremely abundant in neritic biotopes, especially on sandy and muddy grounds in tropical and subtropical settings (Nolf 1980; Nolf & Steurbaut 1989; Schwarzhans 1981, 2010, 2013; Carnevale & Johnson 2015). A sharp turnover occurred at the end of the Oligocene when many genera went extinct and were replaced by species belonging to extant genera (Nolf & Steurbaut 1989; Carnevale & Johnson 2015). As most of the Cretaceous and Palaeogene history of this group primarily occurred in neritic palaeobiotopes, it was suggested that the occupation of the oceanic realm and bathyal zones may have taken place mostly during the Oligocene and Miocene (Nolf & Steurbaut 1989; Carnevale & Johnson 2015).

The fossil record of the Dinematichthyidae, uniquely represented by otoliths so far, was analysed in detail by Møller et al. (2016). Although several otolith-based species referred to the extant genus *Ogilbia* have been reported since the Palaeocene-Eocene boundary of Europe (e.g., Frost 1934; Nolf 1978; Schwarzhans 2003; Schwarzhans & Bratishko 2011), Møller et al. (2016) considered these species to be stem dinematichthyids. Conversely, the earliest reliable occurrence of the family appears to be †*Ogilbia dispar* from the Rupelian of the Mainz Basin, Germany (c. 33 Ma; Koken 1891). Younger reliable fossils of dinematichthyid cuskeels are mostly represented by Oligocene to Pliocene (32.5 to 4.5 Ma) otolith-based species assigned to the genera *Ogilbichthys* and *Ogilbia* (e.g., Koken 1891; Nolf & Steurbaut 1989; Nolf & Stringer 1992; Schwarzhans & Aguilera 2013; Møller et al. 2016). A few otoliths assigned to *Dipulus* are known from the Palaeogene of Europe, but as this genus is endemic to Australia today, these fossil occurrences are considered unlikely by Møller et al. (2016), who evidenced a certain degree of affinity with *Ogilbia*. The most recent timetree (Møller et al. 2016)

is consistent with the fossil record of the Ophidiiformes, suggesting a Cretaceous origin (between 104 and 84 Ma) for cusk-eels, and the appearence of the Dinematichthyidae between 49 and 27 Ma. In this perspective, MGP-PD R661 documents the first skeletal record of dinematichthyid cusk-eels, and together with †*Ogilbia dispar* from the Rupelian of Germany (Koken 1891) one of the earliest occurrences of the family.

The fossil record of cardinalfishes is relatively abundant but strongly biased towards isolated otoliths which appear to occur from theUpper Cretaceous to the Pleistocene (e.g., Nolf 1985, 2003a; Nolf & Stringer 1996), although the Mesozoic occurrences were thought to be doubtful (Bannikov 2005). Conversely, the oldest reliable apogonids based on articulated skeletons are those reported from the upper Ypresian (lower Eocene; about 49 Ma) of Bolca, that include apogonine genera of the tribe †Eoapogonini (†*Apogoniscus*, †*Bolcapogon* and †*Eoapogon*), and the apogonines †*Eosphaeramia* and †*Leptolumamia* of uncertain phylogenetic affinity (Bannikov 2005, 2008; Bannikov & Fraser 2016). Other relatively complete skeletal material includes †*Apogon macrolepis*, represented by a three-dimensionally preserved skull from the Bartonian (upper Eocene) of the Belgian Maldegem Formation (Storms 1896; Schwarzhans et al. 2018), †*Apogon krambergeri* from the (?) Rupelian (lower Oligocene) of Chiavon, Italy (Bassani 1889), †*Apogon transylvanicus* and †*Arambourgia* (= *Apogonoides*) *cottreaui* from Miocene of Romania and Algeria, respectively (Arambourg 1927; Paucă 1935). However, the assignment of †*A. transylvanicus* to the Apogonidae needs to be confirmed. In this perspective, the Rupelian †*Oligopseudamia iancurtisi* gen. et sp. n. represents the only pseudamiine in the fossil record so far, consequently marking the earliest occurrence of the subfamily Pseudamiinae, whereas †*Arconiapogon deangelii* gen. et sp. n. can be considered as the youngest representative of the †Eoapogonini, suggesting the persistence of this apogonine tribe in the western Tethys at least to the early Oligocene.

The earliest occurrences of gobioids are Eocene in age and consist of isolated otoliths from the middle Ypresian (ca. 55 Ma) marine deposits of India (Bajpai and Kapur 2004; Nolf et al. 2006), whereas the oldest skeleton-based taxon is †*Carlomonnius quasigobius* from the upper Ypresian (ca. 49 Ma) of Bolca (Bannikov & Carnevale 2016). According to Gierl & Reichenbacher (2017), none of the Eocene and Oligocene skeletal records belong to the family Gobiidae, including the occurrences of '*Pomatoschistus*' *bleicheri* from the Priabonian of the Isle of Wight in England and those from the Rupelian of the Upper Rhine Valley in France, as well as the genera †*Lepidocottus* (Butidae), †*Paralates* (family incertae sedis) and †*Pirskenius* (†Pirskeniidae) (see also Gierl et al. 2013; Reichenbacher et al. 2020). Conversely, the earliest reliable fossils of the family Gobiidae appear to be otoliths from the Rupelian of southwestern France (Steurbaut 1984) and Japan (Schwarzhans et al. 2017), whereas the oldest reliable skeletal record was thus far represented by †*Gobius jarosi* from the Burdigalian (early Miocene) of the Czech Republic (Reichenbacher et al. 2018). †*Oniketia akihitoi* gen. et sp. n., being of Rupelian age (early Oligocene), seems to represents the oldest occurrence of articulated skeletal remains pertaining to the Gobiidae in the fossil record, suggesting that, consistent with the hypothesis of Thacker (2015), the origin and diversification of the family may have taken place in the Palaeogene, and not in the early Miocene as suggested by Reichenbacher et al. (2018). In addition, the earliest occurrences of gobiids (this study) and of gobioids in general (Bannikov & Carnevale 2016) seem to support the hypothesis of a western Tethyan origin for the group, although some authors proposed an Indo-West Pacific origin (see Thacker 2015).

Although several Eocene articulated skeletons and otoliths were attributed to the Chaetodontidae (e.g., Blot 1980; Stinton 1984), the earliest reliable fossils of butterflyfishes appear to be of Rupelian age (Bannikov 2004; Carnevale 2006; Micklich et al. 2009). These include fossils of the tholichthys larval stage of a chaetodontid from the lower Oligocene (Rupelian; 30.1 Ma) of Frauenweiler (S Germany), together with two probable butterflyfish tholichthys from the lower Oligocene Menilite-Formation (30–28 Ma) of Przemyśl (Outer Carpathians, SE Poland) (Micklich et al. 2009). Younger chaetodontids are represented by articulated specimens from the Chattian (late Oligocene; ca. 25 Ma; Bechtel et al. 2004) Laško-Trbovlje syncline in Slovenia, referred to *Chaetodon hoefleri* by Gorjanovic-Kramberger (1895, 1898). The taxonomic status of †*C. penniger* from Chattian sediments near Siazan, Azerbaijan, described by Bogachev (1964) based on a caudal portion only,

cannot be supported due to the incompleteness of the fossil (Carnevale 2006). The Miocene record of butterflyfishes is represented by †*C.* (*Arambourgchaetodon*) *ficheuri* from lower Messinian deposits of the Chelif Basin, north-western Algeria (Arambourg 1927; Carnevale 2006) and by isolated otoliths from the Badenian of Poland, possibly belonging to the living *C. hoefleri* (Radwanska 1992). Although the systematic status of †*Chelmon fossilis*, described by De Beaufort (1926) from a single specimen from the Miocene of South Celebes, is questionable, it was tentatively retained within the Chaetodontidae, pending further studies (Carnevale 2006). Finally, Landini & Sorbini (1993) figured a single well-preserved specimen of *C. hoefleri* from the lower Pleistocene sapropelites of the Samoggia Torrent, near Bologna, in northern Italy. The origin and early diversification of butterflyfishes is poorly understood and difficult to evaluate due to the paucity of their fossil record. Bellwood (1996) suggested that the absence of chaetodontids in Eocene deposits (where closely related taxa have been found; see Carnevale 2006) possibly reflects their low abundance. According to the molecular analyses by Fessler & Westneat (2007) chaetodontids had a common ancestor with the Scatophagidae and Pomacanthidae about 54 Ma (early Eocene), whereas the origin of the family occurred approximately at 37 Ma (late Eocene), thus implying that the early diversification of the Chaetodontidae may have occurred in the early Oligocene, like many other reef fish clades (Bellwood & Wainwright 2002; Fessler & Westneat 2007). The estimated appearence of the clade comprising *Amphichaetodon, Coradion, Chelmon, Forcipiger, Johnrandallia*, and *Heniochus* is placed at ca. 33 Ma (Rupelian, early Oligocene), whereas *Prognathodes* and *Chaetodon s.l.* originated around 24 Ma (Chattian, late Oligocene) (Fessler & Westneat 2007), with the diversification of the latter lineage that may have begun around 20 Ma (Burdigalian, early Miocene). Because the oldest chaetodontid is Rupelian in age (c. 30.1 Ma; Michlich et al. 2009), and the earliest known occurrence of the genus *Chaetodon* comes from Chattian successions (c. 25 Ma; Gorjanovic-Kramberger 1895, 1898), †*C.* (*Blumchaetodon*) *wattsi* subgen. et sp. n. from the Venetian southern Alps pushes back the origin of the *Chaetodon* clade into the early Oligocene, also supporting the hypothesis of a Tethyan origin of the group.

The Eocene western Tethys marks the earliest record of several extant tropical fish lineages, including the teleost families Acanthuridae, Antennariidae, Apogonidae, Ephippidae, Holocentridae, Labridae, Pomacentridae, and Siganidae (e.g., Bellwood 1996; Bellwood & Wainwright 2002; Carnevale & Pietsch 2009; Bannikov & Carnevale 2010; Marramà et al. 2021b) as well as some dasyatid stingray subfamilies (e.g., Marramà et al. 2019), with most of them having their earliest occurrence in the Ypresian (c. 50 Ma) assemblages of Bolca locality, in NE Italy, known for the abundance and exquisite preservation of the articulated fish skeletons (Carnevale et al. 2014; Friedman & Carnevale 2018). However, teleosts that are numerically dominant in modern coral reefs (Pomacentridae, Gobiidae, Apogonidae, Caesionidae, Chaenopsidae, Tripterygiidae) or, more generally, what are regarded as the typical coral reef fishes (Acanthuridae, Apogonidae, Blenniidae, Carangidae, Chaetodontidae, Holocentridae, Labridae, Mullidae, Pomacentridae, parrotfishes) are not abundant or, in some cases, are even absent (e.g., Gobiidae, Chaetodontidae, parrotfishes) in the Bolca fish assemblages (Bellwood 1996; Bellwood et al. 2017). Some authors suggested that the absence of gobies, butterflyfishes and parrotfishes in the Ypresian of Bolca, might be the result of their late Eocene or Oligocene origin (e.g., Fessler & Westneat 2007; Cowman & Bellwood 2011; Thacker 2015).

In this perspective, most of the Rupelian fossils from Perarolo described herein include the the oldest records for their groups (i.e., †*Oniketia akihitoi* gen. et sp. n. for gobiids; †*Oligopseudamia iancurtisi* gen. et sp. n. for the Pseudamiinae; †*C.* (*Blumchaetodon*) *wattsi* subgen. et sp. n. for the *Chaetodon* lineage; and MGP-PD R661 for the dinematichthyids), supporting the hypothesis that the evolutionary origin and early diversification of several reef fish lineages possibly took place during the early Oligocene in the tropical warm and shallow waters associated with coral reefs of the western Tethys.

Palaeoecology of the Perarolo palaeobiotope

Sedimentological, stratigraphic and palaeontological evidence concurs in indicate that the fossiliferous sediments of Perarolo where the fossils described herein were collected, originated in a tropical, shallow marine basin, possibly represented by a protected lagoon associated with a

coral reef system close to emerged areas (e.g., Frost 1981; Bosellini et al. 2020). Based on the ecology and habitat preferences of their extant relatives, the fish taxa described herein are indicative of a heterogeneous and structured context characterized by soft and vegetated bottoms, thereby consistent with a reefal palaeobiotope (Bosellini et al. 2020). The assemblage consists of epibenthic and (possibly) cryptobenthic fishes, in particular the diminutive pseudamiine apogonid †*Oligopseudamia iancurtisi* gen. et sp. n., and the gobiid †*Oniketia akihitoi* gen. et sp. n. The hypothesis is also supported by the presence of a representative of the extinct reef-associated cardinalfish lineage †Eoapogonini, represented by †*Arconiapogon deangelii* gen. et sp. n., as well as by the butterflyfish †*Chaetodon (Blumchaetodon) wattsi* sp. n., and the indeterminate dinematichthyid cusk-eel, whose extant relatives are commonly associated with tropical shallow settings characterized by coral reefs.

Viviparous brotulas of the family Dinematichthyidae are small sized (up to 20 cm) cusk-eels living in shallow tropical to subtropical waters down to about 70 m (mostly up to 10 m), of the tropical western Central Atlantic and tropical Indian and Pacific Oceans, where they commonly occur associated with coral reef environments, hidden in holes and crevices, algae beds and rocky shores, although a few species occur in non-reefal environments of subtropical rocky shores (e.g., Møller & Schwarzhans 2006; Møller et al. 2016; Bauer et al. 2021). Howes (1992) suggested that possession of the typical features of dinematichtyids and certain bythitids (taxa of 'Group 1'), characterized by the direct contact between the swimbladder and the thickened and expanded ribs and epineurals, is typical of those taxa inhabiting shallow to mid-depths. In this perspective, based on the ecology and habitat preferences of its extant relatives, the presence of a dinematichthyid cusk-eel described herein is in good accordance with the heterogeneous reefal palaeobiotope hypothesized for this region (see Bosellini et al. 2020).

Cardinalfishes of the family Apogonidae occur worldwide and include several nocturnal species (Schmitz & Wainwright 2011; Mabuchi et al. 2014). Most tropical marine cardinalfishes inhabit coral and rocky reefs and adjacent habitats including sand-rubble patches, coralline algal meadows, and seagrass beds, and are among the few marine fishes that have oral egg brooding by males (Allen 1999; Marnane & Bellwood 2002; Schmitz & Wainwright 2011). For these reasons, apogonids are invariably included in faunal surveys of coral reef fishes and are considered typical coral reef fishes (Bellwood 1996; Bellwood & Wainwright 2002; Bellwood et al. 2017). The overall body physiognomy and osteology of †*Oligopseudamia iancurtisi* gen. et sp. n. are clearly consistent with those of the extant pseudamiine genus *Pseudamia*. The seven species of this genus today inhabit tropical marine shallow waters associated with coral reefs down to about 65 meters in the Red Sea, Persian Gulf, and Indian and western Pacific Ocean (Randall et al. 1985; Mabuchi et al. 2014). Moreover, the occurrence of the apogonine †*Arconiapogon deangelii* gen. et sp. n. of the tribe †Eoapogonini is consistent with this palaeoenvironmental scenario, as the other three fossil taxa belonging to this clade, †*Apogoniscus*, †*Bolcapogon* and †*Eoapogon* (Bannikov 2005), are solely known from the celebrated Ypresian Bolca Lagerstätten, whose sediments accumulated in tropical shallow waters associated with coral reefs (e.g., Carnevale et al. 2014; Marramà et al. 2016, 2021a; Friedman & Carnevale 2018).

The family Gobiidae comprises numerous diminutive (usually not exceeding 10 cm) epibenthic and cryptobenthic species, some of which are considered among the smallest living vertebrates (e.g., Lachner & Karnella 1980; Winterbottom & Emery 1981; Winterbottom 1990; Johnson & Brothers 1993). These highly successful fishes primarily inhabit shallow tropical and subtropical waters, occupying nearly all benthic habitats from freshwater to paralic down to depths over 500 m. However, they usually dwell on a variety of very shallow substrates from mud to rubble and especially coral reefs, where they are very abundant (Larson & Murdy 2001; Murdy & Hoese 2003). Although the gobiids represent, together with apogonids and pomacentrids, some of the most abundant fishes on modern coral reefs, playing key roles in the reef ecology (Tornabene et al. 2015; Bellwood et al. 2017; Brandl et al. 2018), they are not regarded as typical coral reef fishes nor are usually included in studies about reef fish biogeography or evolutionary history (e.g., Bellwood 1996; Bellwood & Wainwright 2002; Cowman 2014). The general body size, physiognomy, osteology and meristic counts of †*Oniketia akihitoi* gen. et sp. n., closely resem-

ble the dwarfgoby *Eviota*, a tropical, cryptobenthic marine Indo-Pacific genus that includes about 120 species, with most of them being under 20 mm SL (Lachner & Kamella 1978, 1980; Tornabene et al. 2013; Greenfield & Winterbottom 2016), which are well-known for their rapid lifecycle, high turnover, and overall abundance, making them an important component of trophic food webs in coral reef settings (e.g., Depczynski & Bellwood 2003, 2005, 2006). The morphological similarity between *Oniketia akihitoi* gen. et sp. n. and *Eviota*, may suggest similar ecological affinity, implying that the Oligocene goby from Perarolo represents a diminutive cryptobenthic taxon.

Butterflyfishes of the family Chaetodontidae are small to medium-sized (up to 30 cm) reef-associated fishes usually occurring in tropical to warm-temperate shallow marine waters at depths of less than 20 m of the Atlantic, Indian, and Pacific Oceans (Burgess 1978, 2003; Pyle 2001; Rajan 2010). Chaetodontids are typically diurnal fishes that usually feed on coelenterate polyps, small invertebrates, fish eggs, and filamentous algae, while some species are specialized planktivores or obligate corallivores (e.g., Reese 1975; Harmelin-Vivien & Bouchon-Navarro 1983; Bouchon-Navarro 1986; Motta 1988). Butterflyfishes are one of the most conspicuous elements of the coral reef community, with some species, called 'ecosystem engineers', known to interact with entire environments modifying them and physically manipulating distinct habitat features (Rajan 2010). Stratigraphical and palaeoenvironmental data of the type localities of †*C. (Blumchaetodon) wattsi* suggest that this butterflyfish lived in a tropical coral reef system, possibly represented by a protected lagoon (e.g., Bosellini et al. 2020). The presumed palaeoenvironmental heterogeneity of the palaeobiotope of †*C. wattsi* sp. n. agrees with the results derived from study of its anatomy, which indicates that this taxon was characterized by a primitive, generalized jaw morphology and tooth arrangement, which are linked to an opportunistic feeding behaviour and an omnivorous diet with a wide range of benthic prey items (see e.g., Motta 1988; Carnevale 2006).

Bellwood (1996) established a specific consensus list of coral reef fish families which comprises families that can be found on coral reefs, irrespective of their biogeographic location. These include Acanthuridae, Apogonidae, Blenniidae, Carangidae, Chaetodontidae, Holocentridae, Labridae (including parrotfishes), Mullidae, and Pomacentridae, although some of these are not exclusive to coral reefs (Bellwood 1996; Bellwood & Wainwright 2002). As far as the taxa described herein are concerned, although gobies and viviparous brotulas can be remarkably abundant in modern reef biotopes playing prominent roles in the reef ecology (e.g., Tornabene et al. 2015) only apogonids and chaetodontids are generally regarded as typical coral reef fishes (Bellwood 1996; Bellwood et al. 2017).

Modern coral reefs are dominated by small-sized species, especially those belonging to the Gobiidae, Apogonidae and Pomacentridae (e.g., Bellwood et al. 2017). The Rupelian assemblage of Perarolo also mostly consists of small fishes less than 30 mm SL, including the gobiid †*Oniketia akihitoi* gen. et sp. n. and the pseudamiine cardinalfish †*Oligopseudamia iancurtisi* gen. et sp. n. Several ecological hypotheses have been used to explain the existence of very small-sized fishes in reef biotopes (e.g., Schoener 1974; Werner 1984; Marzluff & Dial 1991; Munday & Jones 1998; Bannikov & Carnevale 2016). In general, small-sized fish species are specialized in exploiting fine-grained (soft bottom) substrates, where they usually occupy sheltered and restricted microhabitats not available to the larger species (e.g., Tyler 1971; Tyler & Böhlke 1972; Patton 1994; Randall et al. 1997; Bannikov & Carnevale 2016). Based on their habitat use, small-sized benthic fish species may be classified as epibenthic or cryptobenthic (Miller 1979). Cryptobenthic species, in particular, are bottom-dwelling, morphologically or behaviourally cryptic fishes, typically adult individuals less than 50 mm in length, representing a large proportion, the so called 'hidden half', of the vertebrate diversity of coral reefs (Depczynski & Bellwood 2003; Brandl et al. 2018). Cryptobenthic fishes play a significant role in trophodynamics of tropical shallow water biotopes, and their diet is notably diverse, encompassing a full range of trophic food groups (e.g., Ackerman & Bellwood 2002). Depczynski & Bellwood (2003) found a clear relationship between diet and body length, with taxa and individuals having a total length less than 30 mm being invariably carnivores and generalists.

Based on these definitions, the gobiid †*Oniketia akihitoi* gen. et sp. n. and the pseudamiine †*Oli-*

gopseudamia iancurtisi gen. et sp. n. being represented by adult individuals of less than 30 mm SL, can be unquestionably considered as representatives of the carnivore and generalist cryptobenthic species of the Perarolo palaeobiotope, whereas the larger butterflyfish †*Chaetodon* (*Blumchaetodon*) *wattsi* subgen. et sp. n., the cardinalfish †*Arconiapogon deangelii* gen. et sp. n., and the indeterminate dinematichthyid cusk-eel, possibily represented part of the original epibenthic assemblage.

Conclusions

Oligocene fish-bearing deposits are known from the Central Europe (e.g., Leriche 1910; Weiler 1928, 1955; Théobald 1934; Pharisat 1991; Pharisat & Micklich 1998; Hovestadt et al. 2010; Maxwell et al. 2016; Gaudant et al. 2018), Alpine region (e.g., Wettstein 1886; Weiler 1932; Fröhlicher & Weiler 1952; Pictet et al. 2013; Pandolfi et al. 2017), Carpathians (e.g., Constantin 1999; Kotlarczyk et al. 2006; Gregorová 2011; Přikryl 2013; Baciu et al. 2016; Bordeianu et al. 2018; Přikryl & Carnevale 2018) and Caucasus (e.g., Bannikov 2010). All these Oligocene fish assemblages document freshwater, paralic and shallow and deep marine settings not associated to coral reefs. On the other hand, geological and palaeoecological data concur to indicate that the Perarolo taxa described herein unquestionably represent the first Oligocene coral reef fish assemblage known so far. This hypothesis is supported by stratigraphic, sedimentary and palaeontological evidence attesting to the presence of a wide shallow lagoon hosting coral bioconstructions and rimmed by a coral reef margin located on the southeastern margin of the Lessini Shelf (Bosellini et al. 2020). Therefore, our knowledge concerning Palaeogene coral reef fish assemblages is currently restricted to the Ypresian of Bolca and the Rupelian of Perarolo.

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