Description of a new stromateoid fish from the Miocene of St. Eugène, Algeria

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Carnevale, G. and Bannikov, A.F. 2006. Description of a new stromateoid fish from the Miocene of St. Eugène, Algeria. *Acta Palaeontologica Polonica* 51 (3): 489–497.

A single specimen of the axial skeleton of an elongate fossil stromateoid fish, collected from the Upper Miocene (Messinian) St. Eugène locality of north-western Algeria, is identified as a new species *Ariomma geslini* sp. nov. of the family Ariommatidae. It is based on a unique combination of features, including morphology and arrangement of pleural ribs, structure and orientation of anterior portion of the anal fin, unique sequential arrangement of anal-fin pterygiophores in relation to the haemal spines, and presence of large cycloid scales and meristics. The morphology and orientation of the first anal-fin pterygiophore indicate that *A. geslini* sp. nov. is probably related to the amphi-Atlantic species *A. bondi* and *A. melanum*. The analysis of the fossil record of the Stromateoidei suggests that the ariommatids were already in existence at least as early as the Eocene.

Key words: Teleostei, Perciformes, Ariommatidae, Miocene, Messinian, Algeria.

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Introduction

The suborder Stromateoidei is a small group of perciform fishes that comprises six families (Amarsipidae, Ariommatidae, Centrolophidae, Nomeidae, Stromateidae, Tetragonuridae), occurring worldwide in tropical and temperate coastal and oceanic waters (Haedrich 1967; Nelson 1994). These fishes have an unmistakable characteristic appearance that develops during their larval phase, resulting mostly from the wide expansion of the lacrimal, the large eye, and the protruding, inflated and naked snout and top of the head (Haedrich 1967; Ahlstrom et al. 1976). They are characterized by a marked tigmotropism and are usually associated symbiotically with jellyfishes, ctenophores and salps (see, e.g., Mansueti 1963). Although these fishes currently are recognized as a distinct and well-defined monophyletic assemblage (Haedrich 1967; Horn 1984; Doiuchi et al. 2004), their relationships with other perciforms are not completely understood (see Johnson 1993). Haedrich (1967) proposed a close relationship between stromateoids and several perciform families (Arripididae, Girellidae, Kuhliidae, Kyphosidae, Nematistiidae, Pomatomidae, Scorpididae, Terapontidae) on the basis of a shared arrangement of one ramus of one of the facial nerves (pattern 10 of the *ramus lateralis accessorius* Freihofer 1963). He also emphasized the potential role of another structure, the so-called *pons moultoni*, a small bony bridge across the inside of the passage for the anterior vertical canal of the ear, in establishing relationships of the Stromateoidei with those perciform families (Haedrich 1967; 1971). The distribution of such features within perciform families was re-evaluated by Johnson and Fritzsche (1989), who added the families Microcanthidae and Oplegnathidae to the assemblage and excluded pomatomids and nematistiids from it.

Stromateoid fishes have a poor fossil record dating from the Late Paleocene (Bonde 1966; Arambourg 1967; Bannikov 1985; 1988; 1993; 1995; 2000; Sorbini 1988; Baciu and Bannikov 2004). The goal of this paper is to describe a new fossil stromateoid recently found among the undescribed materials of the collection of the Miocene fishes from Algeria housed in the Laboratoire de Paléontologie of the Muséum national d'Histoire naturelle, Paris. The detailed osteological analysis of this fossil suggests unequivocally that it is a member of the stromateoid family Ariommatidae, and more precisely that it is the first fossil representative of the genus *Ariomma* based on articulated skeletal remains.

The genus *Ariomma* was created by Jordan and Snyder (1904) based on material collected in Hawaii that they placed in the family Apogonidae. In 1907 the same authors referred the genus to the Nomeidae. The taxonomic status of *Ariomma* was reviewed and extensively discussed by Katayama (1952) and McKenney (1961). Later, Haedrich (1967) erected the new family Ariommatidae (= Ariommidae) to accommodate it. The systematics of this family is rather problematic and confused mostly because meristic and morphometric features are identical or broadly overlapping among the species. Although Haedrich (1968) and Horn (1972) clarified several aspects of the taxonomy and biogeography of ariommatids, more detailed osteological work is needed to properly interpret the limits and relationships of this group of fishes.

Institutional abbreviations.—MNHN, Laboratoire de Paleontologie, Museum national d'Histoire Naturelle, Paris, France; USNM, National Museum of Natural History, Smithonian Institution, Washington D.C., USA.

Sedimentary setting and age

The material was collected in the 1950s by Dr. Léopold Geslin from the massive diatomite deposits outcropping near St. Eugène, a district in the suburbs of Oran, north-western Algeria. These biosiliceous deposits form part of a sedimentary sequence that originated in the south-western portion of the Chelif Basin, mainly during the late Neogene. This sector of the Chelif basin is characterized by the wide development of carbonate platforms and reef complexes that peripherally grade into marls and diatomite deposits (Rouchy 1982; Saint-Martin and Rouchy 1990). In particular, the ichthyolitiferous diatomite of St. Eugène outcrops on the north-eastern edge of the Djebel Murdjadjo carbonate platform. According to the palaeogeographic restoration provided by Perrodon (1957), diatomaceous deposition occurred widely in this part of the Chelif basin on the distal portion of the carbonate platforms, which are exposed to open marine influences. The analysis of the diatom flora of the biosiliceous deposits of the Djebel Murdjadjo carbonate platform system (Mansour and Saint-Martin 1999) indicated a neritic depositional environment characterized by high-productivity related to coastal upwelling phenomena.

The St. Eugène locality lies within the Messinian Djebel Murdjadjo platform system. The diatomites of St. Eugène, as well as other biosiliceous deposits of the Chelif basin, date back to the lower part of this stage. Large scale correlations based on the sequence stratigraphic model for Messinian carbonate platform systems elaborated by Cornée et al. (2004) pointed out that in this basin the onset of the diatomite sedimentation occurred at around 6.73 Ma, ending at around 5.95 Ma.

Materials and methods

The type and only known specimen is deposited in the Laboratoire de Paléontologie of the MNHN. The fossil is preserved on white massive diatomite with bones that appear dark brown-orange. The specimen was examined using a stereomicroscope equipped with a camera lucida drawing tube. Measurements were taken with a dial caliper, to the nearest 0.1 mm. The sequential arrangement of anal-fin pterygiophores in relation to haemal spines is written as a formula, following Forey et al. (2003), where the horizontal lines represent the haemal spine and the numbers refer to the number of pterygiophores that are interleaved. Several radiographs of Recent *Ariomma* species deposited in the USNM, have been used for comparative analysis. These are listed in Appendix 1.

Systematic palaeontology

Subdivision Teleostei *sensu* Patterson and Rosen, 1977

Order Perciformes *sensu* Johnson and Patterson, 1993

Suborder Stromateoidei *sensu* Haedrich, 1967

Family Ariommatidae Haedrich, 1967

Genus *Ariomma* Jordan and Snyder, 1904

Ariomma geslini sp. nov.

Figs. 1, 2A.

Holotype: MNHN ORA1540, incomplete fish from the Messinian of St. Eugène, Oran, Algeria.

Etymology: Specific name in honour of Dr. Léopold Geslin.

Diagnosis.—An *Ariomma* with pleural ribs robust and slender, extending posteriorly on the anteriormost caudal vertebra; posterior parapophyses and anterior haemal spines enlarged antero-posteriorly; proximal shaft of the anteriormost anal-fin pterygiophore bent backward over the four adjacent pterygiophores; sequential arrangement of anal-fin pterygiophores in relation to haemal spines 5_1_1_1_1_1_2_1_2_1; second dorsal-fin and anal-fin formulae (I + 15) and (III + 15) respectively; pectoral fin consisting of 21 elongate rays; body covered with large scales.

Measurements (mm).—Length of incomplete specimen (Fig. 1): 122; maximum body depth: 51.7; (preserved) total dorsal-fin length: 94.5; soft dorsal-fin length: 61; anal-fin length: 59.

Description.—Most of the head skeleton and caudal region are missing (Fig. 1). The body is elongate and laterally compressed; its depth measured at the level of the pelvic-fin origin approximately corresponds to the length of 11 vertebrae.

The cranial bones are missing except for some fragments of the posteroventral portion of the opercular complex.

The vertebral column is robust and almost straight. Twenty-one vertebrae are preserved. The separation of vertebrae into precaudals and caudals is rather problematic in ariommatids, and more generally in stromateoid fishes, because of the co-occurrence of a pair of pleural ribs and a haemal spine on one or more caudal vertebrae (caudal ribs *sensu* Tominaga et al. 1996). Moreover, as pointed out by Ahlstrom et al. (1976), there is a second complicating and obfuscating factor related to the backward protrusion of the organs of the abdominal cavity into the space ordinarily occupied by the anterior haemal spines. Aboussouan (1983) suggested that the separation between precaudal and caudal vertebrae can be defined by the position of the ventral folding

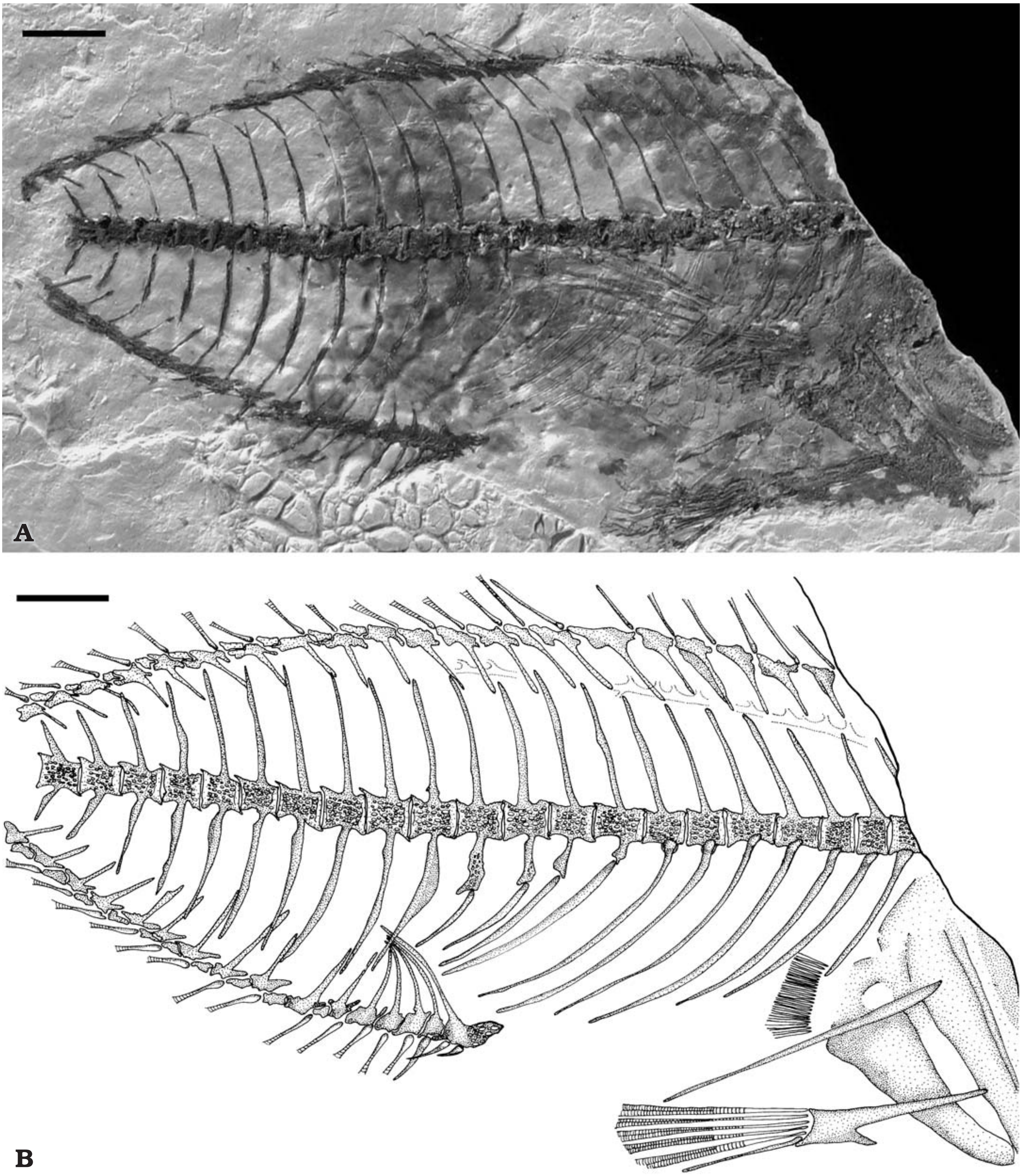

Fig. 1. *Ariomma geslini* sp. nov., Messinian, St. Eugène, Algeria. MNHN ORA1540 (holotype). Entire specimen in lateral view (**A**) with interpretative drawing (**B**). Scale bars 10 mm.

of the caudal vein. Based on the description of Aboussouan (1983), the ventral folding of the caudal vein occurs just anterior to the first haemal spine. Because of preservation there is no way to determine this character on MNHN ORA1540. Ahlstrom et al. (1976) found that the haemal spines never precede the anal fin pterygiophores. Following this criterion, the 11th preserved vertebra is interpreted herein as the anteriormost caudal element of the vertebral column. The vertebral centra are strongly ossified, subrectangular, longer than high. The dorsal pre- and postzygapophyses and the ventral postzygapophyses are well developed on most of the preserved vertebrae, whereas the ventral prezygapophyses are present on the posterior two precaudal and on the caudal vertebrae (Fig. 1). The lateral surface of the vertebral centra is extensively pitted. In general, the neural and haemal spines are relatively slender, moderately elongate, slightly curved and pointed, except for the haemal spine of the first caudal vertebra that is irregular in shape, laterally compressed and widely ornamented. The anteriormost 11 preserved vertebrae bear robust slender pleural ribs. The ribs originate on the parapophyses of the five posterior precaudal centra, and on the ventral tip of the haemal spine of the first caudal centrum. Epineural bones are poorly preserved.

There are two scarcely separated dorsal fins (Fig. 1B). The anterior portion of the spinous dorsal fin and the supraneurals are missing. Of the spinous dorsal fin, six fragile spines are preserved. Based on the meristic values commonly observed in extant congenerics (Table 1), it is possible to estimate that the anterior three or four spines have been lost. The second dorsal fin is nearly complete. This fin consists of a single spine and 14 soft rays; an additional 15th soft ray is not preserved being represented only by its pterygiophore (Fig. 1). The spine associated with the second dorsal fin is longer than the terminal spine of the first dorsal fin. Each spine and ray of the dorsal fins has a non-serial arrangement with the pterygiophore immediately posterior to it (see Ahlstrom et al. 1976) in addition to regular serial association. The dorsal-fin pterygiophores are irregular in shape. Distinctly separated distal pterygiophores are present from the sixth soft ray posteriorly (= from the 12th preserved element backward).

The anal fin inserts slightly posterior to the second dorsal fin origin. There are three spines and 13 soft rays, although 15 soft elements were certainly present, as indicated by the presence of a posterior rayless pterygiophore (Fig. 1). The anal-fin soft rays are widely spaced. The spines progressively increase in size; the two anterior spines are in supernumerary association with the first pterygiophore. The third spine, as well as the following soft rays, articulate in a non-serial arrangement with the pterygiophore immediately posterior to them, in addition to serial articulation to the preceding pterygiophore. The anteriormost pterygiophore is greatly enlarged antero-posteriorly (Figs. 1, 2A). It has an irregular shape and is ornamented on its lateral surface. The proximal shaft of this pterygiophore is bent backward over the four adjacent pterygiophores. The anal-fin pterygiophores are similar to those of the dorsal fin. A distinct separation between proximal + middle and distal pterygiophores occurs from the sixth pterygiophore posteriorly; similar to the condition observed in the dorsal-fin skeleton, such a separation occurs from the pterygiophore lying in the interhaemal space between the second and the third caudal vertebrae. The sequential arrangement of anal-fin pterygiophores in relation to haemal spines is as follows: 5_1_1_1_1_1_2_1_2_1. The five anterior pterygiophores are interpreted herein as lying in the interhaemal space between the first and the second caudal vertebrae (Fig. 1).

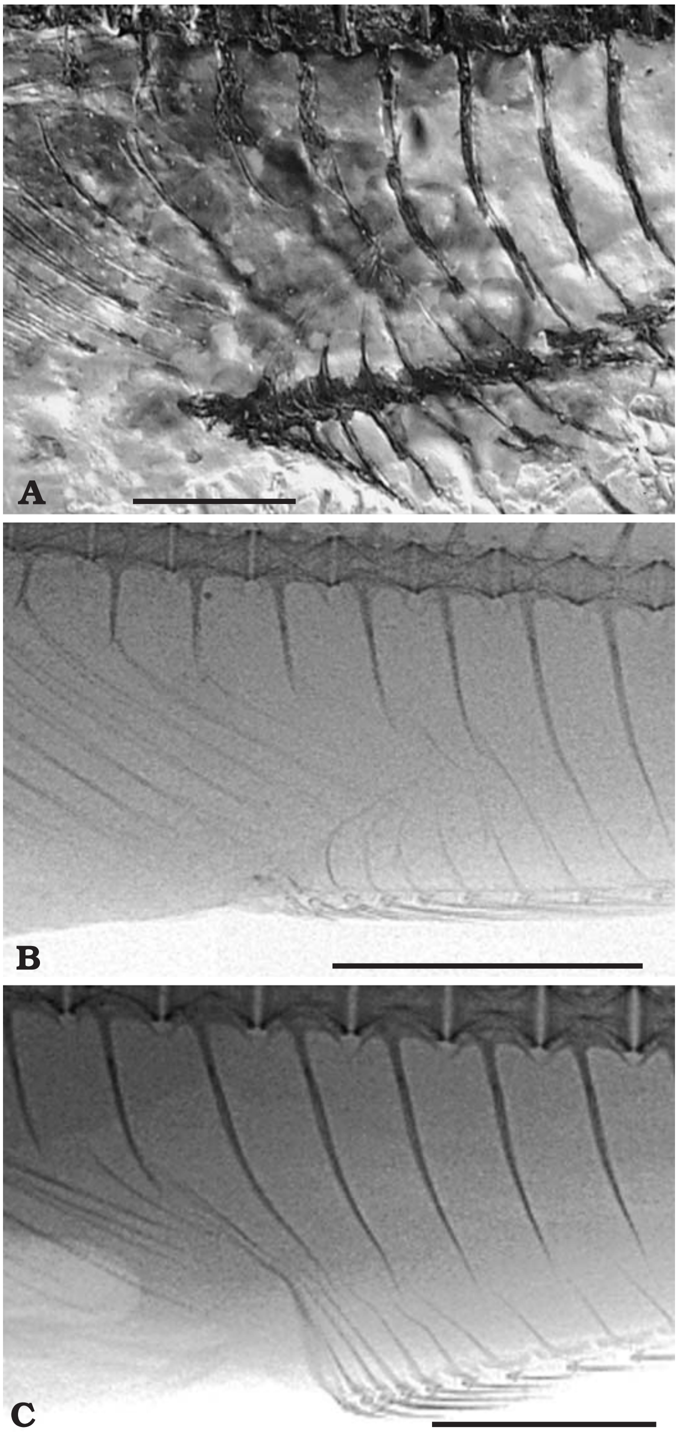

Fig. 2. Patterns of morphological variation of the anterior portion of the anal fin and its supports within the elongate species of the genus *Ariomma*. **A**. *Ariomma geslini* sp. nov., Messinian, St. Eugène, Algeria. MNHN ORA1540 (holotype) (reversed). **B**. *Ariomma bondi* Fowler, 1930, Recent. USNM 304897. **C**. *Ariomma brevimanum* (Klunzinger, 1884), Recent. USNM 057783. Scale bars 10 mm.

Table 1. Body morphology, meristics and geographical distribution of *Ariomma geslini* sp. nov. compared to those of its congenerics (data from Haedrich 1967; 1968; Horn 1972; Piotrovskiy 1987).

Taxon	Body	Dorsal-fin rays	Anal-fin rays	Pectoral-fin rays	Distribution
A. geslini sp. nov.	elongate	?, 15	III, 15	21	Paleomediterranean
A. bondi Fowler, 1930	elongate	XI–XII,13–16	II–III, 15	20–23	W-E Atlantic
A. brevimanum (Klunzinger, 1884)	elongate	XI–XII, 15	III, 14–15	24–25	Indo-Pacific
A. dollfusi (Chabanaud, 1930)	deep	XI–XII, 15	III,15	22	Indo-Pacific
A. indica (Day, 1871)	deep	X–XIII, 14–16	III, 13–15	21–23	Indo-Pacific
A. luridum Jordan and Snyder, 1904	elongate	XI–XII, 14–15	III, 13–15	20–21	Pacific
A. parini Piotrovskiy, 1987	elongate	XII, 15	II, 14–15	18–21	Indian
A. regulum (Poey, 1868)	deep	XI–XII, 15	III, 14–15	21–22	W Atlantic
A. melanum (Ginsburg, 1954)	elongate	XI–XII, 14–17	III, 13–16	21–22	W-E Atlantic

The pectoral girdle is poorly preserved. The lower portion of the cleithrum is partially exposed; its upper portion was probably curved slightly forward. A robust elongate postcleithrum also is present. This bone is obliquely inclined and posteroventrally oriented. The scapula and coracoid are partially preserved. A median foramen appears to be present on the scapula. The pectoral fin inserts low on the flank of the body. The fin is relatively elongate and has at least 21 rays (Fig. 1A).

The pelvic fin origin is situated just behind the pectoral-fin base. The pelvic fin consists of one spine and five soft rays. The basipterygium is relatively long and narrow, wedge-like; an anterior process (see Stiassny and Moore 1992) appears to be present along the ventral margin of this bone.

Large deciduous cycloid scales cover most of the preserved body. A few lateral-line scales also are present; these scales are placed relatively high along the flanks and approximately follow the dorsal profile of the body. The tubes of these scales are branched (see Fig. 1B).

Remarks.—Despite its incompleteness, the specimen examined herein shows several characters that clearly support a well-defined taxonomic placement. Its general appearance could justify its inclusion within the Stromateoidei. As stressed by Haedrich (1967), "…there is no mistaking the stromateoid look…, these fishes nonetheless have a physiognomy that nine times out of ten says stromateoid!…". The relevance of the external morphology as a diagnostic feature of these fishes also was discussed by Regan (1902). However, most of the external features indicated by these authors refer to the head that is almost completely absent in MNHN ORA1540. Fishes of the suborder Stromateoidei have a peculiar modification of the anterior portion of the gut; just behind the last gill arch there are several saccular outgrowths in the gullet that are equipped with numerous small teeth (Haedrich 1967). These structures, called pharyngeal sacs, are present in all stromateoids except for the Amarsipidae (see Haedrich 1969). Based on the absence of the pharyngeal sacs and on the branchial muscles pattern, the placement of the Amarsipidae within the suborder Stromateoidei recently has been considered as questionable by Springer and Johnson (2004) who considered such a monotypic family to be *incertae sedis* among the percomorphs. The teeth of the pharyngeal sacs occasionally can be observed in fossil fishes (Bannikov 1995), although they are usually obscured by the overlying bones of the opercular series and shoulder girdle. There are no traces of such teeth on the specimen described herein. Horn (1975) described a further synapomorphy of the stromateoid fishes, namely the possession of a relatively small, euphysoclistous swimbladder which forms in preflexion larvae and regresses before maturity. This character cannot be determined on the specimen, since it refers to a soft structure clearly not prone to the fossilization processes. In a subsequent paper, Horn (1984) considered the following three features as diagnostic of the Stromateoidei: (1) possession of cycloid scales, (2) preopercle scaled, and (3) presence of six hypurals. Of these characters only the first, presence of cycloid scales, can be observed on the specimen, while the two others cannot be seen because of the incompleteness of the material. However, two additional osteological features allow a well-supported inclusion of the specimen within the Straomateoidei: presence of a median scapular foramen (Regan 1902) and anterior prezygapophyses present on posteriormost precaudal vertebrae as well as on the caudal vertebrae (Doiuchi et al. 2004). MNHN ORA1540 also shares with selected stromateoids the posterior extension of pleural ribs on the caudal vertebrae (shared with *Amarsipus*, *Ariomma*, *Cubiceps*, *Nomeus*, *Pampus*, *Peprilus*, *Psenes*, *Stromateus*, *Tetragonurus*; Doiuchi et al. 2004), the possession of two distinct dorsal fins (shared with *Amarsipus*, *Ariomma*, *Cubiceps*, *Nomeus*, *Psenes*; Doiuchi et al. 2004) and the continued presence of pelvic fins in adult (shared by all the Stromateoidei except for the members of the family Stromateidae; Doiuchi et al. 2004). According to Doiuchi et al. (2004), the family Ariommatidae is defined by several autapomorphies that mostly apply to features not exposed or not preserved on the specimen described herein (e.g., basisphenoid slender and rod-like in lateral view; dorsal end of the basisphenoid articulated only with the prootic; second infraorbital enlarged and slightly separated anteriorly from the first infraorbital; subocular shelf present; adductor arcuus palatini did not occupy the anteroventral part of the orbit; dorsal and ventral hypohyals articulating with one another through an interdigitating suture on the medial aspect; obliquus dorsalis inserts only onto the fourth epibranchial; procurrent spur absent; scapula and coracoid articulating with one another with an interdigitating suture; opercle not scaled). Nevertheless, the assignment of MNHN ORA1540 to the family Ariommatidae, and more precisely to the genus *Ariomma*, is justified by the combination of a number of characters, including: pelvic fins present, dorsal fins scarcely separated, 15 soft rays present in the anal fin, presence of three anal spines not separated from the rays, soft dorsal and anal fins approximately the same length, scales thin cycloid and deciduous, lateral line high following the dorsal profile of the body, tubes in the lateral line scales branched, presence of 21 pectoral-fin rays, anal fin origin behind second dorsal fin origin, and pelvic fin origin behind the pectoral fin base (Haedrich 1967; 1968; Nelson 1994; Doiuchi et al. 2004). The family Ariommatidae consists of two genera, the extant *Ariomma* and the fossil *Isurichthys*. The genus *Isurichthys* from the Lower Oligocene deposits of Canton Glarus, Switzerland traditionally has been interpreted to be related to the Scombridae (see Agassiz 1833–1844; Wettstein 1886; Woodward 1901). Bannikov (1993) and Baciu and Bannikov (2004) tentatively referred it to the Ariommatidae based on several osteological, morphometric, and meristic features. *Isurichthys* clearly differs from *Ariomma* in having a shorter and deeper body. Thus, although a more detailed osteological analysis of *Isurichthys* is necessary in order to understand its phylogenetic placement, there are no substantive characters that would suggest a close relationship between this genus and MNHN ORA1540. The anatomical investigation of MNHN ORA1540 has identified features that strongly support its placement within the genus *Ariomma* (Haedrich 1967; 1968; Doiuchi et al. 2004). Two groups of species can be easily recognized within the genus *Ariomma*: elongate species, with the maximum body depth less than 30% standard length (SL), and deep-bodied species, with the maximum body depth greater than 40% SL. The specimen described herein evidently belongs to the elongate species group. Five extant species constitute the elongate group: *A. bondi* Fowler, 1930, *A. brevimanum* (Klunzinger, 1884), *A. lurida* Jordan and Snyder, 1904, *A. melanum* (Ginsburg, 1954), and *A. parini* Piotrovskiy, 1987 [see Karrer (1984) for synonymies]. According to Haedrich (1967), the problem of delineating the species of *Ariomma* is one of the most perplexing of the entire suborder, because almost all have the same or overlapping morphometric and meristic features (Table 1; see also McKenney 1961; Lamkin 1997). Moreover, the small number of distinguishing features and the widespread and often disjunct distribution of the populations have made the determination of species limits a problematic matter (Horn 1972). Karrer (1984) suggested that the morphology of the anterior anal-fin pterygiophores represents a character useful for the separation of the Pacific species of the genus *Ariomma*. The results of our investigation on extant representatives of the genus support the arguments proposed by Karrer (1984) (Fig. 2). The analysis of the anatomical variability of the anal fin within the family indicates the diagnostic value of the orientation of the anteriormost pterygiophores and their interdigitation with the overlying haemal spines. The species of the elongate group have two different morphological patterns of the anterior sector of the anal fin (Fig. 2). The first pattern is characterized by anteriorly oriented pterygiophores distinctly separated from each other (Fig. 2C). The second pattern is characterized by a completely different arrangement of the anteriormost anal-fin pterygiophores, which are posteriorly oriented and with the proximal shaft of the first pterygiophore bent backward over the adjacent pterygiophores. The second pattern is shared by *A. bondi*, *A. melanum*, and MNHN ORA1540 (Fig. 2A, B). Thus, the specimen described herein seems to be closely related to *A. bondi* and *A. melanum*. *Ariomma bondi* and *A. melanum* are rather similar in body shape. Horn (1972) documented consistent recognizable differences between these species, related to the dimensions of the scales, number of lateral line scales, interorbital squamation, relative development of the cephalic lateral line, distribution of peritoneal melanophores, intestine length, and otolith morphology (see also Schmidt 1968). None these characters, except the dimensions of the scales, can be observed in MNHN ORA1540. The development of relatively large scales (see description above) is indicative of some affinity between MNHN ORA1540 and *A. bondi*. *Ariomma melanum* is characterized by small scales (Horn 1972). However, *A. bondi* and *A. melanum* differ from MNHN ORA1540 in that the pleural ribs are considerably thinner and more slender, the posterior parapophyses and the anterior haemal spines are not enlarged antero-posteriorly, the pleural ribs occur on two caudal vertebrae, the abdominal cavity protrudes further posteriorly into the space usually occupied by the anterior haemal spines, the proximal shaft of the first anal pterygiophore is bent posteriorly over the five posterior pterygiophores and the sequential arrangement of anal-fin pterygiophores in relation to the haemal spines is 6_1_1_1_1_2_1_1_2.

In summary, our study of MNHN ORA1540 has identified several features that unequivocally support its placement as a new species of the genus *Ariomma*.

Discussion

Although L. Geslin donated the specimens to the MNHN in the late 1950s, the fish fauna from St. Eugène is still undescribed. The Messinian fishes of the Chelif Basin were investigated in detail by Arambourg (1927) in an extensive monograph in which he assembled the material collected from five main localities, Gambetta, Les Planteurs, Raz-el-Aïn, Saint Denis du Sig and Sidi-Brahim, describing approximately 80 taxa. The continuous survey of the area by French geologists during the past century resulted in the discovery of a further locality, Renault, located in the north-eastern sector of the basin. The Renault site has provided only a few articulated skeletal remains of the hatchetfish *Argyropelecus logearti*

Arambourg, 1929 (see Carnevale 2003). More recently, Gaudant et al. (1997) described a small assemblage from Chabet Beida, near the Djebel Murdjadjo Massif. The St. Eugène site brings the number of Messinian fish localities known from the Chelif basin to eight. *Ariomma geslini* sp. nov. is the second taxon described up to now from St. Eugène. An incomplete specimen of the butterflyfish *Chaetodon ficheuri* Arambourg, 1927, recently has been described from this locality by Carnevale (2006). A cursory survey of the material from St. Eugène in the MNHN collection has revealed the presence of approximately 230 specimens, among which representatives of at least 9 families can be recognized in addition to the Ariommatidae and Chaetodontidae, including Clupeidae (e.g., *Alosa*, *Etrumeus*), Diodontidae (*Chilomycterus*), Gadidae, Myctophidae (e.g., *Diaphus*, *Lampanyctus*), Pomacentridae, Serranidae, Soleidae, Sparidae, Syngnathidae (*Syngnathus*). Lanternfish (Myctophidae) skeletons are by far the most abundant fishes in the examined material, with more than 150 recognizable specimens. Herrings (Clupeidae) are also well represented in the assemblage with more that 50 specimens. Pipefishes (Syngnathidae) and porgies (Sparidae) are less common, each represented by 6 specimens, while representatives of the other families are restricted to a single specimen. Despite the high percentage of meso- and bathypelagic fish (myctophids), the geological evidence (see, e.g., Perrodon 1957; Rouchy 1982) and the rest of the ichthyofauna are clearly indicative of a shelf environment not far from the coast. In this setting, the lanternfish abundance was probably related to the palaeoceanographical conditions of this sector of the Chelif basin, which was characterized by an intensification of primary production in response to coastal upwelling phenomena (e.g., Moisette and Saint-Martin 1992; Mansour and Saint-Martin 1999). The palaeogeographic and palaeoenvironmental scenario resulted from stratigraphic studies (see Perrodon 1957; Gourinard 1958; Rouchy 1982; Cornée et al. 1994) and analysis of the associated ichthyofauna of the type locality of *A. geslini* suggest that this fish was probably characterized by an ecological behaviour similar to that of the extant Amphi-Atlantic species *A. bondi*. In the eastern Atlantic *A. bondi* is a dominant member of the so-called "sub-thermocline sparid sub-community" that occur in a depth range of 70–200 meters over soft deposits in waters of 14° to 20° (Longhurst 1965; 1969; Fager and Longhurst 1968). As reported by Poll (1959), this demersal species is more abundant in a depth-range of 120–180 m, but it extends less frequently into deeper water towards the shelf edge.

As discussed above, morphological features are indicative of close relationships between *A. geslini* and the extant Atlantic species *A. bondi* and *A. melanum*. In particular, these three species share the same morphological pattern of the anterior sector of the anal fin, which appears to be exclusive of them among the group of species characterized by an elongate body. *Ariomma bondi* and *A. melanum* occur both on the eastern and western sides of the Atlantic Ocean, and the disjunct populations apparently maintain a genetic continuity by larval dispersal across the ocean (Horn 1972). In the eastern Atlantic their geographic range is restricted to the intertropical region, from Mauritania to Angola (Horn 1972). The presence of a representative of the genus *Ariomma* close to the *A. bondi*–*A. melanum* species pair in the Messinian of the Mediterranean provide new evidence of the biogeographic relationships that this basin had with the tropical Atlantic at that time. A similar palaeobiogeographic pattern was also shared by other taxa described from coeval deposits of the Chelif Basin, such the hairy blenny *Labrisomus pronuchipinnis* Arambourg, 1927, and the grunt *Parapristipoma prohumile* Arambourg, 1927. The relationships of *A. geslini* suggest that the characteristic posterior bending of the anteriormost pterygiophore of the anal fin is restricted to the elongate species that inhabit the Atlantic-Paleomediterranean region, thereby indicating that such a morphological pattern of this structure has a probable biogeographical implication.

According to Haedrich (1967), the species of the genus *Ariomma* are the most recently evolved stromateoid fishes; their geographic distribution and their remarkable morphological homogeneity suggest that these fishes apparently derived from a nomeid stock during the Pliocene (Haedrich 1967; 1968). The Late Miocene occurrence of a well-defined species clearly belonging to the genus *Ariomma* evidently contrasts with the hypothesis of a Pliocene origin proposed by Haedrich (1967; 1968). Moreover, Middle Miocene otoliths assigned to this genus were described by Steurbaut (1984) and Schwarzhans (1985), respectively from France and Australia. The origin of ariommatids is not well understood. The placement of *Isurichthys* within this family as argued by Bannikov (1993) and Baciu and Bannikov (2004) further suggests that the divergence of these fishes occurred evidently before the Lower Oligocene. The phylogenetic analysis provided by Doiuchi et al. (2004) proposes that the family Ariommatidae is the sister group of the Nomeidae, Tetragonuridae, and Stromateidae. In his review of the stromateoid fossil record, Bannikov (1995) pointed out that unquestionable representatives of the family Nomeidae already were in existence in the Middle Eocene, and an undescribed possible member of that family was collected from the Upper Paleocene Mo-Clay Formation, Denmark (see Bonde, 1966). The fossil record does not provide a precise age for the origin of ariommatids even if the Eocene record of the nomeids necessarily implies that the ariommatids also existed at that time.

Acknowledgements

Research in Paris by the authors was made possible by a SYNTHESYS grant of the MNHN to GC and a NATO Life Science and Technology collaborative grant (LST.CLG.978836) to AFB. Daniel Goujet and Monette Véran (Département Histoire de la Terre, MNHN, Paris, France) are thanked for permission to examine material under their care and logistic support. We are particularly obliged to Philippe Loubry for the photographs. Many thanks go to Walter Landini (Dipartimento di Scienze della Terra, Pisa, Italy) and Andrea Cerrina Feroni (CNR – Istituto di Geoscienze e Georisorse, Pisa) for useful discussions and support. Nikolai V. Parin (P.P. Shirshov Institute of Oceanology, Moscow, Russia) and Sandra Raredon (USNM) kindly provided radiographs of extant ariommatids. Thanks also are due to Federica Giudice for improvement of the English. Many thanks go to Gloria Arratia (Division of Vertebrate Paleontology, Natural History Museum and Biodiversity Center, University of Kansas, Lawrence, USA) and James C. Tyler (USNM) for constructive advice on improving the manuscript. Not least, our special thanks go to Adrian, Stephanie, and Andrea Di Muro, Angelo Scimia, and Sara and Francesco Santini for their kindness and wonderful hospitality.

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Appendix 1

List of Recent comparative material used (radiographs):
Ariomma bondi Fowler USNM 304897;
Ariomma brevimanum (Klunzinger) USNM 057783;
Ariomma indica (Day) USNM 285971, USNM 325737;
Ariomma lurida Jordan and Snyder USNM 051653;
Ariomma melanum (Ginsburg) USNM 214308;
Ariomma regulus (Poey) USNM 315201.