[Palaeontology, Vol. 49, Part 2, 2006, pp. 391–403]

A NEW SNAKE MACKEREL FROM THE MIOCENE OF ALGERIA

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Typescript received 15 April 2004; accepted in revised form 4 March 2005

Abstract: A new genus and species of gempylid is described from the Late Miocene (Messinian) diatomite deposits of the Chelif Basin, north-east Algeria. Although its skeleton is incomplete, *Chelifichthys goujeti* gen. et sp. nov. possesses a unique combination of features that justifies its recognition as a new genus. *Chelifichthys goujeti* is characterized by remarkably elongate and serrated dorsal-fin spines, the absence of external pelvic-fin elements, and sculptured frontals and opercular bones. *Chelifichthys* appears to be closely related to the living genera *Nealotus*, *Prometichthys*, *Rexea* and *Rexichthys*. *Chelifichthys goujeti* represents the third record of the family Gempylidae in the Neogene of the Mediterranean.

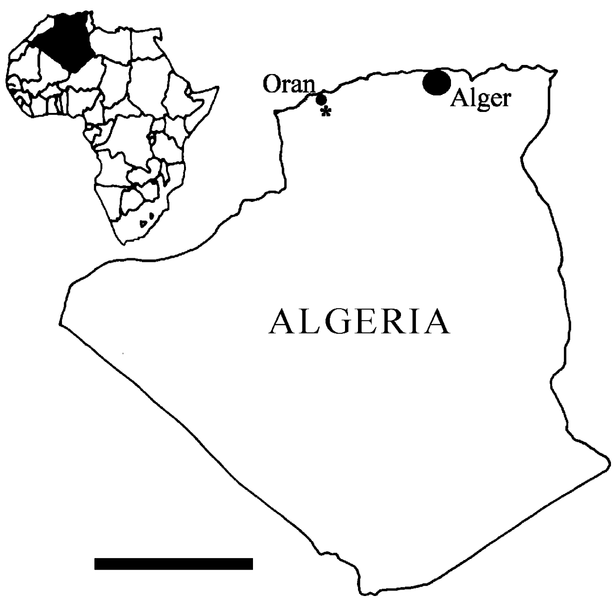
Key words: Teleostei, Perciformes, Gempylidae, *Chelifichthys goujeti*, Algeria, Late Miocene, Messinian.

FOSSIL fishes are relatively common in the Late Miocene (Messinian) deposits of the Mediterranean Basin. Their abundance is primarily related to the euxinic conditions of the bottom that occurred during the cyclic diatomite-sapropel sedimentation that affected the Mediterranean in the early Messinian in response to the precessional forcing of ocean stratification (Filippelli *et al.* 2003; Pérez-Folgado *et al.* 2003). The existence of fish remains in the Messinian diatomites has been well known since the eighteenth century and up to now numerous localities have been discovered in both western and eastern sectors of the Mediterranean. Among these localities, those from the Chelif Basin, north-east Algeria, are the most famous because of the excellent preservation of the specimens and their crucial importance for the fossil record of the Teleostei (Carnevale 2004*a*). Fossil fishes were collected from five main localities: Gambetta, Les Planteurs, Raz-el-Aïn, Saint Denis du Sig and Sidi-Brahim (Arambourg 1927). Arambourg (1927) investigated thousands of specimens and recognized more than 80 taxa among this material. During a re-examination of part of this collection in the last few years, some new taxa were discovered among the still-undescribed or unidentified material. One of these specimens is a small, incomplete, articulated skeleton characterized by remarkably developed dorsal-fin spines and the absence of external pelvic-fin elements. A detailed systematic analysis of the osteology of this fossil suggests unequivocally that it is a member of the family Gempylidae.

Fishes of the family Gempylidae (snake mackerels) are fast-moving, oceanic, epi- and mesopelagic or benthopelagic predators living at 100–2000 m depth in all oceans. Some species of this family support important commercial fisheries and their biology has been extensively investigated (e.g. Colgan and Paxton 1997; Lorenzo and Pajuelo 1999). The systematics of these fishes and their relationships with the Trichiuridae have been discussed by many authors (Günther 1860; Gill 1862; Regan 1909; Gregory 1933; Tucker 1956; Parin and Becker 1972; Russo 1983). Johnson (1986) rediagnosed the Gempylidae in a cladistic context, recognizing their monophyly and placing them as the sister group of scombrids plus billfishes. He defined three gempylid subfamilies (Lepidocybiinae, Gempylinae and Trichiurinae) and concluded that the trichiurids represent a highly derived offshoot of a paraphyletic Gempylinae. However, these results were not supported by successive phylogenetic studies, both morphological and molecular (Carpenter *et al.* 1995; Finnerty and Block 1995). Otoliths referred to the Gempylidae date back to the Late Campanian (Nolf and Stringer 1996). According to Cavin (2001), these fishes crossed the Cretaceous⁄Tertiary boundary by virtue of their belonging to the detritus-based mesopelagic food chain. Skeletal remains clearly belonging to this family are rather common in the Oligocene localities of central and eastern Europe (von Rath 1859; Wettstein 1886; Jonet 1958; Danil'chenko 1960; Jerzmańska 1968; Bannikov and Fedotov 1989; Bannikov and Parin 1996; Micklich and Parin 1996; Pharisat and Micklich 1998; Bannikov 2005).

GEOLOGICAL SETTING

The material was collected during the early years of the twentieth century from the laminated diatomaceous deposits (Tripoli) that crop out in the Ravin Blanc of Gambetta, a suburb situated south of Oran, in the north-east of Algeria (Text-fig. 1). These deposits form part of a sedimentary sequence that accumulated in the south-western portion of the Chelif Basin, mainly during the Late Miocene (Messinian) (Perrodon 1957). A schematic description of the outcrop was given by Arambourg (1927) and Gourinard (1958). Late Miocene deposits here consist of a rhythmic alternation of cherty marls and limestone with thick diatomitic intercalations. Fossil fishes were collected from both marls and diatomites. Pliocene marine calcareous sandstones lie transgressively over the Miocene sequence. A few metres of Quaternary sediments complete the succession (see Gourinard 1958). The diatomaceous and marly deposits of Gambetta represent the peripheral expression of a carbonate platform characterized by wide coral and algal reef complexes (e.g. Rouchy and Saint-Martin 1992; Cornée *et al.* 1994). According to the palaeogeographical restoration provided by Perrodon (1957), diatomaceous deposition occurred widely in the Chelif Basin during the Messinian. The diatomites accumulated in a high-productivity environment related to coastal upwelling. The analysis of the diatom content of an outcrop not far from Gambetta (Mansour and Saint-Martin 1999) revealed the existence of two different environmental episodes of geological and oceanographic changes that occurred in the area surrounding the Djebel Murdjadjo carbonate platform. The first records distal platform sedimentation in an open marine environment characterized by tropical conditions and nutrient richness (abundance of the diatom *Thalassionema nitzschoides s.l.* Grunow, *in* van Heurck 1881). The second episode testifies to marine littoral conditions in a restricted basin characterized by periodic oscillations in salinity. According to Rouchy and Saint Martin (1992) and Mansour and Saint-Martin (1999), this latter episode probably records the onset of the Messinian Salinity Crisis.



TEXT-FIG. 1. Type locality of *Chelifichthys goujeti* gen. et sp. nov. The asterisk indicates the location of Gambetta. Scale bar represents 500 km.

Fossil fishes were collected in diatomites deposited during the first environmental episode. The fish fauna from the Messinian diatomites of Gambetta (Arambourg 1927; Carnevale 2004*b*) consists mostly of myctophids [*Diaphus edwardsi* (Sauvage, 1870), *Diaphus microsomus* (Sauvage, 1870), *Myctophum columnae* (Sauvage, 1873)], but also includes clupeids (*Alosa crassa* Sauvage, 1873, *Alosa elongata* Agassiz, 1843), sternoptychids [*Maurolicus muelleri* (Gmelin, 1789)], sparids [*Boops roulei* Arambourg, 1927, *Diplodus oranensis* (Woodward, 1901)], scombrids (*Euthynnus* sp., *Sarda roulei* Arambourg, 1927) and ammodytids (*Gymnammodytes oranensis* Carnevale, 2004*b*).

MATERIAL AND METHODS

The single holotype specimen was found among the undescribed material of the fossil fish collection of the Laboratoire de Paléontologie, Muséum national d'Histoire naturelle (MNHN), Paris. It consists of an incomplete articulated skeleton preserved on white laminated diatomite. The specimen was studied using a stereomicroscope with an attached camera lucida drawing arm. Measurements were taken using a dial caliper, to the nearest 0·1 mm. Counts and measurements were made following Nakamura *et al.* (1983). The specimen required matrix removal before examination in order to investigate the presence or absence of external pelvic-fin elements. This was achieved using mounted entomological needles. Osteological terminology mainly follows Gago (1998). The term 'interneural space' is used in the sense of Birdsong *et al.* (1988), Baldwin and Johnson (1993) and Tyler *et al.* (2003), with the first space being that between the first and second neural spines. Unless otherwise indicated, the terms Gempylidae and Trichiuridae refer to the Gempylinae plus Lepidocybiinae and Trichiurinae of Johnson (1986), respectively.

Comparative material examined. Blochiidae: *Blochius longirostris* Volta, 1796, Eocene, Monte Bolca (Italy): MNHN BOL0296, BOL0298, BOL0299. Euzaphlegidae: *Palimphyes* sp., Oligocene, Glaris (Switzerland): MNHN GLA4, GLA24. Gempylidae: *Epinnula cancellata* Arambourg, 1967, Oligocene, Elam (Iran): MNHN

EIP193g+d, EIP204g+d, holotype, EIP205, EIP207g+d, EIP216. *Hemithyrsites armatus* Sauvage, 1873, Late Miocene (Messinian), Licata (Italy): MNHN LIC159, syntype, LIC160, syntype, LIC271, syntype, LIC345, LIC477. *Thyrsitoides zarathoustrae* (Arambourg, 1943), Oligocene, Elam (Iran): MNHN EIP192g+d, holotype, EIP196, EIP198, EIP199g+d. Palaeorhynchidae: *Palaeorhynchus altivelis* Arambourg, 1967, Oligocene, Istehbanat (Iran): MNHN EIP39. *Palaeorhynchus glarisianus* Blainville, 1818, Oligocene, Glaris (Switzerland): MNHN GLA52. Scombridae: *Sarda roulei*, Late Miocene (Messinian), Gambetta (Algeria): MNHN ORA402g+d syntype. *Scomber colias* Gmelin, 1789, Late Miocene (Messinian), Raz-el-Aïn (Algeria): MNHN ORA12, ORA13, ORA102g+d, ORA150g+d, ORA151. Trichiuridae: *Ananchelum* sp., Oligocene, Glaris (Switzerland): MNHN GLA41, GLA51, GLA54. *Lepidopus caudatus* (Euphrasen, 1788), Recent, Tyrrhenian Sea: uncatalogued, personal collection. *Lepidopus proargenteus* Arambоug, 1927, Late Miocene (Messinian), Les Planteurs (Algeria) MNHN ORA44, syntype, ORA168 syntype.

Anatomical abbreviations. Ar, articular; Cl, cleithrum; Cor, coracoid; Dfs, dorsal fin spine; Dpcl, dorsal postcleithrum; Dr, distal radial; Epc, epicentral; Edp, endopterygoid; Epi, epioccipital; Epn, epineural; Etp, ectopterygoid; D, dentary; Fr, frontal; H, hyomandibula; Iop, interopercle; Mtp, metapterygoid; Op, opercle; Pa, parietal; Pal, palatine; Pas, parasphenoid; Pmr, proximal + middle radial; Pop, preopercle; Pt, posttemporal; Pto, pterotic; Pts, pterosphenoid; Q, quadrate; Ra, radial; Rar, retroarticular; Sca, scapula; Scl, supracleithrum; Soc, supraoccipital; Sop, subopercle; Spo, sphenotic; Sym, symplectic; Vpcl, ventral postcleithrum.

SYSTEMATIC PALAEONTOLOGY

Subdivision TELEOSTEI *sensu* Patterson and Rosen, 1977
Order PERCIFORMES *sensu* Johnson and Patterson, 1993
Suborder SCOMBROIDEI *sensu* Carpenter, Collette and Russo, 1995
Family GEMPYLIDAE Gill, 1862

Genus CHELIFICHTHYS gen. nov.

Type and only species. *Chelifichthys goujeti* sp. nov.

Derivation of name. After the Chelif Basin (Algeria) where the type locality is situated; and Greek, *ichthys*, a fish.

Diagnosis. Small gempylid with an elongate, compressed body; relatively high median supraoccipital ridge; frontal and opercular bones sculptured; sclerotics present; ventral margin of the posterodorsal notch of the opercle not spinous; presence of two pointed spines on the posterior edge of the preopercle; parapophyses absent; epineurals simple, attached from vertebrae 1–7, unattached posteriorly; epicentral bones present; pectoral fin contains 16 rays; pectoral fin inserts low on the body; posterior pectoral-fin rays longer; pectoral fin length equals 115 per cent of body depth; pectoral girdle dorsoventrally compressed; head of the supracleithrum with a posteriorly expanded process; posterior process of the basipterygium elongate; pelvic fin absent; dorsal-fin spines remarkably elongate (111–163 per cent of body depth) and forming a steeply graduated series; longitudinal anterior keel and posterolateral keels of anterior dorsal-fin spines serrated; anterior dorsal fin inserts just posterior to the occipital region of the neurocranium; proximal portion of the three anterior proximal-middle radials expanded as a bony lamina on both sides of the main shaft.

Distribution. Late Miocene (Messinian), Algeria.

Chelifichthys goujeti sp. nov.
Text-figures 2A, 3–4

Holotype. MNHN ORA1216, anterior portion of body and incomplete head.

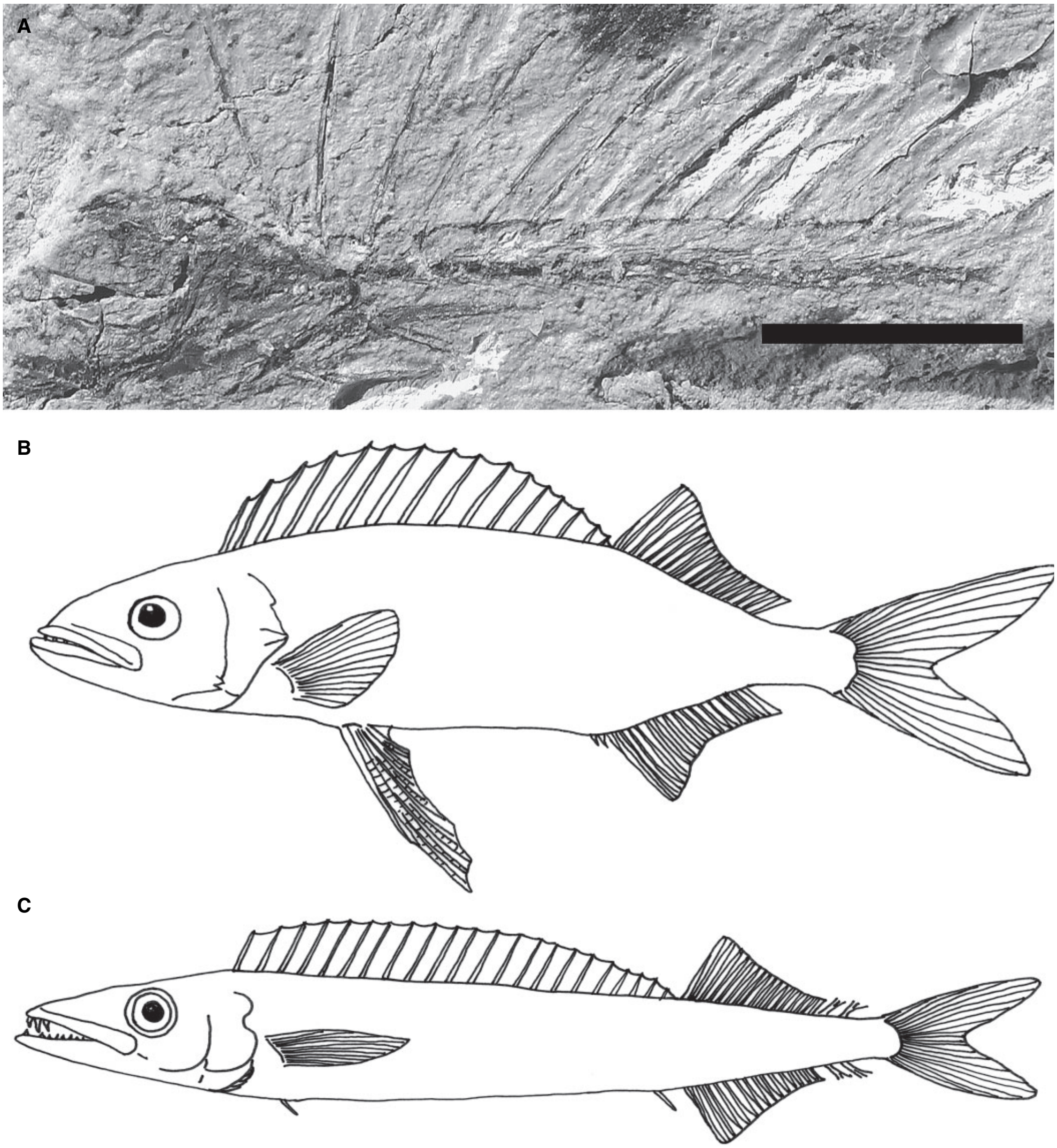
Type locality and horizon. Gambetta, Oran, Chelif Basin, northeast Algeria; Late Miocene, Messinian.

Derivation of name. In honour of the distinguished French palaeoichthyologist Professor Daniel Goujet.

Diagnosis. As for genus.

Description. The holotype of *Chelifichthys* gen. nov. consists of an incomplete postcranial skeleton and a posterior half of the head (Text-fig. 2A). Measurements are given in Table 1. The specimen is small and because of its incompleteness it is not possible to estimate its original length. In general, the body appears to be elongate and considerably compressed, as in many other gempylids, such as *Diplospinus* Maul, 1948, *Gempylus* Cuvier, 1829, *Nealotus* Johnson, 1865 (Text-fig. 2C), *Nesiarchus* Johnson, 1862, *Paradiplospinus* Andrianshev, 1960, *Prometichthys* Gill, 1893, *Rexea* Waite, 1911, *Rexichthys* Parin and Astakhov, 1987, *Thyrsites* Cuvier, 1831 and *Thyrsitoides* Fowler, 1929 (see Nakamura and Parin 1993). It appears to be an adult based on the heavy ossification of most skeletal elements.

The entire preorbital region of the skull is missing. In common with other gempylids, and more generally with the scombroids, the neurocranium of *Chelifichthys* (Text-fig. 3A) is marked by a median supraoccipital ridge and two lateral ridges on each side: epioccipital and pterotic. The prominent supraoccipital ridge is formed by the confluence of two low frontal ridges onto the supraoccipital. The epioccipital and pterotic ridges originate anteriorly, more or less at the same position on the external surface of the frontal ridge. These ridges are separated from each other by three grooves on each side, named by Allis (1903), respectively, as supratemporal, temporal

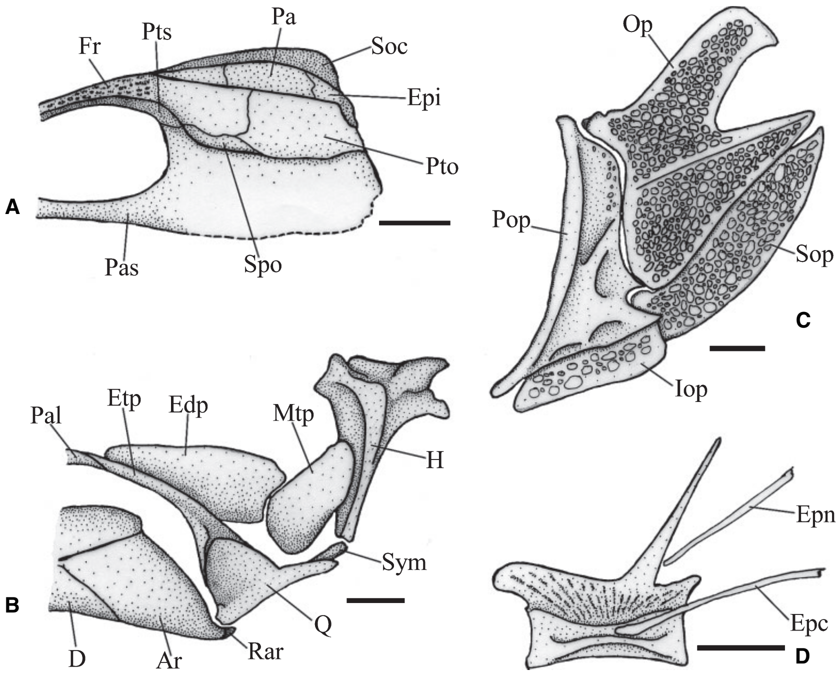


TEXT-FIG. 2. A, *Chelifichthys goujeti* from late Miocene deposits in Algeria. Holotype, MNHN ORA1216, left side, lateral view. Scale bar represents 10 mm. B, *Epinnula magistralis* Poey, 1854 (redrawn from Matsubara and Iwai 1952). C, *Nealotus tripes* Johnson, 1875 (redrawn from Nakamura and Parin 1993).

TABLE 1. Measurements (in mm) for *Chelifichthys goujeti*.

Length of the specimen	39·7
Postorbital length of the head	8·5
Body depth	6
Length of the pectoral fin	6·9
Length of the longest pectoral ray	6·7
Length of the first dorsal base	22·4
Height of first spine of first dorsal fin	9·3
Height of longest first dorsal spine (fourth)	9·8

and dilatator. An additional ridge is situated on the sphenotic, lateral to the pterotic ridge. The shelf formed by the pterotic and sphenotic ridges represents the dilatator groove that housed the dilatator operculi muscle in the living fish. The posterior region of the frontal is preserved. The frontal articulates posteriorly with the parietal and the supraoccipital, posterolaterally with the sphenotic, and ventrally with the pterosphenoid. As described above, the frontal is characterized by two contralateral longitudinal ridges that join each other posteriorly, forming the supraoccipital ridge. At least the



TEXT-FIG. 3. *Chelifichthys goujeti*. A, reconstruction of the braincase, left side, lateral view. B, reconstruction of the suspensorium and posterior end of the lower jaw, left side, lateral view. C, reconstruction of left opercular series, lateral view. D, eleventh precaudal vertebra, left side, lateral view. Scale bars represent 1 mm.

supraorbital portion of the frontal has a sculptured, cancellose texture. The parietal is a small quadrangular bone, separated from its opposite member by the supraoccipital. The epioccipital ridge passes across the parietal. The supraoccipital is an elongate bone bearing a relatively high median ridge. Posterior to the parietal and lateral to the supraoccipital is the epioccipital. This is massive and irregular in shape. Its posterior margin is not clearly recognizable. The epioccipital is the posteriormost bone forming the epioccipital ridge. The braincase is bordered laterally by the sphenotic and the pterotic. The pterotic articulates anteriorly with the frontal and the sphenotic. The dorsolateral border of these bones is characterized by the posteriormost section of the pterotic ridge. The ventral margin of the pterotic, prootic, intercalar and basicranial regions are difficult to interpret because of damage. A small portion of the parasphenoid can be observed as an impression in the lower third of the orbit. Fragments of what appear to be a posterior sclerotic are preserved along the posterior margin of the orbit.

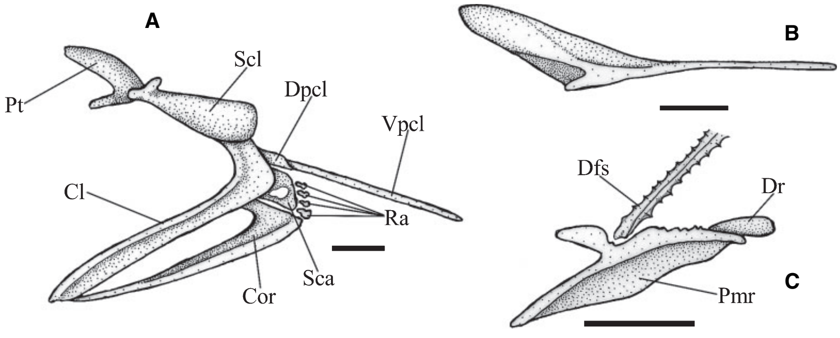
The posterior portion of the mandible, the suspensorium and opercular complex of the right side of the body are exposed in medial view and the counterparts of the left side are missing. The preserved portion of the dentary is characterized by two divergent arms. The articular fits into the dentary at its triangular process. The retroarticular is a small bone attached to the posteroventral margin of the articular (Text-fig. 3B).

The suspensorium (Text-fig. 3B) consists of the hyomandibula, symplectic, quadrate, ectopterygoid, endopterygoid, metapterygoid and palatine. The hyomandibula is a robust, well-ossified bone. Three condyles are present on the upper part of this bone. The two dorsal condyles presumably articulate with a fossa situated in the otic region of the neurocranium but this is not visible in the specimen. The elongate ventral arm of this bone bears a thin bony lamella anteriorly. Along the posterior margin, the hyomandibula articulates with the preopercle. The posterior condyle of this bone articulates with the anterodorsal head of the opercle. The symplectic is a tube-like, elongate splint of bone that fits into the groove on the inner surface of the quadrate. The quadrate is a flat, fan-shaped bone. The posterior margin of the quadrate is thick and bears an elongate process. The metapterygoid and the ectopterygoid are thin, irregular bones. The ectopterygoid is a robust bone that articulates with the quadrate and the endopterygoid. Only the posterior portion of the palatine is preserved. There are no traces of palatine teeth. However, the absence of palatine teeth could be related to the incompleteness of the palatine itself and this character cannot be used to evaluate the relationships of *Chelifichthys* until a better preserved palatine becomes available in additional specimens.

The bones of the opercular apparatus (Text-fig. 3C) are thin and extensively sculptured on the external surface, similar to the frontal. The preopercle is a crescent-shaped bone with a longitudinally orientated lateral-line canal. The posterior edge of the preopercle has two spines; the ventral spine is located at the corner between the ventral and posterior edges. The posterodorsal margin of this bone appears to be slightly convex. The interopercle is a quadrangular bone. The opercle is marked by the presence of a deep notch along its posterior margin. This bone has a thick horizontal crest on the medial surface running back to the posteroventral corner. The articular head of the opercle is partially covered by a flat process. The subopercle is flat, roughly triangular in shape, and characterized by a well-developed anterodorsal articular process.

There is no evidence of the hyoid bar and branchial skeleton.

The preserved portion of the axial skeleton contains 17 precaudal vertebrae. The first vertebra is shorter than those that follow. The centra are elongate and, except for the first centrum, almost twice as long as high. The vertebral centra are



TEXT-FIG. 4. *Chelifichthys goujeti.* A, reconstruction of left pectoral girdle, lateral view. B, basipterygium, left side, lateral view. C, fifth dorsal fin pterygiophore, left side, lateral view. Scale bars represent 1 mm.

sculptured laterally in the dorsal region. The neural spines are stout and short. Haemal arches and spines can be observed at least on the three posterior preserved vertebrae. The parapophyses are apparently absent. The neural prezygapophyses are massive and well developed. These structures arise anterodorsally from the centrum and overlap the postzygapophyses anteriorly. The neural postzygapophyses are smaller than the prezygapophyses. The first two centra lack pleural ribs, as is the case in other gempylids and most teleosts. The pleural ribs are thin, rod-like elements that are present at least until the fourteenth vertebra.

The epineurals are elongate, simple ossifications. These bones articulate directly with the seven anterior vertebrae. The epineural series continues posteriorly as free ossifications. From vertebra 6 a second series of intermuscular bones is present (Text-fig. 3D). According to Gago (1998), these bones can be interpreted as epicentrals. They are simple and their proximal tips appear to be unattached to the centra. The unattached condition of these bones possibly represents an artefact of preservation; each epicentral usually has a ligamentous connection with its corresponding centrum (see e.g. Patterson and Johnson 1995; Gemballa and Britz 1998) that is clearly not prone to the fossilization processes.

The pectoral fin and girdle are missing on the left side of the fossil but present on the right. The pectoral fin has 16 rays and inserts rather low on the body. The pectoral-fin rays are long (115 per cent of body depth), with the dorsal the longest. They articulate with four radials, which lie just behind the scapula. The arrangement of the pectoral girdle (Text-fig. 4A) is similar to that of other gempylids (see Matsubara and Iwai 1958). The structure as a whole is dorsoventrally compressed. The supratemporal is not preserved. The morphology of the posttemporal is not completely clear; however, it appears to be forked, with a robust anteroventral process. The posteroventral process is absent (see Gago 1998). The supracleithrum is nearly ovoid, expanded on its posterior half. The head of the supracleithrum has a posteriorly expanded process. This process carries a canal that bears the lateralis system to the posttemporal. The cleithrum is by the far the largest bone of the pectoral girdle. The coracoid has an elongate anteroventral process. There are two postcleithra. The dorsal postcleithrum is extremely reduced in size and crooked, while the ventral one is very elongate.

The pelvic girdle lies beneath the pectoral girdle. The basipterygium is heavily ossified (Text-fig. 4B). The central part of the basipterygium is dorsally orientated and extends anteriorly between the cleithrum and the coracoid. According to Stiassny and Moore (1992), in this case the basipterygium attaches to the elements of the pectoral girdle by ligaments. The posterior process of the basipterygium is long and styliform. Pelvic spines and rays are absent. Spines and soft rays could have been lost because of taphonomic processes, or, alternatively, were originally absent from the specimen. The taphonomic loss of the external pelvic-fin elements can be excluded because of the relatively good preservation of the anterior part of the body (except the snout), in which even microscopic features, such as skull ornamentation and serrations on the margins of dorsal-fin spines, are clearly observable.

Only the spinous dorsal fin is partially preserved. This fin inserts just posterior to the occipital region of the neurocranium. The preserved portion of the fin contains 13 robust and remarkably elongate spines, supported by 12 pterygiophores and four pterygiophores on which the spines or soft rays have been lost as an artefact of preservation. The anteriormost pterygiophore supports two spines (one supernumerary). The posterior four pterygiophores lack any spine or soft ray. The absence of the external elements of this fin can be easily explained as the result of taphonomic processes, even considering the ontogenetic patterns leading to the morphogenesis of the fin. In general, the dorsal fin of gempylids has an anterior spinous portion and a slightly separate soft-rayed portion posteriorly. The spinous dorsal fin develops prior to the soft dorsal fin (Johnson 1986). According to Potthoff *et al.* (1986), the development of the first dorsal fin proceeds from anterior to posterior in gempylids (see also Gago 1997). As a rule, pterygiophores developed before spines. Gago (1997) pointed out that development of the pterygiophores could be followed in a complete developmental series in a single specimen, because the ossification of the elements proceeds posteriorly from an anterior centre of ossification. Ossification of spines occurs slightly before complete ossification of the endoskeletal elements (Potthoff *et al.* 1986). Thus, considering the ontogenesis of the dorsal fin, the presence of fully developed pterygiophores and the contemporaneous absence of the associated spines were certainly caused by taphonomic processes. The fin is steeply graduated (Text-fig. 2), as in gempylid larvae (see Nishikawa 1987; Richards 1989), and the spines are of approximately the same size (111–163 per cent of body depth). The longitudinal anterior keel and the posterolateral keels of the dorsal-fin spines are widely serrated. Supraneural bones are absent. The anteriormost pterygiophore inserts in the first interneural space.

This pterygiophore supports two spines, one of which is in supernumerary association. The pterygiophores are composed of the proximal-middle and the distal radials that articulate by overlapping widely (Text-fig. 4C). The distal radials of the anterior dorsal fin articulate with their serial spines. The proximal portion of the three anterior proximal-middle radials, particularly the anteriormost, are relatively expanded longitudinally as a bony lamina on both sides of the main shaft. In the other elements, the expansion is present exclusively on the posterior side of the main shaft. Each of the pterygiophores corresponds to a vertebra.

There are no traces of squamation on the fossil.

COMPARISONS

As evident from the description, the incompleteness and unusual morphology of *Chelifichthys* make the identification of relationships difficult. Johnson (1986) discussed 12 apomorphies defining the gempylids. Unfortunately, some of these are uninformative for the interpretation of the status of *Chelifichthys*, because they refer to characters related to the early life history stages or to body portions not preserved on the holotype, such as the lacrymal or the total number of vertebrae.

Although not defined by a robust phylogenetic analysis, the gempylids can be identified by several characters considered as diagnostic of the family. Some additional characters, not widely distributed within the family, are sometimes regarded as useful for the classification of most of the genera. *Chelifichthys* possesses several characters that allow for its inclusion within the Gempylidae, such as: pterotic and temporal crests co-terminating on the supraoccipital ridge; the presence of a flat plate-like process covering most of the articular head of the opercle; the presence of a well-developed anterodorsal process of the subopercle; precaudal vertebrae devoid of parapophyses; epineurals attached to the vertebral centra; spines of the first dorsal fin equal in number to the vertebrae below them; pectoral fins inserting low on the body; the dorsal postcleithrum reduced in comparison with other scombroids (see Johnson 1986); the pelvic bone extending anteriorly beyond the cleithra; the first dorsal pterygiophore relatively expanded and inserting in the first interneural space; extensive overlapping of proximal-middle and distal radials of the spinous dorsal fin; and the presence of (condylar) articulation between the distal radials and the serial spines of the spinous dorsal fin. The combination of all these characters strongly supports the placement of *Chelifichthys* within the Gempylidae (Regan 1909; Starks 1911; Matsubara and Iwai 1952, 1958; Grey 1953; Johnson 1986; Gago 1997, 1998). *Chelifichthys* does exhibit some characters shared with selected gempylid taxa, such as the presence of sclerotics and two series of intermuscular bones. Although these characters appear to be uninformative for understanding the phylogenetic status of the members of this family, they are probably useful diagnostic tools at the generic or specific level. Because of this, their systematic significance is here briefly discussed together with that derived from the comparative analysis of other structures.

The posterior region of the neurocranium of *Chelifichthys* resembles that of *Prometichthys* and *Rexea* in having a similar arrangement of the epioccipital and pterotic ridges (see Starks 1911; Matsubara and Iwai 1958), but the supraoccipital crest is much developed vertically, as in *Epinnula* Poey, 1854 and *Lepidocybium* Gill, 1862 (Matsubara and Iwai 1958). Also, the frontal and the elements of the opercular apparatus are sculptured on the external surface, similar to the Oligocene species *Epinnula cancellata* and *Thyrsitoides zarathoustrae* (see Arambourg 1967). Collette *et al.* (1984) reported the occurrence of cranial ornamentation, mainly rugosities, in the larvae of *Lepidocybium*. However, as a rule, an ornamented cancellose texture of the external surface of the cranial bones of fishes is observed in adult specimens (see e.g. Day 2002).

As described above, *Chelifichthys* exhibits fragments of what appear to be sclerotic bones. Gago (1998) reported the presence of ossified sclerotics in the gempylids *Gempylus* and *Nesiarchus*. He also pointed out that these ossifications are absent from *Diplospinus*, *Paradiplospinus* and the trichiurids, remarking that there is no information about the presence of them in the other gempylid genera. Sclerotic bones are apparently absent in the extinct genus *Hemithyrsites* (see Arambourg 1925; Danil'chenko 1960) and in fossil representatives of *Epinnula* and *Thyrsitoides* (see Arambourg 1967). Ossified sclerotics have been described in many extinct and living scombroids, including *Sphyraena* Röse, 1793 (e.g. Collette and Chao 1975; Collette and Russo 1984; Nakamura and Yamaguchi 1991; Fierstine and Monsch 2002). The absence of sclerotics in *Diplospinus* and *Paradiplospinus* suggests that they could be interpreted as closely related to the trichiurids. Gago (1998) considered the absence of sclerotics as a character of the Trichiuridae, since the presence of these ossifications is widely distributed among the scombroids. According to this hypothesis, it is probable that these ossifications are widely distributed among the gempylids, and their absence in *Diplospinus* and *Paradiplospinus* could be attributed to their derived position within this family. Based on these considerations, the presence of sclerotics in *Chelifichthys* appears to be uninformative for an understanding of its relationships.

Concerning the lower jaw, the posterodorsal margin of the articular is relatively short, its anterior end placed posterior to the articulation between the ectopterygoid and palatine, as in *Lepidocybium* and *Ruvettus* Cocco, 1829 (see Matsubara and Iwai 1958).

The general structure of the suspensorium of *Chelifichthys* is similar to that of other gempylids (e.g. Matsubara and Iwai 1958). As in elongated forms, such as *Diplospinus*, *Gempylus*, *Nesiarchus* and *Paradiplospinus*, the ectopterygoid and endopterygoid of *Chelifichthys* are slender and the angle formed by the anterior and posterior margins of the quadrate is large.

The opercular apparatus of *Chelifichthys* is rather deep, as in *Epinnula*, *Lepidocybium*, *Neoepinnula* Matsubara and Iwai, 1952, and *Ruvettus*. The morphology of the opercular apparatus of *Chelifichthys* as a whole appears to be very similar to that of *Epinnula*. As discussed above, an extensive ornamentation of the bones of the opercular apparatus also characterizes the Oligocene species *Epinnula cancellata* and *Thyrsitoides zarathoustrae*. According to Gago (1998), ornamentation of the bones of the opercular apparatus can sometimes be observed in other gempylids and trichiurids, although it is less developed.

As in *Epinnula*, *Prometichthys* (Matsubara and Iwai 1958; Nakamura and Parin 1993) and juveniles of *Nealotus* (Nakamura and Paxton, 1977), the preopercle of *Chelifichthys* bears two spines along the lower region of the posterior margin. As in *Diplospinus*, *Gempylus*, *Lepidocybium*, *Nealotus* (see Text-fig. 2C), *Nesiarchus*, *Rexea*, *Thyrsites* and *Thyrsitoides*, the ventral margin of the posterodorsal notch of the opercle of *Chelifichthys* is not spinous. The posteroventral margin of the subopercle is convex, as in other gempylids, except *Prometichthys* (see Tucker 1956).

Chelifichthys has two series of intermuscular bones that co-occur from the sixth vertebra posteriorly. Two series of intermuscular bones are widely distributed throughout members of the family Gempylidae, except *Neoepinnula*, which lacks them (Nakamura and Parin 1993). The arrangement of these bones is very variable within this family. Starks (1911) considered the presence of two sets of intermuscular bones to be diagnostic of this group. Nakamura and Parin (1993) interpreted them as epineurals and epipleurals. However, according to Patterson and Johnson (1995), epipleural bones are absent in all Acanthomorpha except *Polymixia* Lowe, 1838, *Velifer* Temminck and Schlegel, 1850, and holocentrids (see also Forey *et al*. 2003). As a rule, higher acanthomorphs have a single bony series of intermusculars, which are considered homologues of epineurals of lower teleosteans (Johnson and Patterson 1993; Patterson and Johnson 1995). The model proposed by these authors suggests that the single series of intermuscular bones in percomorphs corresponds to the epineural series shifted ventrally towards the horizontal septum. The progressive ventral displacement of the epineural series is balanced by the emergence of neomorphic tendinous structures, named neoneurals, which replace them epaxially. The hypothesis of Patterson and Johnson (1995) was contradicted by Gemballa and Britz (1998), who based their analysis on a new technique, and homologized the single intermuscular series of higher acanthomorphs with the epicentrals of lower teleosteans, as previously stated by Owen (1866). Johnson and Patterson (2001) presented a detailed response to Gemballa and Britz (1998), and reiterated the arguments regarding the single series of intermusculars in most acanthomorphs as being epineurals. The presence of two intermuscular bone series in most gempylids appears to be unique among the Percomorpha. Gago (1998) considered the bones of the lower series to be epicentrals based on their morphology and relative position on the body. Epicentrals are present as ligaments in several percomorph families (Patterson and Johnson 1995). As a rule, the anteriormost epicentral ligament is placed after the last epineural. Westneat *et al*. (1993) and Patterson and Johnson (1995) noted that some scombroids have overlapping series of epineurals and epicentrals, but the latter are always present as ligaments. The configuration of intermuscular bones and ligaments observed in scombroids (mainly in *Scomberomorus* Lacépède 1801; see Westneat *et al*. 1993) provides a key to interpret the peculiar condition found in gempylids. The intermuscular elements of the lower series of gempylids could represent the ossified version of the epicentral ligaments commonly observed in other scombroids and are interpreted as such in this paper. As pointed out above, the intermuscular bone arrangement is rather variable within the Gempylidae. Although a detailed comparative analysis of this character within gempylids is currently unavailable, a cursory survey of the literature reveals that variation may be considered diagnostically useful at the specific level.

The number of pectoral-fin rays ranges between 11 and 17 within the Gempylidae (Nakamura and Parin 1993). As in *Lepidocybium*, *Neoepinnula*, *Thyrsitops* Gill, 1862 and *Tongaichthys* Nakamura and Fuji, 1983, the pectoral fin of *Chelifichthys* contains 16 rays. The pectoral girdle of *Chelifichthys* is rather compressed dorsoventrally, as in elongated forms such as *Paradiplospinus* (see Gago 1998) and the trichiurids. The morphology of the bones is consistent with that of *Diplospinus*, *Paradiplospinus* and *Prometichthys* (Matsubara and Iwai 1958; Gago 1998). The head of the supracleithrum is characterized by a posteriorly expanded process similar to that in *Diplospinus*, *Paradiplospinus*, *Prometichthys*, *Nesiarchus* and *Thyrsites* (Russo 1983). This process bears a canal that houses the lateral line to the posttemporal. The ventral postcleithrum (postcleithrum 3 *sensu* Gottfried 1989) is straight and resembles that of *Prometichthys* (Matsubara and Iwai 1958), although it is better developed.

Chelifichthys has a well-developed pelvic girdle devoid of external fin elements. The basipterygium resembles that of most gempylids, except *Gempylus*, *Prometichthys* and *Rexea*. According to Matsubara and Iwai (1958), the pelvic girdle is reduced in these genera. The loss of external pelvic-fin elements also characterizes *Prometichthys*, *Rexichthys* and some species of *Rexea* (Nakamura and Parin 1993). Gago (1997) suggested that the loss of these elements could have occurred independently in these genera.

The preserved portion of the dorsal fin allows the observation of many features that are diagnostic of the family Gempylidae, and useful for the placement of the new species in a new genus. As indicated above, supraneural bones are absent. Johnson (1986) considered the absence of supraneural bones as a synapomorphy of the Gempylidae (including Trichiuridae), Scombridae and billfishes (Istiophoridae and Xiphiidae). However, based on the developmental analysis of Potthoff *et al.* (1986), Johnson (1986) indicated that *Ruvettus*, *Thyrsitops* and *Tongaichthys* possess a single supraneural bone inserting in the preneural space. The highly elongate spines of the dorsal fin represent an unusual feature of *Chelifichthys*. Similar spines are characteristic of the first dorsal fin of larval gempylids. The spines are heavily serrated on their anterior and posterolateral keels, as in the larvae of *Diplospinus*, *Epinnula*, *Lepidocybium*, *Nealotus*, *Neoepinnula*, *Nesiarchus*, *Prometichthys* and *Ruvettus*. The dorsal-fin spines of the other gempylid genera, except *Thyrsitops*, bear serrations at least on their posterolateral keels. *Thyrsitops* larvae are characterized by smooth spines on the first dorsal fin (Gago 1997).

THE AFFINITIES OF *CHELIFICHTHYS*

As detailed above, *Chelifichthys* shares one or more features with each of the gempylid genera. However, some of these features, such as the presence of a convex posteroventral margin of the subopercle, well-developed basipterygium and absence of supraneural bones, cannot be used to determine the relationships of the genus because they are widely distributed throughout the family, or they are diagnostic of one or several genera. For example, supraneural bones are absent in most gempylids, and more generally in all the members of the families Istiophoridae, Scombridae and Xiphiidae. The occurrence of a single supraneural bone in the gempylid genera *Ruvettus*, *Thyrsitops* and *Tongaichthys* (Potthoff *et al.* 1986) is viewed as due to reversal (Johnson 1986), and can be considered as an important diagnostic feature of those genera.

The comparative analysis reveals that *Chelifichthys* shares many features with *Epinnula*, *Lepidocybium* and *Prometichthys*. These genera strongly differ from each other from a morphological point of view. Only a single feature, the presence of widely serrated longitudinal anterior and posterolateral keels of the dorsal-fin spines, is apparently shared by *Chelifichthys*, *Epinnula*, *Lepidocybium* and *Prometichthys*, but in the three extant genera this character refers only to their larval stage. *Chelifichthys* shares with *Epinnula* the presence of sculptured frontal and opercular bones (but only with *Epinnula cancellata*). It shares with *Lepidocybium* the presence of a short posterodorsal margin of the articular, and presence of 16 pectoral-fin rays. It also resembles both *Epinnula* and *Lepidocybium* in having a wide vertical development of the supraoccipital crest.

Chelifichthys shares with *Prometichthys* the following features: physiognomy of the posterior portion of the neurocranium, arrangement of the epioccipital and pterotic ridges, head of the supracleithrum expanded posteriorly, absence of pelvic-fin elements and presence of a straight ventral postcleithrum. In addition, *Chelifichthys* shares with both *Epinnula* and *Prometichthys* the presence of two spines along the posterior margin of the preopercle. The characters that it shares with *Epinnula* (Text-fig. 2B) and *Lepidocybium*, except those also observed in *Prometichthys*, are clearly related to a similar basic morphology, which probably results from a similar lifestyle. For example, the ornamentation on the external sides of the frontal and opercular bones confers a vesicular texture to the head, which is commonly found in midwater fishes. According to Johnson and Cohen (1974), these additional ossifications in the head skeleton (struts and ridges forming the ornamentation described above) were probably required to support the dentition and the strains to which the teeth were subjected, and may also have represented a system to reduce weight. This feature arose several times in the evolutionary history of teleosts (e.g. Weitzman 1967; Carnevale 2002) due to convergent ecological specializations, and for this reason it is not useful for the interpretation of the phylogenetic relationships of *Chelifichthys*. The comparative analysis of *Chelifichthys* suggests a possible affinity to the extant *Prometichthys*. According to Russo (1983) and Collette *et al.* (1984), *Prometichthys*, together with *Nealotus*, *Rexea* and *Rexichthys*, are thought to form a monophyletic group within the gempylids. The fishes of this group, commonly named gemfishes, are characterized (Parin 1990; Roberts and Stewart 1997) by a slightly elongated body, a moderate number of vertebrae, the presence of supernumerary finlets on the caudal peduncle, a reduction of pelvic fins and the presence of small fangs on the lower jaws. Only one of these characters (absence of pelvic fins) is seen in *Chelifichthys* because of its incompleteness. The fossil genus *Hemithyrsites* Sauvage, 1873 could also be included within this group. Arambourg (1925) considered it to be a junior synonym of *Prometichthys*, but Danil'chenko (1960) subsequently pointed out that some of its characters are also observed in *Nealotus*. The precise taxonomic and phylogenetic status of *Hemithyrsites* is unclear, and a new detailed anatomical and comparative analysis of type specimens from Sicily and Russia will be necessary to interpret it properly.

Therefore, it is not possible to provide a precise phylogenetic assessment of *Chelifichthys*. It could be related to the so-called gemfishes, but this hypothesis needs to be tested by a complete phylogenetic analysis of the Gempylidae (including the Trichiuridae), which is not the purpose of this paper. *Chelifichthys* is without doubt a gempylid but its relationships within this family are still to be determined.

CONCLUSIONS

Despite its incompleteness, *Chelifichthys goujeti* gen. et sp. nov. can be regarded without doubt as a member of the family Gempylidae. A comparative osteological study of the fossil suggests that *Chelifichthys* may be related to the so-called gemfishes, a group of gempylid genera (*Nealotus*, *Prometichthys*, *Rexea*, *Rexichthys*) recognized as monophyletic by Russo (1983) and Collette *et al.* (1984). It has an unusual morphology, mainly deriving from the remarkable development of dorsal-fin spines and the parallel absence of external pelvic-fin elements. *Chelifichthys* also differs from gemfishes in having a dorsoventrally compressed suspensorium and pectoral girdle, as in elongated gempylids, and in the sculptured, cancellose external surface of some cranial bones.

The controversial, and still unresolved, phylogenetic status of the Gempylidae and the incompleteness of the single specimen examined make it difficult to understand the relationships of *Chelifichthys*. Additional, more complete specimens will provide the information necessary to clarify its affinities. The characters observed in MNHN ORA1216 are sufficiently unique to warrant the placement of *Chelifichthys* within the family Gempylidae. A detailed osteological survey of this group (including trichiurids) and its fossil representatives is required to resolve the issue of intrafamilial relationships.

Chelifichthys goujeti represents the second gempylid taxon recorded from the Mediterranean Miocene. This family is poorly represented in the diverse Neogene palaeoichthyological record of the Mediterranean area. *Hemithyrsites* was described from the Messinian of Licata, Sicily, and is represented by fewer than ten specimens (see Arambourg 1925). Two indeterminate specimens collected from the diatomites of Sidi-Brahim (Chelif Basin), and housed at the MNHN, probably belong to this genus (MNHN ORA1211, ORA1212). Nolf and Cappetta (1988) identified some otoliths from the Lower Pliocene of Saint-Martin-du-Var and Le-Puget-sur-Argens (southern France) as *Prometichthys prometheus* (Cuvier, 1832). *Ruvettus pretiosus* Cocco, 1833 is the only gempylid that inhabits the Mediterranean today (Parin 1986).

Acknowledgements. I am very much indebted to Daniel Goujet, Hervé Lelièvre and Monette Véran (Département Histoire de la Terre – Paléontologie, MNHN, Paris) for permission to examine material in their care. My special thanks go to Walter Landini (Dipartimento di Scienze della Terra, Università di Pisa), James C. Tyler (National Museum of Natural History, Smithsonian Institution, Washington), Alexandre F. Bannikov (Paleontological Institute, Russian Academy of Sciences, Moscow), Francesco Santini (Département Systématique et Évolution, MNHN, Paris), Joseph L. Russo (Office of Information Research Resource Management, Smithsonian Institution, Washington) and Jean Sébastien Steyer (Département Histoire de la Terre – Paléontologie, MNHN, Paris) for their suggestions and critical reviews of the text. Thanks are also due to Federica Giudice for improving the English. Peter L. Forey (Department of Palaeontology, The Natural History Museum, London) and an anonymous reviewer helped considerably to improve the manuscript with their valuable comments. Thanks are extended to David J. Batten (School of Earth, Atmospheric and Environmental Sciences, University of Manchester) and Susan E. Evans (Department of Anatomy and Developmental Biology, University College London) for editorial work. This study was financially supported by COLPARSYST grants of the MNHN.

REFERENCES

AGASSIZ, L. 1833–44. *Recherches sur les poissons fossils.* Petitpierre, Neuchâtel, 1420 pp.

ALLIS, E. P. 1903. The skull, and the cranial and first spinal muscles and nerves in *Scomber scomber*. *Journal of Morphology*, **18**, 45–328.

ANDRIANSHEV, A. P. 1960. Families of fishes new to the Antarctic. 1. *Paradiplospinus antarcticus* gen. et sp. n. (Pisces, Trichiuridae). *Zoologicheskii Zhurnal*, **39**, 244–249. [In Russian].

ARAMBOURG, C. 1925. Révision de poissons fossiles de Licata (Sicile). *Annales de Paléontologie*, **14**, 39–132.

—— 1927. Les Poissons fossiles d'Oran. *Matériaux pour la Carte Géologique de l'Algérie, 1er Série, Paléontologie*, **6**, 1–218.

—— 1943. Note préliminaire sur quelques Poissons fossiles nouveaux. *Bulletin de la Société Géologique de France*, **43**, 281–288.

—— 1967. Les poissons oligocene de l'Iran. *Notes et Mémoires sur le Moyen Orient*, **8**, 1–210.

BALDWIN, C. C. and JOHNSON, G. D. 1993. Phylogeny of the Epinephelinae (Teleostei: Serranidae). *Bulletin of Marine Science*, **52**, 240–283.

BANNIKOV, A. F. 2005. A new species of the snake mackerel genus *Abadzhekia* (Perciformes, Gempylidae) from the Lower Oligocene of northern Caucasus. *Paleontological Journal*, **39**, 62–65.

—— and FEDOTOV, V. F. 1989. On the systematic position of perch-like genera *Lednevia* and *Abadzekhia* from the Maikop Series in southern USSR. *Byulleten, Moskovskogo Obs-*

chestva Ispytateliy Prirody, Odtel Geologicheskii, **64**, 85–90. [In Russian].

—— and PARIN, N. N. 1996. The list of marine fishes from Cenozoic (Upper Paleocene–Middle Miocene) localities in southern European Russia and adjacent countries. *Journal of Ichthyology*, **37**, 133–146.

BIRDSONG, R. S., MURDY, E. O. and PEZOLD, F. L. 1988. A study of the vertebral column and median fin osteology in gobioid fishes with comments on gobioid relationships. *Bulletin of Marine Science*, **42**, 174–214.

BLAINVILLE, H. 1818. Sur les ichthyolites ou les poissons fossils. 310–395. *In: Nouveau Dictionaire d'Histoire Naturelle*. Volume 37, Paris, 630 pp.

CARNEVALE, G. 2002. A new barbeled dragonfish (Teleostei: Stomiiformes: Stomiidae) from the Miocene of Torricella Peligna, Italy: *Abruzzoichthys erminioi* gen. & sp. nov. *Eclogae Geologicae Helvetiae*, **95**, 471–479.

—— 2004*a*. The first fossil ribbonfish (Teleostei, Lampridiformes, Trachipteridae). *Geological Magazine*, **141**, 573–582.

—— 2004*b*. New species of sand lance (Teleostei: Ammodytidae) from the Miocene of Algeria. *Geodiversitas*, **26**, 297–307.

CARPENTER, K. E., COLLETTE, B. B. and RUSSO, J. L. 1995. Unstable and stable classifications of scombroid fishes. *Bulletin of Marine Science*, **56**, 379–405.

CAVIN, L. 2001. Effects of the Cretaceous-Tertiary boundary event on bony fishes. 141–158. *In* BUFFETAUT, E. and KOEBERL, C. (eds). *Geological and biological effects of impact events*. Springer-Verlag, Berlin, 285 pp.

COCCO, A. 1829. Su di alcuni nuovi pesci de' mari di Messina. *Giornale di Scienze, Lettere ed Arti per la Sicilia*, **26**, 138–147.

—— 1833. Cenni sul genere *Ruvettus* e sui caratteri che lo distinguono. *Osservationes Peloritani*, **8**, 18.

COLGAN, D. J. and PAXTON, J. R. 1997. Biochemical genetics and recognition of a western stock of the common gemfish, *Rexea solandri* (Scombroidea: Gempylidae), in Australia. *Marine and Freshwater Research*, **48**, 103–118.

COLLETTE, B. B. and CHAO, L. 1975. Systematics and morphology of the bonitos (*Sarda*) and their relatives (Scombridae, Sardini). *Fishery Bulletin*, **73**, 516–615.

—— and RUSSO, J. L. 1984. Morphology, systematics, and biology of the Spanish mackerels (*Scomberomorus*, Scombridae). *Fishery Bulletin*, **82**, 545–692.

—— POTTHOFF, T., RICHARDS, W. J., UEYANAGI, S., RUSSO, J. L. and NISHIKAWA, Y. 1984. Scombroidei: development and relationships. 591–620. *In* MOSER, H. G., RICHARDS, W. J., COHEN, D. M., FAHAY, M. P., KENDALL, A. W. Jr and RICHARDSON, S. L. (eds). *Ontogeny and systematics of fishes.* American Society for Ichthyology and Herpetology, Special Publication **1**, 760 pp.

CORNÉE, J.-J., SAINT MARTIN, J.-P., CONESA, G. and MULLER, J. 1994. Geometry, palaeoenvironment and relative sea-level (accommodation space) changes in the Messinian Murdjadjo carbonate platform (Oran, western Algeria): consequences. *Sedimentary Geology*, **89**, 143–158.

CUVIER, G. 1829. *Le Règne Animal, distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée.* Paris, 460 pp.

—— and VALENCIENNES, A. 1831. *Histoire naturelle des poissons. Tome septième. Livre septième. Des Squamipennes. Livre huitième. Des poissons à pharyngiens labyrinthiformes.* F. G. Levrault, Paris-Strasbourg, 531 pp.

—— —— 1832. *Histoire naturelle des poissons. Tome huitième. Livre neuvième. Des Scombéroïdes.* F. G. Levrault, Paris-Strasbourg, 509 pp.

DANIL'CHENKO, P. G. 1960. Bony fishes of the Maikop deposits of the Caucasus. *Trudy Paleontologicheskogo Instituta, Akademii Nauk SSSR*, **78**, 1–247. [In Russian].

DAY, J. J. 2002. Phylogenetic relationships of the Sparidae (Teleostei: Percoidei) and implications for convergent trophic evolution. *Biological Journal of the Linnean Society*, **76**, 269–301.

EUPHRASEN, B. A. 1788. Beskrifning på trenne fiskar. *Kongliga Svenska Vetenskaps Academiens Handlingar, Stockholm*, **9**, 51–55.

FIERSTINE, H. L. and MONSCH, K. A. 2002. Redescription and phylogenetic relationships of the family Blochiidae (Perciformes: Scombroidei), Middle Eocene, Monte Bolca, Italy. *Studi e Ricerche sui Giacimenti Terziari di Bolca*, **9**, 121–163.

FILIPPELLI, G. M., SIERRO, F. J., FLORES, J. A., VAZQUEZ, A., UTRILLA, R., PEREZ-FOLGADO, M. and LATIMER, J. C. 2003. A sediment-nutrient-oxygen feedback responsible for productivity variations in Late Miocene sapropel sequences of the western Mediterranean. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **190**, 335–348.

FINNERTY, J. R. and BLOCK, B. A. 1995. Evolution of cytochrome b in the Scombroidei (Teleostei): molecular insights into billfish (Istiophoridae and Xiphiidae) relationships. *Fishery Bulletin*, **93**, 78–96.

FOREY, P. L., YI, L., PATTERSON, C. and DAVIES, C. E. 2003. Fossil fishes from the Cenomanian (Upper Cretaceous) of Namoura, Lebanon. *Journal of Systematic Palaeontology*, **1**, 227–330.

FOWLER, H. W. 1929. New and little-known fishes from the Natal coast. *Annals of the Natal Museum*, **6**, 245–264.

GAGO, F. J. 1997. Character evolution and phylogeny of the cutlassfishes: an ontogenetic perspective (Scombroidei: Trichiuridae). *Bulletin of Marine Science*, **60**, 161–191.

—— 1998. Osteology and phylogeny of the cutlassfishes (Scombroidei: Trichiuridae). *Contributions in Science, Natural History Museum of Los Angeles County*, **476**, 1–79.

GEMBALLA, S. and BRITZ, R. 1998. Homology of intermuscular bones in acanthomorph fishes. *American Museum Novitates*, **3214**, 1–25.

GILL, T. N. 1862. On the limits and arrangement of the family of scombroids. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **14**, 124–127.

—— 1893. A comparison of antipodal faunas. *Memoirs of the National Academy of Sciences*, **6**, 91–124.

GMELIN, J. F. 1789. *Caroli a Linné … Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species; cum characteribus, differentiis, synonymis, locis. Editio decimo tertia, aucta, reformata. 3 vols in 9 parts.* Leipzig, 1516 pp.

GOTTFRIED, M. D. 1989. Homology and terminology of higher teleost postcleithral elements. *Transactions of the San Diego Society of Natural History*, **21**, 283–290.

GOURINARD, Y. 1958. Recherches sur la géologie du littoral oranais. *Publications du Service de la Carte Géologique de l'Algerie*, **6**, 1–111.

GREGORY, W. K. 1933. Fish skulls: a study of the evolution of natural mechanisms. *Transactions of the American Philosophical Society*, **23**, 75–481.

GREY, M. 1953. Fishes of the family Gempylidae, with records of *Nesiarchus* and *Epinnula from the western Atlantic and descriptions of two new subspecies of Epinnula orientalis*. *Copeia*, **1953**, 135–141.

GÜNTHER, A. 1860. *Catalogue of the fishes in the British Museum. Catalogue of the acanthopterygian fishes in the British Museum. Squamipinnes, Cirrhitidae, Triglidae, Trachinidae, Sciaenidae, Polynemidae, Sphyraenidae, Trichiuridae, Scombridae, Carangidae, Xiphiidae*. Volume 2. Taylor and Francis, London, 548 pp.

HEURCK, H. VAN 1881. *Synopsis de Diatomées de Belgique*. J. F. Dieltjens, Antwerp, 235 pp.

JERZMAŃSKA, A. 1968. Ichthyofaune des couches à ménilite (Flysch des Karpathes). *Acta Palaeontologica Polonica*, **13**, 379–481.

JOHNSON, G. D. 1986. Scombroid phylogeny: an alternative hypothesis. *Bulletin of Marine Science*, **39**, 1–41.

—— and PATTERSON, C. 1993. Percomorph phylogeny: a survey of acanthomorphs and a new proposal. *Bulletin of Marine Science*, **52**, 554–626.

—— —— 2001. The intermuscular system of acanthomorph fishes: a commentary. *American Museum Novitates*, **3312**, 1–24.

JOHNSON, J. Y. 1862. Descriptions of some new genera and species of fishes obtained at Madeira. *Proceedings of the Zoological Society of London*, **1862**, 167–180.

—— 1865. Descriptions of a new genus of trichiuroid fishes obtained at Madeira (*Nealotus tripes*), with remarks on the genus *Dicrotus* Günther, and on some allied genera of Trichiuridae. *Proceedings of the Zoological Society of London*, **1865**, 434–437.

JOHNSON, R. K. and COHEN, D. M. 1974. Results of the research cruises of FRV 'Walther Herwig' to South America. XXX. Revision of the chiasmodontid fish genera *Dysalotus* and *Kali*, with descriptions of two new species. *Archiv für Fischereiwissenschaft*, **25**, 13–46.

JONET, S. 1958. *Contributions à l'étude des schistes disodyliques oligocènes de Roumanie. La faune ichthyologique de Homoraciu District de Prahova*. Sociedade Tipográfica, Lda, Lisboa, 112 pp.

LACÉPÈDE, B. G. E. 1801. *Histoire naturelle des poissons*. Volume 3. Paris, 558 pp.

LORENZO, J. M. and PAJUELO, J. G. 1999. Biology of a deep benthopelagic fish, roudi escolar *Prometichthys prometheus* (Gempylidae), off the Canary Islands. *Fishery Bulletin*, **97**, 92–99.

LOWE, R. T. 1838. A synopsis of the fishes of Madeira, with the principal synonyms, Portuguese names, and characters of the new genera and species. *Transactions of the Zoological Society of London*, **2**, 173–200.

MANSOUR, B. and SAINT-MARTIN, J.-P. 1999. Conditions de depôt des diatomites messiniennes en contexte de plateforme carbonatée d'après l'etude des assemblages de diatomées: exemple du Djebel Murdjadjo (Algérie). *Geobios*, **32**, 395–408.

MATSUBARA, K. and IWAI, T. 1952. Studies on some Japanese fishes of the family Gempylidae. *Pacific Science*, **6**, 193–212.

—— —— 1958. Anatomy and relationships of the Japanese fishes of the family Gempylidae. *Memoirs of the College of Agriculture, Kyoto University, Fisheries Series, Special Number*, 23–54.

MAUL, G. E. 1948. Quatro peixes novos dos mares da Madeira. *Boletim do Museu Municipal do Funchal*, **3**, 41–55.

MICKLICH, N. and PARIN, N. N. 1996. The fishfauna of Frauenweiler (Middle Oligocene, Rupelian; Germany): first results of a review. *Publicaciones Especiales de l'Instituto Español de Oceanografia*, **21**, 129–148.

NAKAMURA, I. and FUJI, E. 1983. A new genus and species of Gempylidae (Pisces: Perciformes) from Tonga Ridge. *Publications of the Seto Marine Biology Laboratory*, **27**, 173–191.

—— —— and ARAI, T. 1983. The gempylid, *Nesiarchus nasutus* from Japan and the Sulu Sea. *Japanese Journal of Ichthyology*, **29**, 408–415.

—— and PARIN, N. V. 1993. Snake mackerels and cutlassfishes of the world (families Gempylidae and Trichiuridae). An annotated and illustrated catalogue of the snake mackerels, snoeks, escolars, gemfishes, sackfishes, domine, oilfish, cutlassfishes, scabbardfishes, hairtails and frostfishes known to date. *FAO Fisheries Synopsis*, **15** (125), 1–136.

—— and PAXTON, J. R. 1977. A juvenile gempylid fish *Nealotus tripes*, from eastern Australia. *Australian Zoologist*, **19**, 179–184.

NAKAMURA, K. and YAMAGUCHI, H. 1991. Distribution of scleral ossicles in teleost fishes. *Memoirs of the Faculty of Fisheries, Kagoshima University*, **40**, 1–20.

NISHIKAWA, Y. 1987. Studies on the early life history of gempylid fishes. *Bulletin of the Far Seas Fisheries Research Laboratory*, **24**, 1–154. [In Japanese].

NOLF, D. and CAPPETTA, H. 1988. Otolithes de poissons pliocènes du Sud-Est de la France. *Bulletin de l'Institute Royal des Sciences Naturelles de Belgique*, **58**, 209–271.

—— and STRINGER, G. L. 1996. Cretaceous fish otoliths – a synthesis of the North American record. 433–459. *In* ARRATIA, G. and VIOHL, G. (eds). *Mesozoic fishes – systematics and paleoecology*. Verlag Dr. Friedrich Pfeil, München, 576 pp.

OWEN, R. 1866. *The anatomy of vertebrates. Volume 1. Fishes and reptiles*. Longmans, London, 600 pp.

PARIN, N. V. 1986. Gempylidae. 967–973. *In* WHITEHEAD, P. J. P., BAUCHOT, M.-L., HUREAU, J.-C., NIELSEN, J. and TORTONESE, E. (eds). *Fishes of the north-eastern Atlantic and the Mediterranean*. Unesco, Paris, 1473 pp.

—— 1990. An updated diagnosis of the genus *Rexichthys* and its position in the family Gempylidae. *Journal of Ichthyology*, **30**, 14–20.

—— and ASTAKHOV, D. A. 1987. *Rexichthys johnpaxtoni* – a new fish of the family Gempylidae from the Tasman Sea. *Voprosy Ikhtiologii*, **27**, 149–151. [In Russian].

—— and BECKER, V. E. 1972. Materials on taxonomy and distribution of some trichiuroid fishes (Pisces, Trichiuroidae:

Scombrolabracidae, Gempylidae, Trichiuridae). *Transactions of the P.P. Shirshov Institute of Oceanology*, **93**, 110–204. [In Russian].

PATTERSON, C. and JOHNSON, G. D. 1995. The intermuscular bones and ligaments of teleostean fishes. *Smithsonian Contributions to Zoology*, **559**, 1–85.

—— and ROSEN, D. E. 1977. Review of ichthyodectiform and other Mesozoic teleost fishes and the theory and practice of classifying fossils. *Bulletin of the American Museum of Natural History*, **158**, 81–172.

PÉREZ-FOLGADO, A., SIERRO, F. J., BÁRCENA, M. A., FLORES, J. A., VÁZQUEZ, A., UTRILLA, R., HILGEN, F. J., KRIJGSMAN, W. and FILIPPELLI, G. M. 2003. Western versus eastern Mediterranean paleoceanographic response to orbital forcing: a high-resolution microplankton study of precessional-controlled sedimentary cycles during the Messinian. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **190**, 317–334.

PERRODON, A. 1957. Étude géologique des bassins Néogènes sublittoraux de l'Algérie Occidentale. *Publications du Service de la Carte Géologique de l'Algérie*, **12**, 1–328.

PHARISAT, A. and MICKLICH, N. 1998. Oligocene fishes in the western Paratethys of the Rhine Valley Rift System. *Italian Journal of Zoology*, **65** (Supplement), 163–168.

POEY, F. 1851–54. *Memorias sobre la historia natural de la Isla de Cuba, acompañadas de sumarios Latinos y extractos en Francés.* La Habana, 463 pp.

POTTHOFF, T., KELLEY, S. and JAVECH, J. C. 1986. Cartilage and bone development in scombroid fishes. *Fishery Bulletin*, **84**, 647–678.

RATH, G. von 1859. 6. Beiträge zur Kenntis der fossilen Fische des Plattenberges im Kanton Glarus. *Zeitschrift der Deutschen Geologischen Gesellschaft*, **11**, 108–132.

REGAN, C. T. 1909. On the anatomy and classification of the scombroid fishes. *Annals and Magazine of Natural History*, **8**, 66–75.

RICHARDS, W. J. 1989. Preliminary guide to the identification of the early life history stages of scombroid fishes of the western central Atlantic. *NOAA Technical Memoirs NMFS-SEFC*, **240**, 1–101.

ROBERTS, C. D. and STEWART, A. L. 1997. Gemfishes (Scombroidei, Gempylidae, *Rexea*) of New Caledonia, southwest Pacific Ocean, with description of a new species. 125–141. *In* SÉRET, B. (ed.). *Résultats des Campagnes MUSORSTOM, Volume 17.* Mémoires du Muséum National d'Histoire Naturelle, **174**, 213 pp.

RÖSE, A. F. 1793. *Petri Artedi Angermannia – Sueci synonymia nominum piscium fere omnium; …Ichthyologiae pars IV*. Greifswald, 140 pp.

ROUCHY, J.-M. and SAINT-MARTIN, J.-P. 1992. Late Miocene events in the Mediterranean as recorded by carbonate-evaporite relations. *Geology*, **20**, 629–632.

RUSSO, J. L. 1983. Interrelationships of the gempylid fishes (Teleostei, Scombroidei). Unpublished PhD thesis, George Washington University, Washington, DC, 243 pp.

SAUVAGE, H.-E. 1870. Synopsis des Poissons tertiares de Licata (Sicile). *Annales des Sciences Naturelles (Zoologie et Paléontologie)*, **14**, 1–26.

—— 1873. Mémoire sur la faune ichtyologique de la période tertiaire, et plus spécialement sur les Poissons fossiles d'Oran (Algérie) et sur ceux découverts par M. R. Alby à Licata en Sicile. *Annales des Sciences Géologiques*, **4**, 1–272.

STARKS, E. C. 1911. The osteological characters of the scombroid fishes of the families Gempylidae, Lepidopidae and Trichiuridae. *Leland Stanford Junior University Publications, University Series*, **5**, 17–27.

STIASSNY, M. L. J. and MOORE, J. A. 1992. A review of the pelvic girdle of acanthomorph fishes, with comments on hypotheses of acanthomorph interrelationships. *Zoological Journal of the Linnean Society*, **104**, 209–242.

TEMMINCK, C. J. and SCHLEGEL, H. 1850. Pisces. 270–324. *In: Fauna Japonica, sive descriptio animalium quae in itinere per Japoniam suscepto annis, 1823–30 collegit, notis observationibus et adumbrationibus illustravit P. F. de Siebold.*

TUCKER, D. W. 1956. Studies on the trichiuroid fishes – 3. A preliminary revision of the family Trichiuridae. *Bulletin of the British Museum (Natural History), Zoology*, **4**, 73–130.

TYLER, J. C., O'TOOLE, B. and WINTERBOTTOM, R. 2003. Phylogeny of the genera and families of zeiform fishes, with comments on their relationships with tetraodontiforms and caproids. *Smithsonian Contributions to Zoology*, **618**, 1–110.

VOLTA, G. S. 1796. *Ittiolitologia Veronese*. Giuliari, Verona, 323 pp.

WAITE, E. R. 1911. Additions to the fauna of New Zealand. II. *Proceedings of the New Zealand Institute*, **43**, 9–51.

WEITZMAN, S. H. 1967. The osteology and relationships of the Astronesthidae, a family of oceanic fishes. *Dana-Report*, **71**, 1–54.

WESTNEAT, M. W., HOESE, W., PEEL, C. A. and WAINWRIGHT, S. A. 1993. The horizontal septum: mechanisms of force transfer in locomotion of scombrid fishes (Scombridae, Perciformes). *Journal of Morphology*, **217**, 183–204.

WETTSTEIN, A. 1886. Über die Fishfauna des tertiären Glarnen-schiefers. *Abhandlungen der Schweizerischen Paläontologischen Gesellschaft*, **13**, 1–103.

WOODWARD, A. S. 1901. *Catalogue of the fossil fishes in the British Museum (Natural History), Volume 4.* British Museum (Natural History), London, 636 pp.