



General palaeontology, systematics and evolution (Vertebrate Palaeontology)

Miocene bristlemouths (Teleostei: Stomiiformes: Gonostomatidae) from the Makrilia Formation, Ierapetra, Crete



Les bristlemouths miocènes (Teleostei : Stomiiformes : Gonostomatidae) de la formation Makrilia, Ierapetra, Crète

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ABSTRACT

Bristlemouths of the genus *Cyclothone* are currently regarded as the most abundant vertebrates on Earth. The fossil record seems to suggest that these fishes diversified during the Miocene in the Pacific Ocean, but there is no evidence of their presence in the Miocene of the Atlantic Ocean and Mediterranean basin. A new bristlemouth, *Cyclothone gaudanti* sp. nov. (Teleostei, Stomiiformes, Gonostomatidae), is described herein based on 16 specimens from the Upper Miocene Makrilia Formation (late Tortonian of Crete, Greece). The small sized species is characterized by light pigmentation, 30–31 (14–15 + 15–16) vertebrae, dorsal fin with 10–13 rays, anal fin with 10–14 rays, premaxilla bearing seven closely spaced teeth, maxilla with 42–55 teeth, epipleurals, and autogenous parhypural. The presence of epipleurals appears to be unique of this Miocene species, and the re-establishment of this ancestral character state may be possibly interpreted as related to a phylogenetic character reversal. Morphological and paleoecological considerations suggest that this species possibly inhabited the upper mesopelagic layer, at depths ranging from 2–300 and 500 meters.

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R É S U M É

Les bristlemouths du genre *Cyclothone* sont actuellement considérés comme étant les plus abondants vertébrés sur Terre. Le registre fossile suggère que ces poissons se sont diversifiés durant le Miocène dans l'océan Pacifique, mais il n'y a aucune évidence de leur présence dans le Miocène de l'océan Atlantique et du Bassin méditerranéen. Un nouveau bristlemouth, *Cyclothone gaudanti* sp. nov. (Teleostei, Stomiiformes, Gonostomatidae), est décrit ici basé sur 16 spécimens du Miocène supérieur de la formation Makrilia (Tortonien supérieur de Crète, Grèce). Cette espèce de petite taille est caractérisée par une pigmentation claire, 30–31 (14–15 + 15–16) vertèbres, une nageoire dorsale avec 10–13 rayons, une nageoire

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anale avec 10–14 rayons, un prémaxillaire portant sept dents légèrement espacées, un maxillaire avec 42–55 dents, épipleurales, et parhypurale autogène. La présence d'épipleurales semble être unique chez cette espèce miocène, et le rétablissement d'un caractère ancestral peut être éventuellement interprété comme lié à un caractère phylogénétique inversé. Les considérations morphologiques et paléocéologiques suggèrent que cette espèce vivait probablement dans la couche mésopélagique supérieure, à une profondeur comprise entre 2–300 et 500 mètres.

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1. Introduction

The 13 species of the deep-sea fish genus *Cyclothone* (see [Badcock, 1982](#); [Miya, 1994](#); [Mukhacheva, 1964, 1974](#)) are the numerically dominant and ubiquitous meso- and bathypelagic micronektonic components, comprising about 50–70% of the midwater fish catches globally (e.g., [Badcock and Merrett, 1976](#); [Miya and Nemoto, 1991](#); [Miya and Nishida, 1996](#)). Because of their remarkable abundance, these fishes are often referred to as the most abundant vertebrates on earth (see [Ahlstrom et al., 1984](#)). Unlike other midwater fishes, they do not undertake diurnal vertical migrations, remaining in meso- and/or bathypelagic layers both day and night ([DeWitt, 1972](#); [Badcock and Merrett, 1976](#); [Miya and Nemoto, 1991](#)). Although the basic structure is very similar among the species of this genus, they exhibit diversity in size, body coloration and ecology (see, e.g., [Miya and Nemoto, 1991](#); [Miya and Nishida, 1996](#)). As pointed out by [Miya and Nishida \(1996\)](#), the shallow-dwelling transparent species exhibit small size at maturity, semelparity, low fecundity and early age at first reproduction, while the deep-dwelling black or dark-colored species exhibit a larger size at maturity, iteroparity and high fecundity and retarded reproduction. Molecular studies hypothesized that the *Cyclothone* radiation occurred between 20 and 17 Ma ([Miya and Nishida, 1996](#)), and the fossil record clearly reveals that this genus was widely distributed in the Pacific Ocean since the Middle Miocene, with species known from the Middle Miocene Morozaki Group, Japan (*Cyclothone* sp.; [Ohe, 1993](#); [Yabumoto and Uyeno, 1994](#)), Middle to Upper Miocene Kurasi Formation, Sakhalin Island (*Cyclothone mukhachevae*; [Nazarkin, 2015](#)) and Upper Miocene Modelo Formation, California (*Cyclothone solitudinis*; [David, 1943](#); [Fierstine et al., 2012](#)). Additional fossils belonging to this genus are known from the Pliocene and Pleistocene of the Mediterranean basin, including representatives of the extant species *Cyclothone braueri* and *C. pygmaea* (see [Landini and Menesini, 1978, 1986](#); [Landini and Sorbini, 1992](#); [Sorbini, 1988](#)). Finally, [Gaudant \(2004\)](#) reported the presence of several specimens belonging to an indeterminate *Cyclothone* species from the Upper Miocene deposits of the Makrilia Formation, Ierapetra basin, Crete. The purpose of this paper is therefore to describe a new *Cyclothone* species from the Makrilia Formation based on the material formerly documented by [Gaudant \(2004\)](#).

The Makrilia Formation consists of an alternation of laminated hemipelagic marls and sandy turbiditic layers. According to [Fortuin \(1977\)](#), the sediments of the Makrilia Formation accumulated in an active half-graben system in

the Ierapetra Basin, which formed in the subduction zone south of Crete. The laminated marls of the Makrilia Formation contain abundant fossils, mainly articulated fish remains ([Bachmeyer and Symeonidis, 1978](#); [Bürgin, 1994](#); [Gaudant, 2004](#); [Symeonidis, 1969](#)) and plants ([Sachse et al., 1999](#)). The late Tortonian age of these fossiliferous deposits has been established based on planktonic foraminiferans and calcareous nannoplankton (NN11a; see [Bachmeyer and Symeonidis, 1978](#); [Fortuin, 1977](#); [Sachse and Mohr, 1996](#)).

2. Materials and methods

This study is based on 16 specimens from the Upper Miocene Makrilia Formation currently housed in the Geologisch-Paläontologische Abteilung of the Naturhistorisches Museum Wien (NHMW). The specimens were collected by Richard and Getrude Weixler during the second half of the seventies in two sites, the first of which is located 400 meters north of the Chapel Aghia Paraskevi (specimens NHMW 1999z0042/0013–1999z0042/0026); the second one is placed next to the Chapel Aghia Paraskevi (NHMW 1976/1813/19 and 1977/1907/23) and was described in much detail by [Symeonidis \(1969\)](#); additional data were provided by [Gaudant \(2004\)](#). The fossils were studied using a stereomicroscope Leica MZ12 with an attached camera lucida drawing arm. Measurements were taken using a vernier caliper. Comparative information was derived mainly from the literature. Photophores nomenclature follows [Badcock \(1982\)](#).

Abbreviations: A: anal fin; AC: anal series of photophores; ang: agulo-articular; bo: basioccipital; br: gill rakers; bsph: basisphenoid; C: caudal fin; D: dorsal fin; den: dentary; ect: ectopterygoid; end: endopterygoid; hm: hyomandibula; hyp: hypural; IV: isthmus-ventral series of photophores; mx: maxilla; NHMW: Naturhistorisches Museum in Vienna; P: pectoral fin; pa: palatine; phb: pharyngobranchial; php: parhypural; pmx: premaxilla; pro: prootic; psph: parasphenoid; pu: preural vertebra; q: quadrate; SL: standard length; smx: supramaxilla; sy: symplecticum; V: pelvic fin; VAV: ventral-anal series of photophores; vert: vertebra; vo: vomer; ?: unidentified element.

3. Systematic paleontology

Order Stomiiformes *sensu* [Harold and Weitzman, 1996](#)
Infraorder Gonostomata *sensu* [Harold, 1998](#)

Family Gonostomatidae Gill, 1893
 Genus *Cyclothone* Goode and Bean, 1883
Cyclothone gaudanti sp. nov.

Cyclothone sp. – Gaudant, 2004, p. 262, pl. 2, fig. 1, pl. 4, fig. 3

Diagnosis – A small sized and lightly pigmented species of *Cyclothone* with 30–31 (14–15 + 15–16) vertebrae; dorsal fin with 10–13 rays; anal fin with 10–14 rays; premaxilla bearing seven closely spaced teeth; maxilla with 42–55 teeth; epipleurals present; parhypural autogenous.

Holotype – NHMW 1999z0042/0020, nearly complete articulated skeleton, 24.6 mm SL (Fig. 1A).

Paratypes – NHMW 1999z0042/0018, nearly complete articulated skeleton, 26.4 mm SL (Fig. 1B); NHMW 1999z0042/0025, nearly complete articulated skeleton, 18.7 mm measurable length.

Referred material – NHMW 1976/1813/19, nearly complete articulated skeleton, 19.0 mm SL (Fig. 1C); NHMW 1977/1907/23, partially complete articulated skeleton, 21.6 mm SL (Fig. 1F); NHMW 1999z0042/0013, partially complete articulated skeleton, 23.0 mm SL; NHMW 1999z0042/0014, partially complete articulated skeleton, 25.5 mm SL; NHMW 1999z0042/0015, partially complete articulated skeleton, 19.5 mm SL, in part and counterpart (NHMW 1999z0042/0016, Fig. 1D); NHMW 1999z0042/0017, partially complete articulated skeleton, 23.0 mm SL; NHMW 1999z0042/0019, partially complete articulated skeleton, 22.8 mm measurable length; NHMW 1999z0042/0021, partially complete articulated skeleton, 24.1 mm SL; NHMW 1999z0042/0022, partially complete articulated skeleton, 23.0 mm estimated SL; NHMW 1999z0042/0023, nearly complete articulated skeleton, 17.9 mm SL (Fig. 1E); NHMW 1999z0042/0024, partially complete articulated skeleton, 28.0 mm estimated SL; NHMW 1999z0042/0026, two partially complete articulated skeletons, 18.3 mm SL and 18.4 mm estimated SL.

Locality and age – About 400 meters north of the Chapel Agia Paraskevi, Crete, Greece; Makrilia Formation, Late Miocene, Tortonian, NN11a (see Gaudant, 2004).

Derivation of name – Named in honor to our friend and colleague Dr. Jean Gaudant, in recognition of his contribution to paleoichthyology.

Measurements – (based on NHMW 1976/1813/19; SL = 19.0 mm). As percentage of SL: maximum body depth = 15.8%; head length = 28.9%; predorsal distance = 57.9%; preanal distance = 55.8%; prepectoral distance = 30.5%; lower jaw length = 22.1%.

Description – The body is elongate and laterally compressed. The dorsal and anal fins are located in the posterior half of the body; the anal fin inserts slightly anterior to dorsal fin origin. The pelvic fin originates approximately at the midlength of the distance between pectoral and anal fins. The caudal fin is deeply forked. The meristic features are listed in the Table 1.

Although the head skeleton is inadequately preserved in many cases, some general morphological features are clearly recognized, including orbit located in the anterior-most part of the head, and snout length measuring about

two times the orbit diameter. Neurocranial fragments are exposed in the paratype NHMW 1999z0042/0018, in which it is possible to recognize the long and thin parasphenoid, and parts of the prootic, basisphenoid and basioccipital (Fig. 2). The vomer is recognizable in the specimen NHMW 1999z0042/0026, mostly preserved as impression only and bearing lateral processes (Fig. 3).

The premaxilla is short, its length is contained about ten times in that of the toothed portion of the maxilla; the ascending process is moderately developed and the alveolar process bears about seven closely spaced teeth of which the third is the smallest (Fig. 4C, D). The maxilla is elongated and curved, bearing 42 to 55 closely spaced teeth subequal in length arranged into a single row along its ventral border (Fig. 4E, F). The supramaxilla (= posterior supramaxilla; see Harold, 1998) consists of an ovoid main body with a pointed anterior process emerging from its anteroventral corner. The dentary is elongate and approximately triangular in outline, bearing about 70 teeth along its dorsal border.

The bones of the suspensorium are thin and laminar. The quadrate is triangular. The hyomandibula is arched and characterized by a short opercular process. The symplectic is short and rod-like. The ectopterygoid resembles a very elongate triangle. The triangular endopterygoid is rather large. The metapterygoid is not preserved in any of the available specimens. The palatine is rod-like and bears several short conical teeth.

Fragments of the opercle are preserved in the specimen NHMW 1999z0042/0022.

A poorly preserved and incomplete hyoid skeleton can be recognized in the paratype NHMW 1999z0042/0025. What appears to be the first pharyngobranchial is exposed in lateral view in the specimen NHMW 1999z0042/0019; it is ventrally bifurcated (Fig. 5).

The vertebral column consists of 30–31 (14–15 abdominal plus 15–16 caudal) vertebrae. The centra are subrectangular, longer than high and constricted in the middle. The first abdominal vertebra is slightly more elongated than those following, being clearly exposed in the specimen NHMW 1999z0042/0019. The neural arches of the abdominal vertebrae appear to be not fused to each other into a median neural spine. The accessory neural arch seems to be absent. The two posterior abdominal vertebrae bear well-developed parapophyses. There are 11 or 12 (or possibly 13 in a few cases) pleural ribs articulating with the ventral portion of the vertebral centra and with the parapophyses. Ribs appear to be absent on the two anterior and the posteriormost vertebrae. Thin and elongated epineurals (Fig. 6) articulate with the neural arches of the vertebrae third through ninth or tenth vertebrae (see specimens NHMW 1977/1907/23, NHMW 1999z0042/0019, NHMW 1999z0042/0020, NHMW 1999z0042/0021, NHMW 1999z0042/0022, and NHMW 1999z0042/0025). Eight pairs of thin and elongated epipleurals can be observed in the specimens (NHMW 1999z0042/0014, NHMW 1999z0042/0018, NHMW 1999z0042/0020, NHMW 1999z0042/0021, NHMW 1999z0042/0023, and NHMW 1999z0042/0025), associated with the third through tenth abdominal vertebrae (Fig. 6).

The caudal skeleton (Fig. 7) is in large part formed by the urostyle fused with two large triangular hypural plates

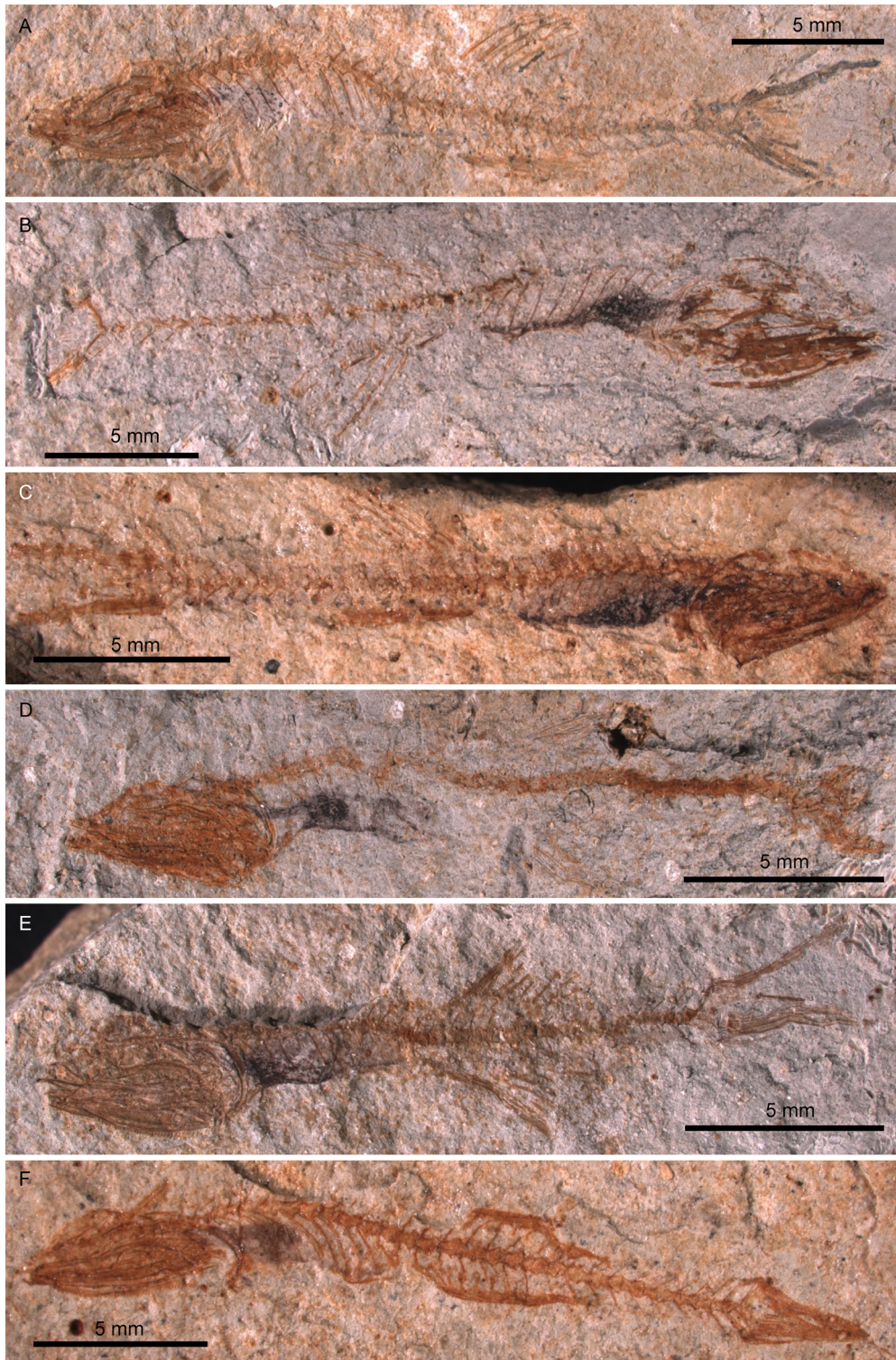


Fig. 1. *Cylothone gaudanti* sp. nov. A: holotype, NHMW 1999z0042/0020, left lateral view; B: paratype, NHMW 1999z0042/0018, right lateral view; C: NHMW 1976/1813/19, right lateral view (dark spots along the ventral margin of the postanal part of the body are remains of the photophores); D: NHMW 1999z0042/0016, left lateral view; E: NHMW 1999z0042/0023, left lateral view; F: NHMW 1977/1907/23, left lateral view.

Fig. 1. *Cylothone gaudanti* sp. nov. A : holotype, NHMW 1999z0042/0020, vue latérale gauche ; B : paratype, NHMW 1999z0042/0018, vue latérale droite ; C : NHMW 1976/1813/19, vue latérale droite (les points foncés le long de la marge ventrale de la partie post-anale du corps sont des restes de photophores) ; D : NHMW 1999z0042/0016, vue latérale gauche ; E : NHMW 1999z0042/0023, vue latérale gauche ; F : NHMW 1977/1907/23, vue latérale gauche.

Table 1Selected meristic features of *Cylothone gaudanti* sp. nov.**Tableau 1**Sélection de caractéristiques méristiques de *Cylothone gaudanti* sp. nov.

Specimen	Abdominal vertebrae	Caudal vertebrae	D	A	P	V	C	Ribs (pairs)	VAV	AC	IV
1976/1813/19	15	16	7+?	10	8	?	?	12	2 or 3	13	?
1977/1907/23	15	16	9+?	10	?	?	III+10+9+IV	11	?	?	?
1999z0042/0013	?	?	?	?	?	?	?	?	?	?	?
1999z0042/0014	14	16	?	?	?	?	?	10	?	?	?
1999z0042/0016	15	16	6+?	9+?	8 or 9	?	?	?	?	?	?
1999z0042/0017	?	?	?	?	8	?	?	?	?	?	?
1999z0042/0018 (paratype)	12+?	16	9 or 10	8+?	9	6	?	11	?	?	3
1999z0042/0019	14	9+?	13	12+?	?	?	?	11	?	?	?
1999z0042/0020 (holotype)	15	15	13	14	8	7	IV+10+9+?IV	12	?	?	?
1999z0042/0021	15	16	13	14	?	?	?	11	?	?	?
1999z0042/0022	13+?	15	12 or 13	?	8	?	10+9	11	?	?	?
1999z0042/0023	?	16	12	8+?	7+?	?	?	10	?	?	?
1999z0042/0024	?	16	>10	>10	?	6	?	?	?	?	?
1999z0042/0025 (paratype)	15	7+?	?	?	8	6	?	13	?	?	?
1999z0042/0026-A	13+?	8+?	?	12 or 13	8 or 9	5+?	?	11	?	?	?
1999z0042/0026-B	11+?	15	10+?	11	8	?	?	11	?	?	?

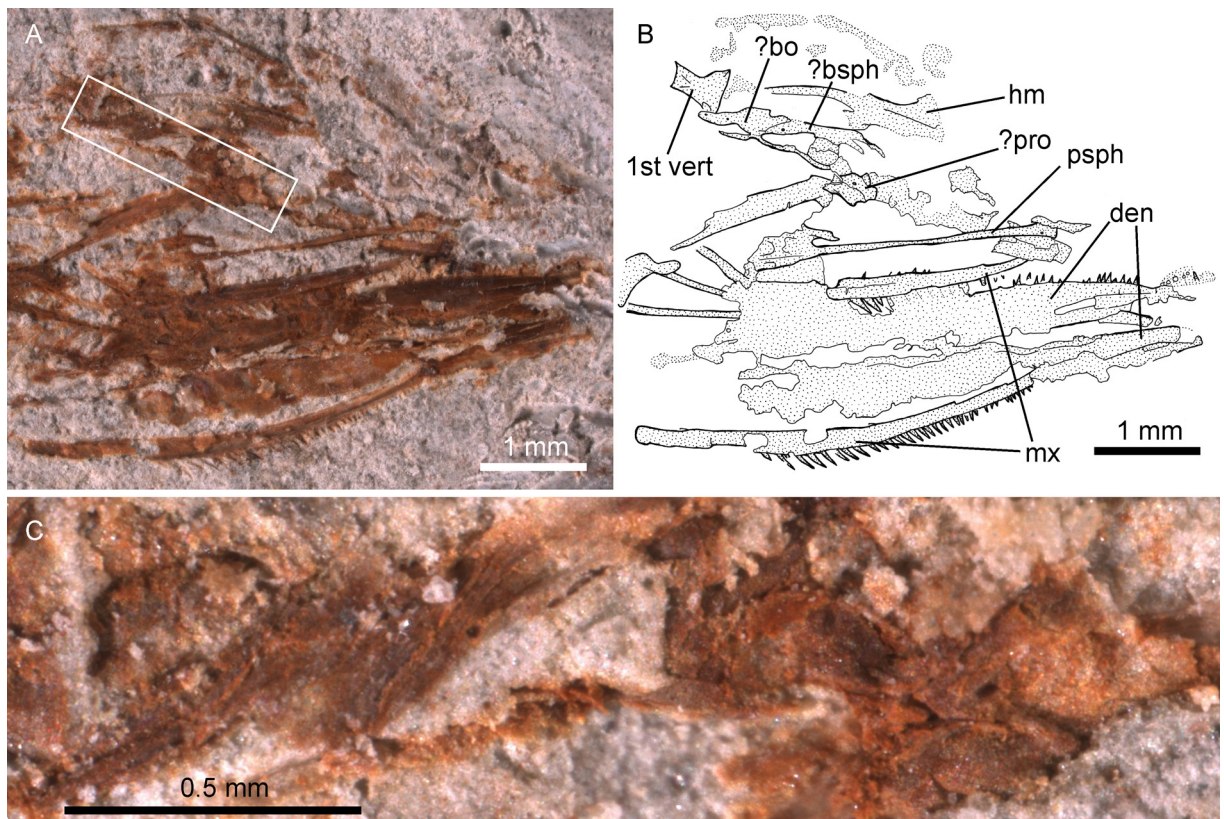


Fig. 2. *Cylothone gaudanti* sp. nov., paratype, NHMW 1999z0042/0018; A: general view of the head, right lateral view; B: interpretative drawing of A; C: detail of white box in A.

Fig. 2. *Cylothone gaudanti* sp. nov., paratype, NHMW 1999z0042/0018 ; A : vue générale de la tête, vue latérale droite ; B : dessin interprétatif de A ; C : détail de la boîte blanche dans A.

(hypurals 1 + 2 and hypurals 3 + 4 + 5). A small autogenous sixth hypural can be observed along the dorsal margin of the epaxial hypural plate. Its anterior margin articulates with a thin uroneural for most of its length (the element is tightly attached, but not fused!). The autogenous parhypural is moderately developed. There is no

evidence of epurals. The second preural vertebra has a well-developed neural spine and a distally expanded haemal spine. Two neural spines emerge from the centrum of the antepenultimate caudal vertebra in the specimens NHMW 1999z0042/0014 and NHMW 1999z0042/0022 (Fig. 7C,D). Due to the notable shortening of the posterior half of

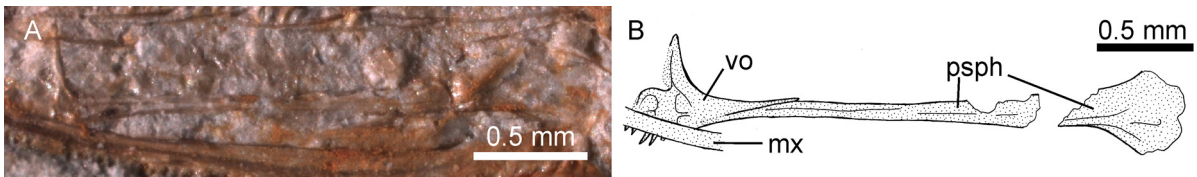


Fig. 3. *Cylothone gaudanti* sp. nov., NHMW 1999z0042/0026, parasphenoid and vomer; A: detail, left lateral view; B: interpretative drawing of A.
Fig. 3. *Cylothone gaudanti* sp. nov., NHMW 1999z0042/0026, parasphénoïde et vomer ; A : détail, vue latérale gauche ; B : dessin interprétatif de A.

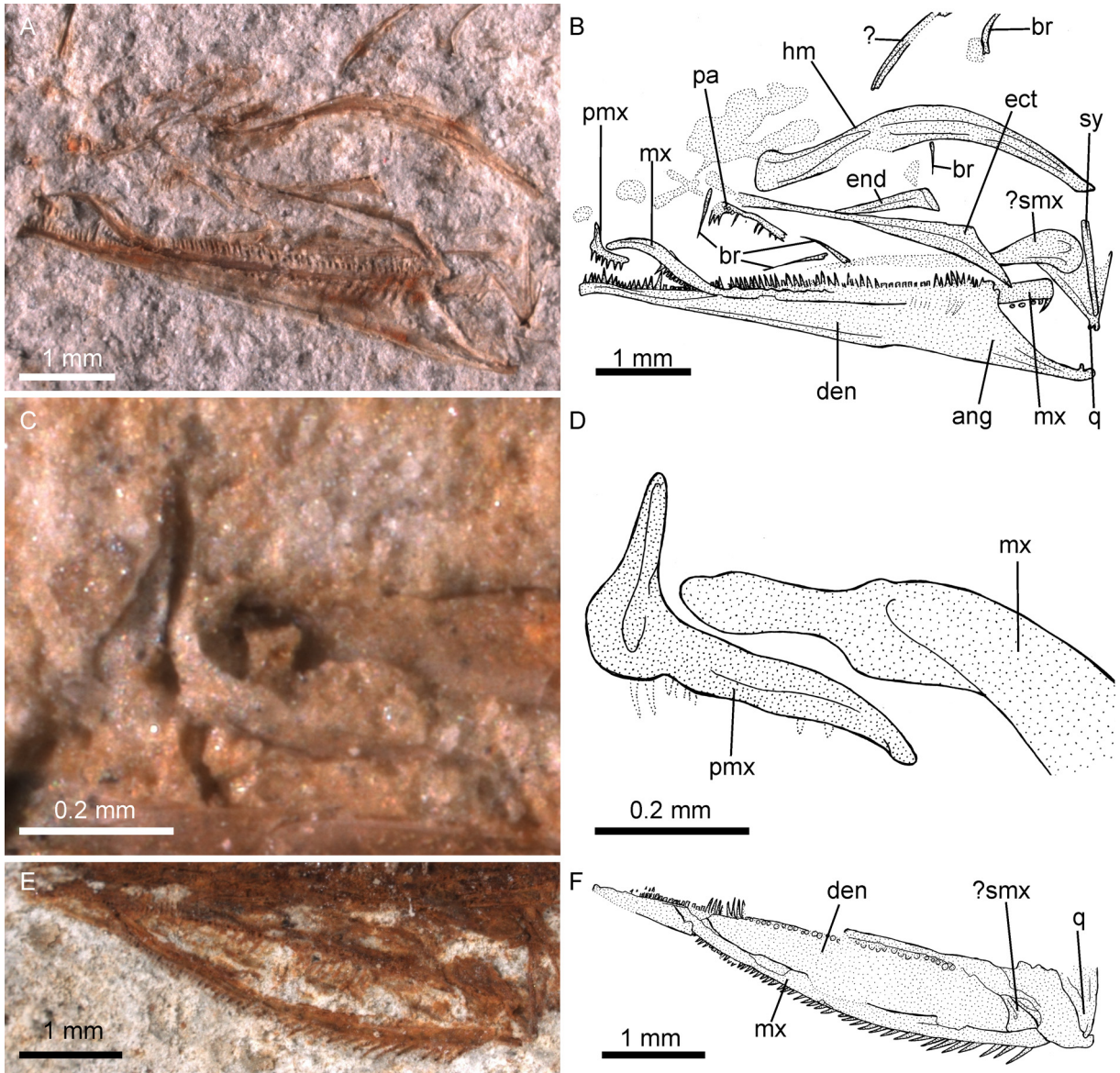


Fig. 4. *Cylothone gaudanti* sp. nov.; A: paratype, NHMW 1999z0042/0025, part of the splanchnocranium, left lateral view; B: interpretative drawing of A; C: holotype, NHMW 1999z0042/0020, premaxilla, left lateral view; D: interpretative drawing of C; E: NHMW 1999z0042/0017, maxilla, left lateral view; F: interpretative drawing of E.
Fig. 4. *Cylothone gaudanti* sp. nov. ; A : paratype, NHMW 1999z0042/0025, partie du splanchnocrâne, vue latérale gauche ; B : dessin interprétatif de A ; C : holotype, NHMW 1999z0042/0020, prémaxillaire, vue latérale gauche ; D : dessin interprétatif de C ; E : NHMW 1999z0042/0017, maxillaire, vue latérale gauche ; F : dessin interprétatif de E.

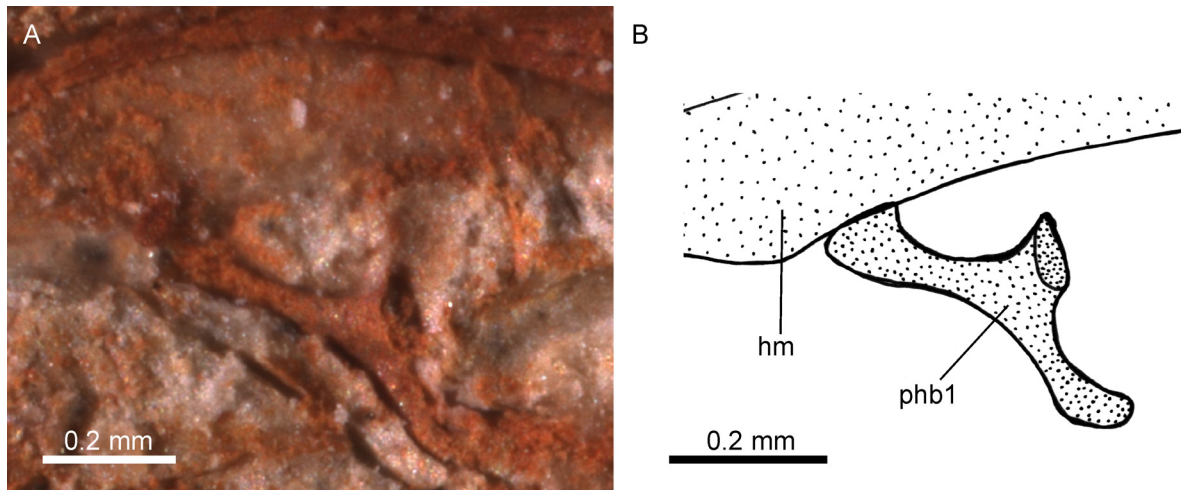


Fig. 5. *Cylothone gaudanti* sp. nov.; A: NHMW 1999z0042/0019, first pharyngobranchial, left lateral view; B: interpretative drawing of A.

Fig. 5. *Cylothone gaudanti* sp. nov. ; A : NHMW 1999z0042/0019, premier pharyngobranchial, vue latérale gauche ; B : dessin interprétatif de A.

the centrum of the second preural vertebra in the specimen NHMW 1999z0042/0021, the posterior margin of its haemal spine is closely associated to the parhypural (Fig. 7E, F). The caudal fin is deeply forked and contains 19 (10+9) principal rays plus three or four dorsal and four ventral procurent rays.

Three supraneurals seem to insert in the third, fourth and fifth interneural spaces. The dorsal fin contains ten to 13 rays. The first ray is the shortest of the series, whereas the second and third are the longest ones.

The anal fin contains ten to 14 rays. Like in the nearly opposite dorsal fin, the first ray is the shortest of the series, whereas the second and third rays are the longest ones. There are two or three prehaemal anal fin pterygiophores. Distal pterygiophores of the dorsal and anal fins appear to be recognizable in the specimen NHMW 1999z0042/0019 (Fig. 8).

The posttemporal is V-shaped and articulates ventrally with the straight supracleithrum. The cleithrum is elongate and crescent-shaped. The coracoid is short and rod-like, clearly recognizable in the specimen NHMW 1999z0042/0019. The pectoral fin inserts close to the ventral margin of the body and consists of eight or nine relatively elongate rays. The distal ends of the pectoral fin rays extend posteriorly up to the eighth or ninth abdominal vertebrae (see NHMW 1999z0042/0019).

The pelvic fin originates at the level of the tenth or 11th abdominal vertebra and contains six or seven rays. The basipterygium is inadequately preserved in all the specimens examined.

There is no trace of the original squamation. The absence of a dark or black body coloration (see, e.g., Miya and Nishida, 1996; Nazarkin, 2015), together with presence of the dark pigmented peritoneum, suggests that the preservation of dermal pigments was favored during the fossilization process, thereby suggesting that the body was transparent or semitransparent in origin. Photophores are preserved in many specimens (see e.g.,

Fig. 1C), including 13 elements of the AC series, the posteriormost two or three of the VAV series (both series easily recognizable in the specimen NHMW 1976/1813/19), and the posteriormost three of IV series (recognizable in the paratype NHMW 1999z0042/0018). What appear to be the peritoneum and part of the digestive system, are preserved in many specimens (NHMW 1976/1813/19, NHMW 1999z0042/0018, NHMW 1999z0042/0023, NHMW 1999z0042/0024, NHMW 1999z0042/0025, and NHMW 1999z0042/0026) as a dark pigmented film in the abdominal cavity, extending back slightly anterior to the anal fin origin, approximately at the level of the 13th or 14th vertebrae.

4. Taxonomic discussion

The specimens documented herein exhibit a suite of features that unquestionably support their assignment to the Stomiiformes (see Fink and Weitzman, 1982; Harold and Weitzman, 1996), including the overall physiognomy of the body, jaw teeth closely spaced, mouth gape extending posteriorly to the orbit, and presence of photophores. Within stomiiform fishes, the possession of a ventrally bifurcated first pharyngobranchial and a well-developed neural spine in the second preural vertebra, together with a short premaxilla and the presence of short, straight and subequal maxillary teeth clearly indicate that the fossils from Ierapetra belong to the family Gonostomatidae (Harold, 1998).

The limits and composition of the family Gonostomatidae have been broadly modified in the past decades. Grey (1964) assigned 21 genera to this family. Ten year later, Weitzman (1974) reduced the number of gonostomatid genera to six, namely *Bonapartia*, *Cylothone*, *Diplophos*, *Gonostoma*, *Margrethia* and *Triplophos*. The exclusion from the family of *Diplophos* and *Triplophos* by Ahlstrom et al. (1984) and Fink (1984), further restricted the number of genera to four. Subsequently, Miya and Nishida (2000) conclusively demonstrated the paraphyletic

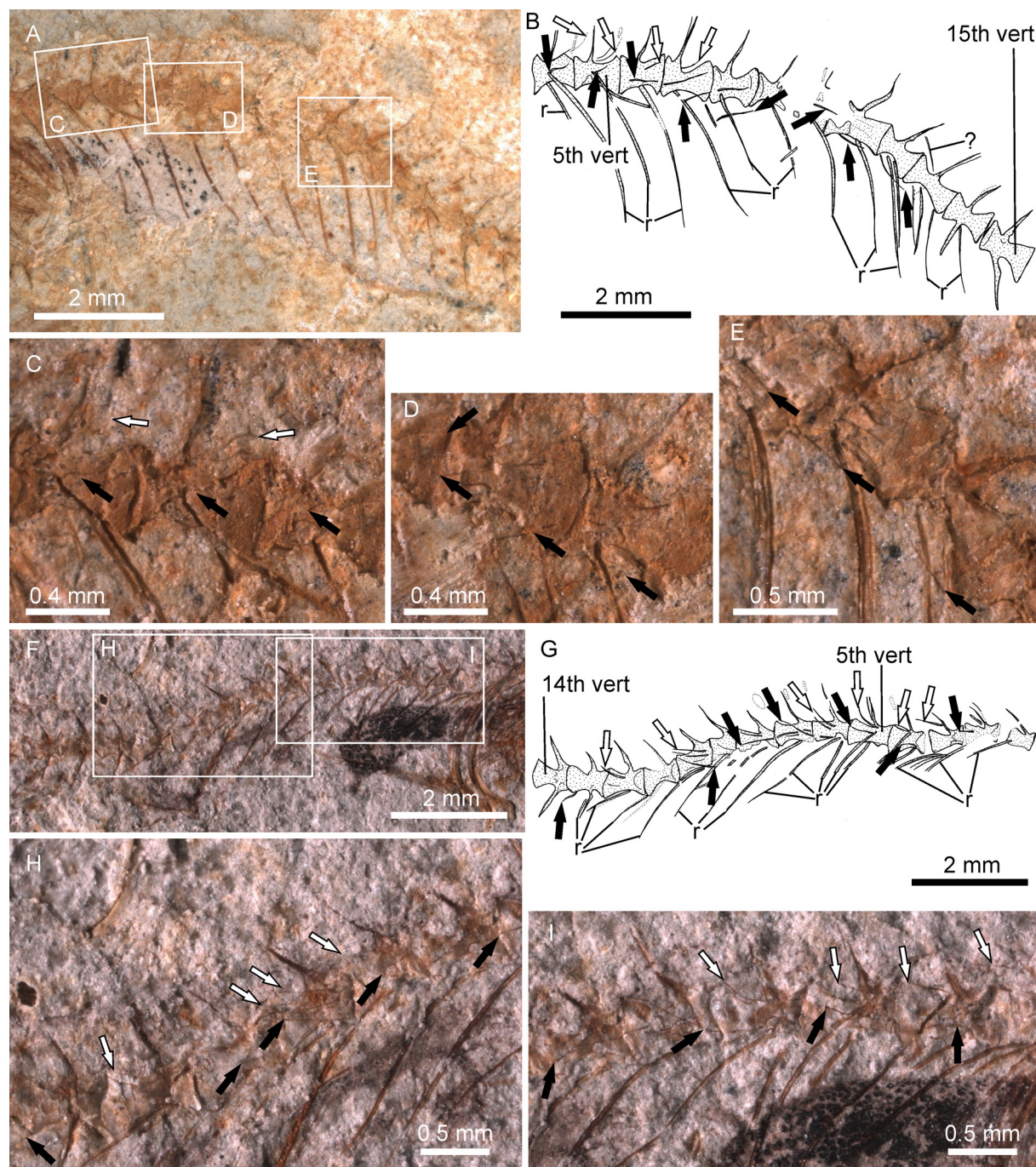


Fig. 6. *Cylothone gaudanti* sp. nov. abdominal region of the vertebral column, with associated intermuscular bones (white arrows indicate epineurals; black arrows indicate epipleurals); A: holotype, NHMW 1999z0042/0020, left lateral view; B: interpretative drawing of A; C–E: details of white boxes in A; F: paratype, NHMW 1999z0042/0025, abdominal vertebrae and associated skeletal elements, right lateral view; G: interpretative drawing of F; H–I: details of white boxes in F.

Fig. 6. *Cylothone gaudanti* sp. nov. région abdominale de la colonne vertébrale, avec ossements intermusculaires associés (les flèches blanches indiquent les épineurales; les flèches noires indiquent les épipleurales); A: holotype, NHMW 1999z0042/0020, vue latérale gauche; B: dessin interprétatif de A; C–E: détails de la boîte blanche dans A; F: paratype, NHMW 1999z0042/0025, vertèbres abdominales et éléments squelettiques associés, vue latérale droite; G: dessin interprétatif de F; H–I: détails de la boîte blanche dans F.

status of *Gonostoma* and resurrected the genus *Sigmops*, bringing the number of extant gonostomatid genera to five. The earliest representative of this family (cf. *Scopeloides*) dates back to the late Early Eocene of Italy (e.g., [Giusberti](#)

[et al., 2014](#)), and at least three additional genera are known from Eocene (*Primaevistomias*; [Prokofiev and Bannikov, 2002](#)), Oligocene (*Kotlarczykia*, *Scopeloides*; e.g., [Jerzmańska, 1974](#); [Gregorová, 1997](#)) and Miocene (*Ohuus*;

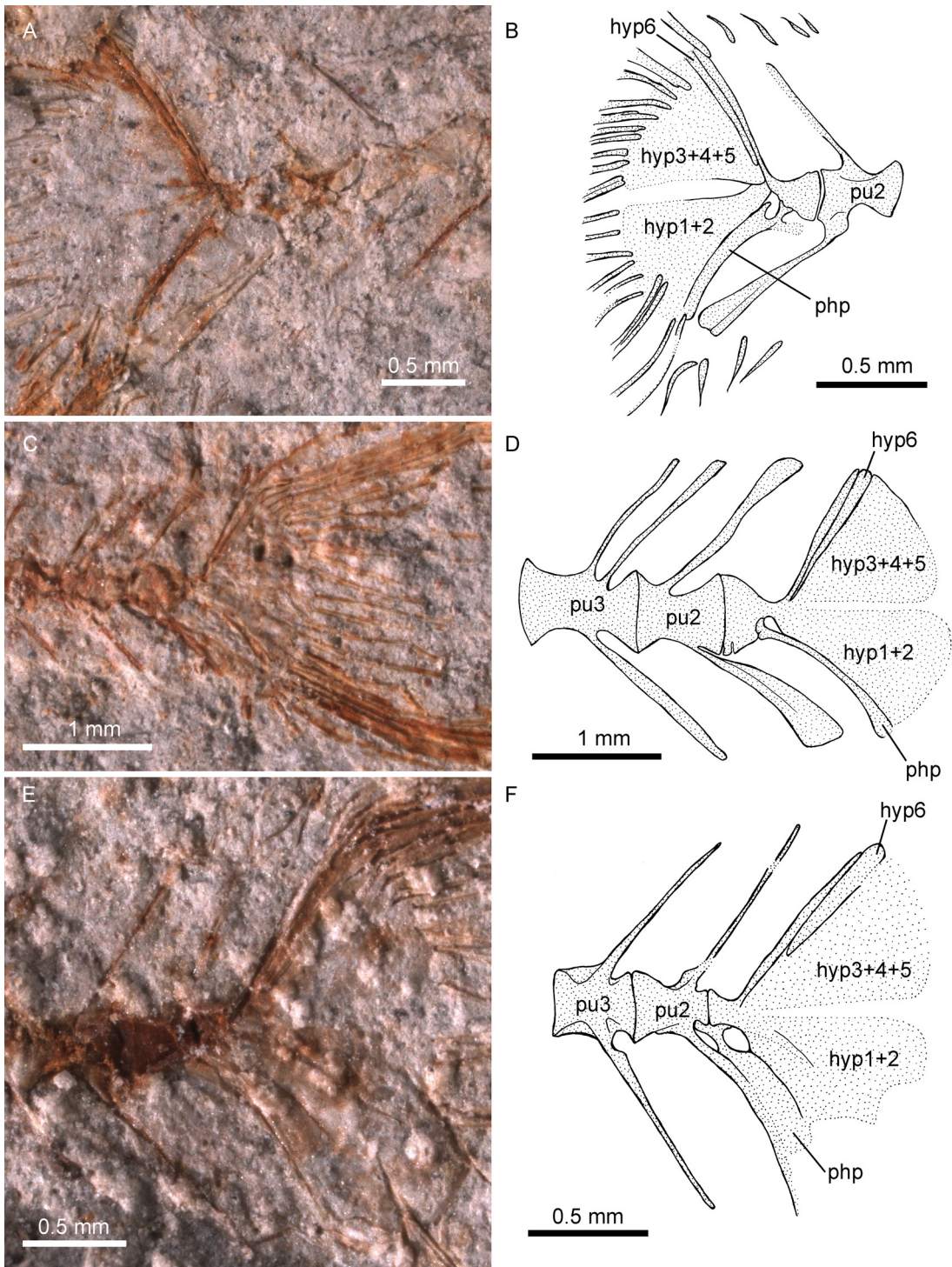


Fig. 7. *Cylothone gaudanti* sp. nov., caudal skeleton; A: paratype, NHMW 1999z0042/0018, right lateral view; B: interpretative drawing of A; C: NHMW 1999z0042/0022, left lateral view; D: interpretative drawing of C; E: NHMW 1999z0042/0021, left lateral view; F: interpretative drawing of E. Caudal fin rays omitted.

Fig. 7. *Cylothone gaudanti* sp. nov., squelette caudal ; A : paratype, NHMW 1999z0042/0018, vue latérale droite ; B : dessin interprétatif de A ; C : NHMW 1999z0042/0022, vue latérale gauche ; D : dessin interprétatif de C ; E : NHMW 1999z0042/0021, vue latérale gauche ; F : dessin interprétatif de E. Les rayons des nageoires caudales ont été omis.

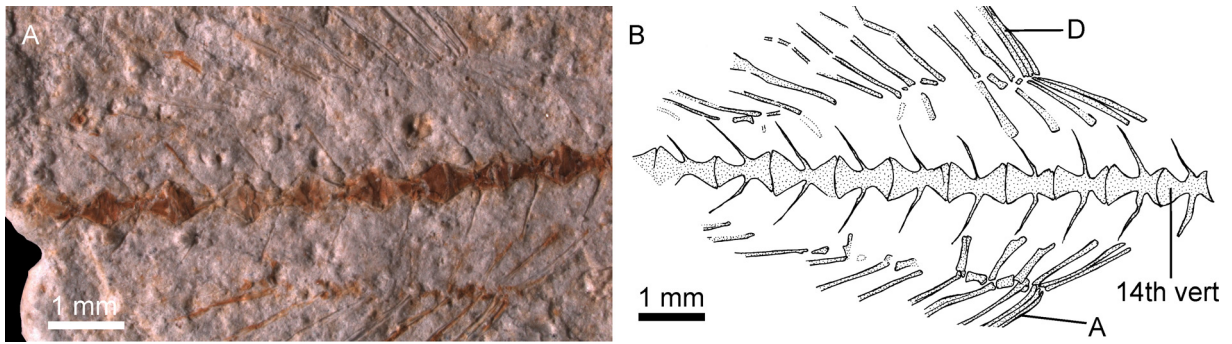


Fig. 8. *Cylothone gaudanti* sp. nov.; A: NHMW 1999z0042/0019, median fins and supports, right lateral view; B: interpretative drawing of A.

Fig. 8. *Cylothone gaudanti* sp. nov. ; A : NHMW 1999z0042/0019, nageoires médianes et supports, vue latérale droite ; B : dessin interprétatif de A.

Sato, 1962). Therefore, considering both extant and extinct taxa, the family Gonostomatidae is known to include at least nine genera.

The overall morphology of the specimens described herein (see also Fig. 9) exhibits a strong similarity to that of the species of the genus *Cylothone* to which they are referred; such a remarkable similarity is also supported by a number of additional features, including body proportions, mutual position of median fins, structure and relative size of jaw teeth, abdominal vertebrae bearing unfused neural arches, possession of an arched and elongate hyomandibula bearing a short opercular process, and overall structure of caudal skeleton (e.g., Günther and Deckert, 1953; Harold, 1998; Nazarkin, 2015). The presence of epipleurals appears to contrast with such a generic attribution since the absence of this series of intermuscular bones is currently regarded as synapomorphic of *Cylothone* (Harold, 1998). The absence of epipleurals has been recorded in at least eight of the 13 extant *Cylothone* species (Harold, 1998) and in the fossil *Cylothone mukhachevae* (Nazarkin, 2015). Considering that a comprehensive survey of the distribution of intermuscular bones within the genus *Cylothone* remains elusive, if the possession of epipleurals will be confirmed as uniquely present in *Cylothone gaudanti* sp. nov., this feature might be regarded as a re-establishment of an ancestral character state through the mechanism of phylogenetic character reversal. This phenomenon, also known as taxic atavism, is regarded as a mechanism of considerable relevance in generating morphological variation within clades (Stiassny, 1992). Alternatively, the epipleurals have been lost independently in all other *Cylothone* species, or *C. gaudanti* sp. nov. represents the sister taxon to all other *Cylothone* species.

Another peculiar feature of *Cylothone gaudanti* sp. nov. is the presence of an autogenous parhypural in the caudal skeleton. Also in this case, although a comprehensive survey of the variability of the caudal skeletal structure is not available, the parhypural is usually fused with the hypaxial hypural plate in both extant and extinct species of this genus (see, e.g., Fujita, 1990; Nazarkin, 2015). *Cylothone gaudanti* sp. nov. also exhibits a notably reduced number of anal fin rays (10–14 vs. 16–22 of other congeners; see Table 2); a similar very low number has been reported in the fossil *Cylothone solitudinis* (see Jordan, 1907; Nazarkin, 2015); however, the inadequate preservation of the known

material assigned to this Miocene eastern Pacific species does not allow to conclusively define the actual composition of its anal fin (see Fierstine et al., 2012). Overall, the other recognizable meristic features, together with the overall small size and body pigmentation reveal an overall similarity with the extant species *Cylothone alba*, *C. braueri*, and *C. signata* (see Table 2).

5. Associated ichthyofauna and paleoecology

The Tortonian fish fauna from the Makrilia Formation has been described based on a few hundreds of specimens collected from different sites located next to the route connecting Ierapetra and Makrilia (see Symeonidis, 1969; Bachmeyer and Symeonidis, 1978; Bürgin, 1994; Gaudant, 2004). Gaudant (2004) described material deriving from two sites, one of which located close to the Chapel Aghia Paraskevi and the other located about 400 meters north of the Chapel. The first of these sites yielded a diverse assemblage clearly dominated by the codlet *Bregmaceros albyi* and also including taxa of the families Clupeidae, Sternoptychidae, Gonostomatidae, Myctophidae, Priacanthidae [erroneously identified by Gaudant (2004) as boarfishes of the genus *Capros*], Syngnathidae, Carangidae, Acanthuridae, Trichiuridae, and Bothidae, in large part represented by very small individuals. As discussed above, *Cylothone gaudanti* sp. nov. is solely represented by two specimens from this locality. The taxonomic composition of the fish assemblage and the abundance of plant remains in the fossiliferous laminated marls cropping out close to the Chapel Aghia Paraskevi suggest that these deposits originated close to the coast at a moderate depth (Gaudant, 2004). The fish assemblage of the second site consists of pelagic taxa and is sharply dominated by specimens belonging to *Cylothone gaudanti* sp. nov., representing about 44% of the whole assemblage, associated with sternoptychids, myctophids and bregmacerotids (Gaudant, 2004). Such taxonomic composition seems to indicate a deeper depositional environment for the laminated marls exposed about 400 meters north of the Chapel Aghia Paraskevi. As pointed out above, *Cylothone gaudanti* sp. nov. exhibits a certain morphological affinity with the extant small sized and lightly pigmented species *Cylothone alba*, *C. braueri*, and *C. signata*. These three extant species form a monophyletic assemblage inhabiting the upper mesopelagic layer (at

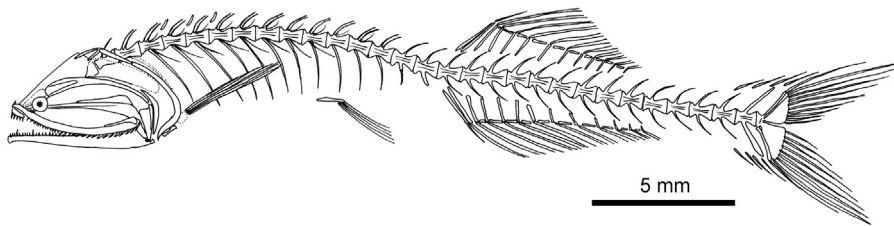


Fig. 9. *Cylothone gaudanti* sp. nov., interpretative reconstruction of the skeleton, left lateral view.

Fig. 9. *Cylothone gaudanti* sp. nov., reconstruction interprétative du squelette, vue latérale gauche.

Table 2

Summary of selected morphological and meristic features used to discriminate *Cylothone* species. Included, new data and data from David (1943), Fierstine et al. (2012), and Nazarkin (2015).

Tableau 2

Sommaire de la sélection de caractéristiques morphologiques et méristiques utilisées pour la discrimination des espèces de *Cylothone*. Incluses, des données nouvelles et les données de David (1943), Fierstine et al. (2012) et Nazarkin (2015).

Species	Pigmentation	Maximum SL (mm)	Premaxillary teeth	Maxillary teeth	Abdominal vertebrae	Caudal vertebrae	Total vertebrae	Dorsal fin rays	Anal fin rays
<i>C. acclinidens</i>	Dark	60.0	8–10	30–58	?	?	30–32	13–15	17–20
<i>C. alba</i>	Light	34.0	6–7	30–65	?	?	31–32	12–15	17–20
<i>C. atraria</i>	Dark	62.4	7–12	73–92	14	18	30–32	12–14	17–20
<i>C. braueri</i>	Light	38.0	6–8	40–53	?	?	30–32	13–14	18–20
<i>C. gaudanti</i> sp. nov.	Light	26.4	7	42–55	14–15	15–16	30–31	10–13	10–14
<i>C. kobayashii</i>	Light	50.0	4–10	38–45	12–14	19–22	32–35	13–16	19–22
<i>C. livida</i>	Dark	50.0	8–10	88–97	?	?	30–32	14–16	17–19
<i>C. microdon</i>	Dark	66.0	6–11	50–85	13	19	31–33	13–14	17–20
<i>C. mukhachevae</i>	Dark	47.4	≥6	62–64	14–15	18–20	32–34	13–14	18
<i>C. obscura</i>	Dark	70.0	14	88	?	?	31–33	13–15	17–19
<i>C. pallida</i>	Dark	70.0	8–14	51–90	12–13	18–20	31–33	12–15	16–19
<i>C. parapallida</i>	Dark	75.0	4–10	69–82	13–14	18–20	31–33	13–15	17–20
<i>C. pseudopallida</i>	Light	58.0	5–8	32–75	12–13	17–20	30–33	12–15	17–21
<i>C. pygmaea</i>	Dark	30.0	10–11	46–52	?	?	32–33	12–14	17–19
<i>C. signata</i>	Light	35.0	6–7	?	?	?	30–32	12–14	17–20
<i>C. solitudinis</i>	Light	51.0	?	?	?	~22	~40–42	~10	~10
<i>C. cf. solitudinis</i>	Light	41.0	?	?	14	17	31	11 or 12	16 or 17

depths ranging from 2–300 and 500 meters), and therefore defined as the upper mesopelagic group by Miya and Nishida (1996). Consequently, considering the possible affinities of *Cylothone gaudanti* sp. nov., it is reasonable to hypothesize that this Late Miocene species possibly occupied the upper mesopelagic layer and that the depositional environments of the fossiliferous marls exposed in the two sites occurred at depths ranging from 2–300 to 500 meters.

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