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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.

Mots clés :
Teleostei
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RÉSUMÉ

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 paléoécologiques suggèrent que cette espèce vivait probablement dans la couche mésopélagique supérieure, à une profondeur comprise entre 2–300 et 500 mètres.

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 (*Cylothone mukhachevae*; Nazarkin, 2015) and Upper Miocene Modelo Formation, California (*Cylothone 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 NNMW 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