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GEOBIOS

Geobios 43 (2010) 283–304

Original article

Review of the fossil pufferfish genus *Archaeotetraodon* (Teleostei, Tetraodontidae), with description of three new taxa from the Miocene of Italy☆

Révision du genre tétraodon fossile Archaeotetraodon *(Teleostei, Tetraodontidae), avec description de trois nouveaux taxons du Miocène d'Italie*

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Received 31 July 2009; accepted 9 October 2009
Available online 1 February 2010

Abstract

Three new species of the extinct pufferfish genus *Archaeotetraodon* are described from the Middle to Upper Miocene of Italy (*A. bannikovi* nov. sp., *A. dicarloi* nov. sp. and *A. zafaranai* nov. sp.), and compared in detail with the three previously described taxa of the genus [*A. jamestyleri* (Bannikov), *A. winterbottomi* Tyler and Bannikov and *A. cerrinaferoni* Carnevale and Santini], which are known, respectively, from the Miocene of Ukraine, the Oligocene of Russia, and the Miocene of Algeria. The three new species described herein bring the number of known *Archaeotetraodon* species to six, thereby making it by far the most speciose extinct genus of the order Tetraodontiformes. The monophyly of *Archaeotetraodon* is supported by two derived conditions: bifid scale spinules (*versus* single spinules in all other tetraodontids), and the fusion of the haemal spine of the penultimate vertebra to the centrum (*versus* autogenous in all other tetraodontids). We compare a large suite of morphological features of *Archaeotetraodon* to those found within the group of more basal tetraodontid genera to which we believe it belongs, but we are unable to determine the closest relationships of *Archaeotetraodon* within that group. Morphofunctional and paleoenvironmental considerations suggest that the species of the genus *Archaeotetraodon* were adapted to a pelagic or deep-sea lifestyle and were probably able to tolerate relatively low oxygen concentrations. The entire fossil record of the family Tetraodontidae is discussed.

Keywords: Teleostei; Tetraodontidae; *Archaeotetraodon*; New species; Paleoecology; Fossil record

Résumé

Trois nouvelles espèces de tétraodons fossiles du genre *Archaeotetraodon* sont décrites du Miocène moyen et supérieur d'Italie (*A. bannikovi* nov. sp., *A. dicarloi* nov. sp. et *A. zafaranai* nov. sp.), et comparées en détail aux trois espèces préalablement décrites pour ce genre [*A. jamestyleri* (Bannikov), *A. winterbottomi* Tyler et Bannikov et *A. cerrinaferoni* Carnevale et Santini], espèces respectivement connues du Miocène d'Ukraine, de l'Oligocène de Russie, et du Miocène d'Algérie. Les trois nouvelles espèces décrites ici portent le nombre d'espèces d'*Archaeotetraodon* connues à six, faisant de ce taxon le genre fossile de loin le plus diversifié au sein de l'Ordre des Tetraodontiformes. La monophylie d'*Archaeotetraodon* est supportée par deux conditions dérivées : spinules d'écailles bifides (*vs.* spinules simples chez tous les autres tétraodontidés), et fusion de l'épine hémale de l'avant-dernière vertèbre au centrum (*vs.* épine autogène chez tous les autres tétraodontidés). Nous comparons un large ensemble de caractères morphologiques d'*Archaeotetraodon* à ceux trouvés au sein du groupe des genres les plus basaux de tétraodontidés, auquel nous pensons qu'il appartient, mais nous ne parvenons pas à déterminer plus précisément les relations de parenté d'*Archaeotetraodon* au sein de ce groupe. Des considérations morphofonctionnelles et paléo-environnementales suggèrent que les espèces

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0016-6995/$ – see front matter
doi:10.1016/j.geobios.2009.10.005

d'*Archaeotetraodon* étaient adaptées à un mode de vie pélagique ou profond et étaient probablement capables de tolérer des taux relativement bas d'oxygène. L'ensemble du registre fossile de la Famille des Tetraodontidae est discuté.

Mots clés : Teleostei ; Tetraodontidae ; *Archaeotetraodon* ; Nouvelle espèce ; Paléoécologie ; Registre fossile

1. Introduction

The family Tetraodontidae comprises more than 25 genera with more than 150 species in the Recent fauna (e.g., Nelson, 2006). Most of these fishes are primarily marine, but some species inhabit the fresh- and brackish waters of tropical Africa, southern Asia and South America (e.g., Tyler, 1964; Dekkers, 1975; Ebert, 2001). Tetraodontids, commonly known as pufferfishes, are characterized by a vast array of structural and functional peculiarities, most notably by an extremely steady swimming mode with a simultaneous use of the median and pectoral fins (see Gordon et al., 1996; Plaut and Chen, 2003), the ability to inflate the body by swallowing mouthfuls of water that are pumped into an expandable stomach (see Wainwright et al., 1995; Wainwright and Turingan, 1997), a skeleton constituted by fewer elements than most other fishes (see Tyler, 1980), and a high visceral content of the alkaloid tetrodotoxin, a strong neurotoxin produced by symbiotic bacteria (Noguchi et al., 1987; Simidu et al., 1987) that is the cause of pufferfish poisoning (see e.g., Su et al., 1986, for a clinical account of a fatality). Moreover, pufferfishes are characterized by a highly reduced genome size, in the range of 0.7–1.0 pg (∼400 Mb), representing the smallest vertebrate genome but with a gene repertoire similar to that of other vertebrates (Hinegardner and Rosen, 1972; Brenner et al., 1993; Brainerd et al., 2001). Because of their compact genome, pufferfishes are currently regarded as excellent model systems in comparative genomics and evolutionary biology (Koop and Nadeau, 1996; Venkatesh et al., 2000; Santini and Stellwag, 2002; Neafsey and Palumbi, 2003; Mulley and Holland, 2004; Yamanoue et al., 2006, 2009), and the genomes of two species, *Takifugu rubripes* and *Tetraodon nigroviridis*, have been completely sequenced, making it possible to infer about the basic structure of the ancestral bony vertebrate genome, and to interpret the evolutionary mechanisms of genome size reduction (e.g., Aparicio et al., 2002; Jaillon et al., 2004).

Numerous genomic studies in the last few years have stimulated the production of molecular phylogenetic hypotheses concerning pufferfishes and their allied groups (see Holcroft, 2004, 2005; Alfaro et al., 2007; Yamanoue et al., 2008), and led to an increased interest in the fossil record of the crown members of the family (e.g., Benton and Donoghue, 2006; Benton et al., 2009). In this context, a detailed knowledge of the fossil tetraodontids is important in order to improve our knowledge of the past diversity and evolutionary patterns of these fishes through time. With the exception of the relatively common but taxonomically uninformative disarticulated jaws, and of the largely incomplete Pliocene material referred to the extant genus *Sphoeroides* (Tyler et al., 1992), the only known articulated skeletal remains assigned to the crown Tetraodontidae are those referred to the extinct genus *Archaeotetraodon* (see Tyler and Santini, 2002). This genus was established by Tyler and Bannikov (1994) based on several specimens representing two species from the Oligocene of north Caucasus, Russia and from the Miocene of Crimea, Ukraine. Subsequently, an additional species was described by Carnevale and Santini (2006) based on an incomplete specimen from the Miocene of Algeria. Soon thereafter, Carnevale (2007) presented a brief description of an additional fragmentary specimen from the Miocene of central Italy, leaving it indeterminate at the specific level. Being aware of our interest in fossil tetraodontids, we were independently informed by Salvatore Zafarana from Niscemi (Sicily) and Jean Gaudant from Paris that new specimens of fossil pufferfishes from Italy were available for study in several collections. Because of their diagnostic bifid scale spinules (Fig. 1) and other osteological features, we recognized that these specimens represent new species of the genus *Archaeotetraodon*.

Our purpose is to describe this new material and compare it with the other previously described taxa of this genus, as well as to compare *Archaeotetraodon* with relevant extant genera of the family Tetraodontidae and to discuss its possible relationships with them. We also discuss the paleobiology of *Archaeotetraodon* and review the fossil record of the entire family Tetraodontidae.

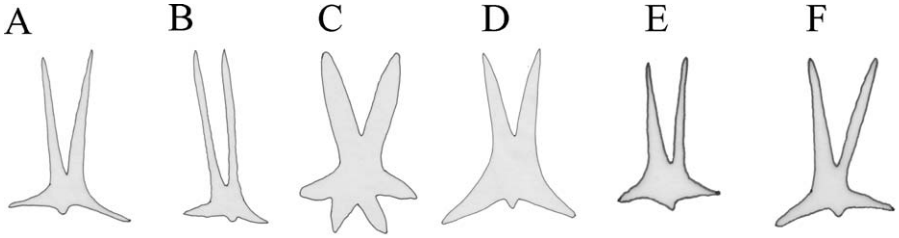

Fig. 1. Scale spinule of: **A**: *Archaeotetraodon bannikovi* nov. sp.; **B**: *A. cerrinaferoni* Carnevale and Santini, 2006; **C**: *A. dicarloi* nov. sp.; **D**: *A. jamestyleri* (Bannikov, 1990); **E**: *A. winterbottomi* Tyler and Bannikov, 1994; **F**: *A. zafaranai* nov. sp.