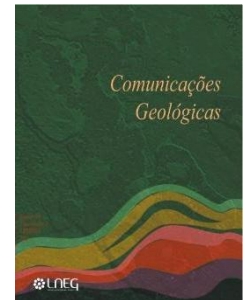


# The first occurrence of tuna *Thunnus* sp. (Family Scombridae) in the Miocene fossil record of Portugal

## A primeira ocorrência do atum *Thunnus* sp. (Família Scombridae) no registo fóssil Miocénico de Portugal



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**Abstract:** The fossil record of tunas (tribe Thunnini, family Scombridae) is sparse due to their pelagic lifestyle. Yet such finds are essential for reconstructing evolutionary and biogeographic patterns of these marine apex predators. We report the first occurrence of *Thunnus* sp. in Portugal, based on a well-preserved caudal vertebra from Burdigalian (Lower Miocene) deposits at Praia da Foz da Fonte (Baixo Tejo Basin, Setúbal Peninsula). The specimen, although recovered *ex situ*, is confidently attributed to the Lower Miocene shallow-marine succession of the locality. Morphological features—including an amphicoelous centrum, paired lateral foramina, and distinct growth rings—support its assignment to a large scombrid, consistent with the taxon *Thunnus*. Estimated body length exceeds 284 cm, indicating the presence of large pelagic predators from this genus in Miocene seas of western Iberia. This find represents the earliest tuna record from Portugal and supports a widespread Miocene distribution and diversification of the genus *Thunnus* across Europe and the Americas.

**Keywords:** Tuna, *Thunnus* sp., Scombridae, Burdigalian, Portugal.

**Resumo:** O registo fóssil dos atuns (tribo Thunnini, família Scombridae) é relativamente escasso devido ao seu modo de vida pelágico, que limita o potencial de preservação. Ainda assim, esses registos são fundamentais para compreender a história evolutiva e a paleobiogeografia de um dos grupos de peixes mais importantes do ponto de vista ecológico e económico. Neste trabalho reporta-se a primeira ocorrência de *Thunnus* sp. no registo fóssil de Portugal, com base numa única vértebra bem preservada proveniente de depósitos do Burdigaliano (Miocénico Inferior) na Praia da Foz da Fonte, localizada na Bacia do Baixo Tejo (Península de Setúbal). O espécime foi encontrado *ex situ* na base de uma arriba, mas é atribuído com confiança à sucessão marinha miocénica local, caracterizada por biocalcarenítos, calcarenítos e margas interestratificadas, representativos de ambientes deposicionais marinhos pouco profundos. A análise morfológica da vértebra caudal revela características diagnósticas de grandes escombrídeos, incluindo o centro anficélico, centrum robusto, pares de forâmenes laterais e anéis de crescimento bem definidos, consistentes com um indivíduo de tamanho médio a grande do género *Thunnus*. Com um comprimento corporal estimado superior a 284 cm, este fóssil evidencia a presença de predadores pelágicos altamente adaptados nos mares miocénicos do oeste da Ibéria. Comparações com outros registos miocénicos de *Thunnus* da Europa, América do Norte e do Sul, sugerem uma distribuição mais ampla e a diversificação do grupo neste período. Embora vértebras isoladas sejam geralmente não diagnósticas ao nível específico, o espécime enquadra-se na morfologia “tipo-*Thunnus*”

reconhecida noutros depósitos miocénicos a nível mundial. Este achado não só amplia o registo fóssil português de Scombridae, anteriormente pouco documentado, como também constitui a evidência mais antiga de espécies de atum na região. A presença de *Thunnus* nestes depósitos reflete tanto a importância ecológica dos atuns nos ecossistemas marinhos de idade Miocénica, como o seu papel de predadores pelágicos de topo durante uma fase crítica da evolução oceânica do período Neogénico.

**Palavras-chave:** Atum, *Thunnus* sp., Scombridae, Burdigaliano, Portugal.

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## Introduction

The family Scombridae includes mostly epipelagic marine fishes, such as mackerel, bonito and tunas, the latter being a large predator (Collette and Nauen, 1983). The fossil record of the Scombridae extends back to the middle Paleocene of Angola (Friedman *et al.*, 2023). *Thunnus* is a genus of ocean-dwelling, ray-finned bony fish from this family. More specifically, *Thunnus* is one of five genera which make up the tribe Thunnini – collectively known as the tunas (Graham and Dickson, 2004). Also called the true tunas, the genus *Thunnus* consists of eight species (more than half of the overall tribe), divided into two subgenera (Gibbs and Collette, 1986). The Atlantic bluefin tuna, the largest member of this genus,

can grow on average to 2 m to 2.5 m in length, up to a maximum of 4.6 m, and weigh up to 680 kg (Collette and Nauen, 1983).

As with all tunas, members of this genus have endothermic capabilities, which is a rare trait among fish; this enables them to tolerate cold waters and to dive to great depths (Bernal *et al.*, 2017). Bluefin tunas, for example, are found in Newfoundland and Iceland, and also in the tropical waters of the Gulf of Mexico and the Mediterranean Sea, where they migrate each year to spawn (Cermeño *et al.* 2015). Tunas are powerful swimmers, and the yellowfin tuna is known to reach speeds of up to 80 km/h when pursuing prey, primarily consisting of smaller fish, squid, and crustaceans.

This group's fossil record is relatively sparse but important for understanding its evolutionary history. Fossils attributed to *Thunnus* and close relatives date back to the Late Oligocene-Miocene epochs (*e.g.*, Kotlarczyk *et al.*, 2006; Di Celma *et al.*, 2018), which corresponds to a time of diversification in many modern fish groups, including scombroids. Most fossils consist of isolated vertebrae, fin spines, and some teeth. Complete skeletons are rare due to the pelagic lifestyle of these fishes which decreases the chances of preservation.

The Miocene deposits of the Setúbal Peninsula (Fig. 1), which are exposed in the coastal cliffs between Cacilhas (North) and Praia da Foz da Fonte (South), provide an important paleontological archive for reconstructing the marine ecosystems of the Lower Tejo Basin. These sediments preserve a diverse assemblage of marine mammals, birds and ichthyofauna (*e.g.*, Estevens *et al.*, 1999; Estevens, 2000; Fialho *et al.*, 2021; Figueiredo *et al.*, 2023), mainly in the sediments from the Middle and Upper Miocene. The most common remains of ichthyofauna are elasmobranch teeth and teleost otoliths. Early systematic work by Jonet (1966, 1978a, b, 1979) described rich selachian faunas and detailed assemblages of teleost otoliths from the Tortonian, demonstrating that these deposits were inhabited by a broad spectrum of marine predators and demersal fishes. Subsequent studies expanded this picture (Fialho, 2022; Fialho *et al.*, 2021).

Beyond their taxonomic importance, these findings emphasize the significance of the Setúbal Miocene as a key paleontological area in Portugal and in the broader European context, preserving both high faunal diversity and valuable paleoenvironmental indicators of shallow, warm-temperate to tropical marine environments, comparable to modern coastal ecosystems in subtropical settings (E Stevens *et al.*, 1999). Together, the Miocene fish assemblages of the Setúbal Peninsula offer critical insights into the evolutionary and ecological history of the northeastern Atlantic during the Neogene.

The fossil record of Scombridae is seldom known in Portugal (Zbyszewski, 1949). Here we describe a single large vertebra from the Burdigalian of Foz da Fonte (Baixo Tejo basin) that can be attributed to *Thunnus* sp. and therefore considered one of the earliest occurrences of this genus in the fossil record.

## Materials and methods

A single vertebra (CPM-BFF034) was found by José Costa and Hugo Silva at the base of the cliff pile of debris at Praia da Foz da Fonte as a result of erosion. The level from which the vertebra came off could not be determined. The vertebra was eventually acquired by one of the co-authors (P.M.), who prepared and consolidated it. Currently included in P. Marreca's private collection, it is available for further study upon request. This work focuses on the morphological characterization of the vertebra to determine its taxonomic identification.

## Stratigraphic setting

Foz da Fonte is a referential section for the Lower Miocene of Baixo Tejo Basin (Pais *et al.*, 2012; Fig. 1). It was thoroughly studied and dated from the lower Burdigalian by Zbyszewski (1967), Antunes *et al.* (1998, 1999), Manuppella *et al.* (1999), Cachão and Silva (2000), and Silva *et al.* (2000), and references herein.

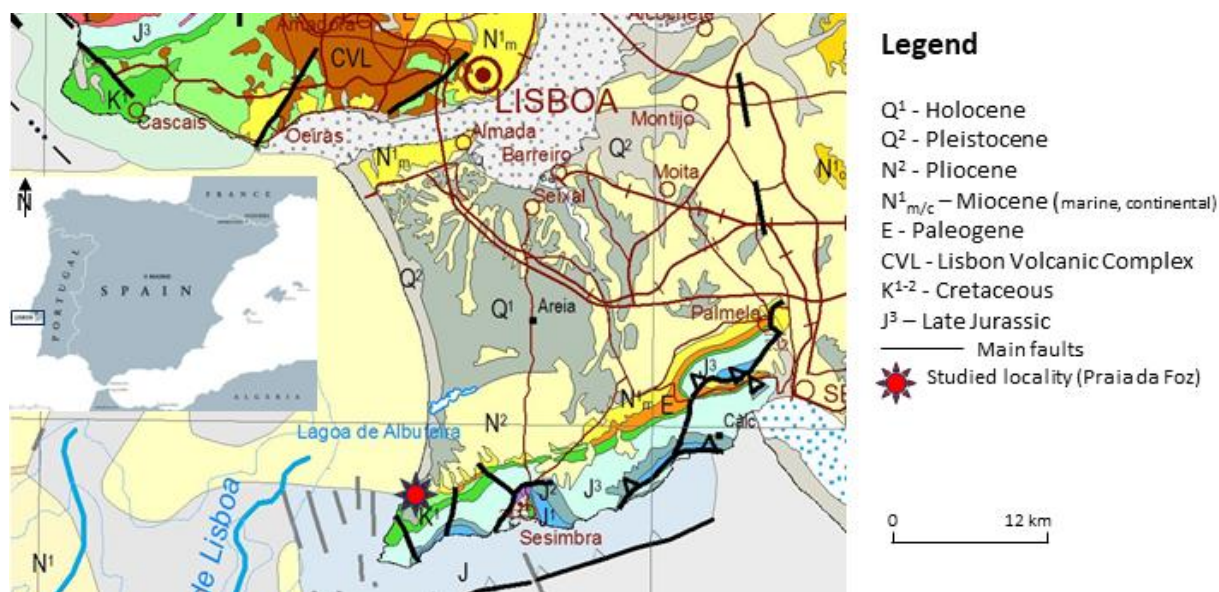


Figure 1. Simplified geological map of the Lower Tejo river region, showing the distribution of the main Miocene deposits (extract adapted from the geological map of Portugal at 1:1,000,000 scale edited in 2010 by Laboratório Nacional de Energia e Geologia, I.P.); symbol indicates the approximate location of the studied locality.

Figura 1. Mapa geológico simplificado da região do Baixo Tejo, mostrando a distribuição dos principais depósitos do Miocénico (extrato adaptado do mapa geológico de Portugal à escala 1:1 000 000, editado em 2010 pelo Laboratório Nacional de Energia e Geologia, I.P.); o símbolo indica a localização aproximada da área estudada.

The cliffs and small coastal exposures around Praia da Foz (Foz da Fonte / Penedo sector of the Setúbal Peninsula; Fig. 2) uncover condensed Lower Miocene (Burdigalian) marine deposits dominated by biocalcarenes and calcarenites with interbedded marls and thin siliciclastics (“Calcarenes and marls from Foz da Fonte and Penedo Sul” unit described in Manuppella *et al.*, 1999). These outcrops are part of the broader Setúbal Peninsula Miocene succession. The Burdigalian record here is often condensed and locally shows hiatuses and regional unconformities related to early Miocene tectono-sedimentary events and later basin inversion/uplift of the Arrábida domain (Antunes *et al.*, 1999; Manuppella *et al.*, 1999), therefore, the thickness and facies change rapidly along strike. This makes the Foz da Fonte section important for regional correlation and for reconstructing the early Miocene paleogeography of western Iberia (Pais *et al.*, 2012). Here, maximum measured thickness is approximately 35 m (Antunes *et al.*, 1998) of biocalcarenes and calcarenites, overlying Albian (Early Cretaceous) strata along an angular or slightly oblique unconformity defined by bioerosion (Santos *et al.*, 2010).

The lower unit (0–12 m) exhibits high-energy, shallow carbonate shoreface deposits reworked by storms, rich in coarse biocalcarenes with rhodoliths and *Ophiomorpha*. A disconformity marks a sedimentological and perhaps tectonic hiatus (Antunes *et al.*, 1999). Overlying siltstones (12–20 m) represent quieter, more offshore conditions. Due to the aforementioned ecological characteristics of the genus *Thunnus*, this is where the vertebra most likely came from. The upper section at Foz da Fonte (20–35 m) is composed of mixed carbonate-siliciclastic facies with abundant marine fossils, indicating a more distal, yet still shallow, marine setting.

These units form part of the local Lower–Middle Miocene succession that records a shallow-marine carbonate to mixed carbonate-siliciclastic depositional setting. Medium-to-coarse biocalcarenes, often with cross-lamination, predominate but there are also shell-beds and storm-packstone textures - signaling deposition on a shallow carbonate shelf or shoreface that was periodically reworked by waves and storms. Those thin marly intervals and local siliciclastic layers record minor changes to

muddier or quieter conditions. The Burdigalian units at Foz da Fonte contain diverse shallow-marine faunas (mollusks, bryozoans, echinoids, foraminifera; *e.g.*, Zbyszewski, 1967) and have produced vertebrate remains (notably sirenian/other marine mammal fossils and Chondrichthyes reported from Foz da Fonte/Penedo localities; see synthesis in Esteves, 2000; Fialho *et al.*, 2021; Prista *et al.*, 2023). That assemblage supports interpretation as warm-temperate to subtropical shallow-marine environments with high benthic productivity.

### Systematic Paleontology

Order Perciformes  
Suborder Scombroidei  
Family Scombridae  
Tribe Thunnini

Genus *Thunnus* South (1845)

Type-species: *Thunnus thynnus* (Linnaeus, 1758)

*Thunnus* sp.

Description with remarks: The CPM-BFF034V specimen is a caudal vertebra shown in the six different views (Fig. 3a–f) and clearly belongs to a large teleost fish. Key features include (see figure 4 for nomenclature based on Collette *et al.*, 2001):

#### a) General Shape

The vertebra (Fig. 3) is amphicoelous, with both articular surfaces deeply concave and connected, a condition typical of teleost fish which allows flexibility and efficient transmission of forces during swimming. The vertebral centrum is relatively robust and cylindrical, with smooth articular surfaces and shows distinct concentric striations related to endochondral ossification and growth (Fig. 3). Lateral transverse and articular processes are also present, contributing to additional muscular attachment. The centrum exhibits minimal surface ornamentation, show slightly flattened articular surfaces, restricting flexibility to the caudal peduncle region.



Figure 2. The Burdigalian age succession of Praia da Foz da Fonte from which the caudal vertebra of *Thunnus* sp. is originated.

Figura 2. A sucessão de idade Burdigaliano da Praia da Foz de onde provém a vértebra caudal de *Thunnus* sp..

### b) Neural and Hemal Arch

In dorsal and ventral views (Fig. 3a, b), the neural arch bases and hemal arch attachments are visible, but the neural and hemal spines are missing (broken off). The lower angle made by the hemal arch attachment and the presence and morphology of a transverse foramen at the base of the hemal spine possibly places this as vertebra 24 or 25 (according to figure S10 of Appendix 2 by Andrews *et al.*, 2022a). Lateral views (Fig. 3c, d) reveal depressions and foramina for the spinal nerve roots, seen as two oval openings above the midline, indicating attachment points for muscles, ligaments, and blood vessels. Prezygophyses project cranially from the neural arch.

### c) Centrum

The centrum is progressively more elongate posteriorly. It is circular to slightly oval in transverse view (Figs. 3e, f and 4),

showing concentric growth increments, visible as fine rings radiating from the notochordal pit, common in large pelagic fishes. It lacks the heavy ornamentation seen in some other fish groups.

### d) Surface Texture

Porous texture in some areas suggests vascularization, typical of fast-swimming fishes.

### e) Size

The vertebra's centrum width is between 6 cm and 6.5 cm, making it consistent with a large *Thunnus* individual, likely over 284 cm  $\pm$  10% total length based on allometric relationships from tuna vertebra studies calculated using [www.tunaarchaeology.org/lengthestimations](http://www.tunaarchaeology.org/lengthestimations) for vertebra types between 23 and 31 (see also Andrews *et al.*, 2022a and the supplementary material provided by these authors). The



Figure 3. *Thunnus* sp. vertebra from the Burdigalian age of Praia da Foz da Fonte: (a) – dorsal view showing the base of the neural spine and the neural prezygophysis; (b) – ventral view with the base of the hemal arch; (c and d) – lateral views (dorsal and ventral, respectively) showing the robust centrum and the bases of neural spine and hemal arch, besides the elliptical scars for intermuscular ribs (clearly seen in d); (e) – anterior view of the centrum showing the articular surface; (f) – posterior view. Scale is 10 mm.

Figura 3. Vértebra de *Thunnus* sp. de idade Burdigaliano da Praia da Foz da Fonte: (a) – vista dorsal mostrando a base da espinha neural e a pré-zigapófise neural; (b) – vista ventral com a base do arco hemal; (c e d) – vistas laterais mostrando o corpo vertebral robusto e as bases da espinha neural e do arco hemal, além das cicatrizes elípticas das costelas intermusculares (claramente visíveis em d); (e) – vista posterior do corpo vertebral mostrando a superfície articular; (f) – vista anterior. Escala de 10 mm.

thickness of the lateral ridge also points to a large individual, the thickness of this ridge increases with size (Sakashita *et al.*, 2023).

The combination of size, growth ring pattern, and the centrum morphology is diagnostic of large scombrids, particularly *Thunnus*. This fossil is a classic *Thunnus* centrum: a thick, round, amphicoelous vertebra with low neural/hemal arch bases and clear growth rings—exactly the features used to recognize tuna vertebrae in the archeological record (Andrews *et al.*, 2022b). Caudal vertebrae in *Thunnus* are defined by the presence of hemal arches and hemal spines projecting ventrally from the centrum. We think this could be vertebra 24 or 25, according to the lower angle provided by the hemal arch attachment and large thickness of the lateral ridge.

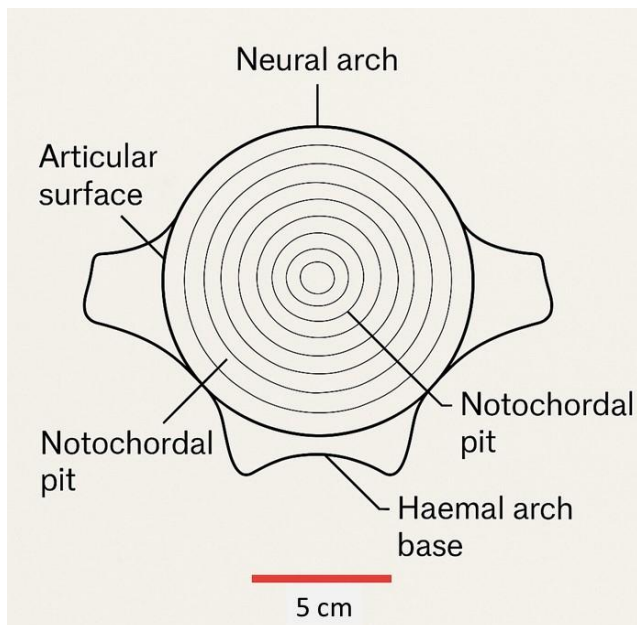


Figure 4. Sketch of the vertebra with the general nomenclature used for its description.  
Figura 4. Esquema da vértebra com a nomenclatura genérica utilizada para a sua descrição.

## Discussion

Fossil fish vertebrae—especially from tunas and related scombrids—are generally nondiagnostic at the species level. Many vertebral finds from tunas show similarities but tend to lack the fine anatomical details needed to separate species. Besides, the vertebral column of a tuna usually has 39 vertebrae with their morphological variants (Andrews *et al.*, 2022a), divided into a precaudal series (20–21 centra) and a caudal series (19–20 centra) (Kishinouye, 1923; Collette and Nauen, 1983). All centra are amphicoelous, with deeply concave anterior and posterior articular surfaces, and are strongly calcified with reduced notochordal remnants (Fierstine and Walters, 1968; Baxter *et al.*, 2022). The morphology of the vertebral column in tunas reflects their specialization for thunniform locomotion. The stiffened precaudal column provides a stable framework for the attachment of massive myomeres, minimizing lateral undulation and allowing efficient transmission of muscular forces (Collette *et al.*, 2001). This rigidity contrasts with more generalized teleosts (*e.g.*, Clupeidae, Gadidae), where flexibility is distributed along the entire body

axis. Comparatively, tunas exhibit a more heavily ossified and rigid vertebral column than most non-scombrid teleosts, a condition shared with other fast pelagic taxa such as istiophorid billfishes and xiphiids (Nauen and Shadwick, 1999) and also observed in the vertebra analyzed in this study. These features are interpreted as structural adaptations to sustained high-speed swimming, large-scale migrations, and a pelagic predatory lifestyle (Block and Stevens, 2001). Overall, the morphology of this caudal vertebral centrum reflects adaptations to sustained, high-speed swimming, facilitating the transmission of muscular forces to the caudal peduncle and tail fin propulsion.

Early Miocene scombrids are reported, but most determinations are family/genus-level and based on isolated elements; detailed species-level diagnoses from single centra are rare (Kotlarczyk *et al.*, 2006). Monsch and Bannikov (2012) described two species of *Thunnus* in the Middle Eocene of Russia and Late Oligocene of West Ukraine. According to these authors, these species are provisionally attributed to the genus *Thunnus* because they possess some, but not all, diagnostic features of that genus. The centrum shape, size, and the paired lateral foramina of the Foz da Fonte vertebra matches the global Miocene “*Thunnus*-type” pattern seen especially well in Atlantic Coastal Plain material from the Langhian (Middle Miocene) Pungo River Formation (Aurora, North Carolina; Purdy *et al.*, 2001) and resembles isolated records elsewhere, such as in the Early Miocene of Chilcatay Formation at Ullujaya (Pisco basin, Peru; Di Celma *et al.*, 2018). Definite *Thunnus* fossils are documented from Late Miocene to Early Pliocene marine units in northern Chile (Long, 1993).

Several teleostean vertebrae from the Burdigalian sites of Areiro and Horta das Tripas (Arroios) in Lisbon were attributed to the family Scombridae without description by Zbyszewski (1949: pl. XXII, figs. 136, 141, 142, 149, 154, 159, 161 and 171). The figured material cannot be compared taxonomically with our material. Jonet (1966) revised the numerous teeth described by Serralheiro (1954) under different species of the mackerel *Cybium* and erected the species *C. serralheiroi* from the upper Serravallian of Portela de Sacavém, Olivais and Costa da Caparica. Moreover, the author described in more detail three different morphotypes attributed to *Cybium* sp. from the upper Serravallian and upper Tortonian from Caparica. *Cybium* was considered a junior synonym of *Scomberomorus* (Collette and Nauen, 1983). Jonet (1978a, b) described the scombrid *Pelamys teixeirae* (*Pelamys* is a junior synonym of the bonito genus *Sarda sensu* Collette and Chao, 1975) from the late Serravallian and late Tortonian of Caparica and Fonte da Telha, respectively, based mainly on rare teeth.

The presence of a small tuna (*Thunnus* sp.) in the second phase of occupation of Vidigal site on the SW coast of Portugal constitutes the first record of its kind in archaeological sites from the Prehistory of Portugal (Gabriel *et al.*, 2022). The Vidigal site is one of the Late Mesolithic sites on the coastal plain between Sines and Cabo Sardão. The “Tuna Archaeology — Database of records” that consolidates archaeological records of tuna (*Thunnus thynnus*) in the Atlantic and Mediterranean (see Andrews *et al.*, 2022b) includes entries for Tavira (1176 vertebrae; recorded as “Unpublished” and dated between the 8th century BC and the 1st century AD, Iron Age period) and Castro Marim (194 vertebrae; “Unpublished”, from the same period as the previous entries).

Due to the morphology observed, we consider the vertebra CPM-BFF034 from the lower Burdigalian of Praia da Foz da Fonte to be the first and earliest evidence of tuna in the fossil record of Portugal.

## Conclusions

The discovery of a large amphicoelous vertebra from Praia da Foz da Fonte (Early Miocene, Burdigalian, Baixo Tejo Basin) provides the first unequivocal fossil evidence of tuna (*Thunnus* sp.) in Portugal. The specimen exhibits diagnostic features consistent with large individuals of the genus, representing a highly adapted pelagic predator, already well established in Miocene marine ecosystems of western Iberia. This finding not only extends the Portuguese fossil record of Scombridae, which was previously poorly documented, but also contributes to the broader understanding of tuna distribution and diversification during the Neogene. Comparisons with coeval material from Europe, North and South America confirm that *Thunnus* was a widespread and ecologically important component of the Miocene oceans. The record from Foz da Fonte thus represents both the earliest evidence of tuna in Portugal and a significant data point for reconstructing the paleobiogeography of scombrids in the Atlantic domain.

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