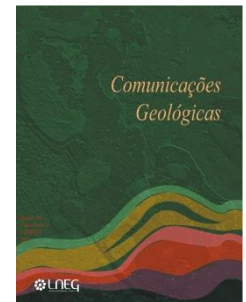


The hybodontiform sharks (Chondrichthyes: Euselachii) from the Upper Jurassic of Torres Vedras, Portugal

Os tubarões hybodontiformes (Chondrichthyes: Euselachii) do Jurássico Superior de Torres Vedras, Portugal

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Artigo original
Original article

DOI: <https://doi.org/10.34637/rx8a-5283>

Recebido em 15/03/2021 / Aceite em 02/12/2021

Publicado online em maio de 2022

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Abstract: In this work, the description and classification of a set of fossil shark tooth specimens, from the upper Kimmeridgian-lower Tithonian (Upper Jurassic) of Torres Vedras, was developed. The material, currently housed in the paleontological collection of Sociedade de História Natural, was collected on the surface of the marine deposits at the top of the Praia Azul Member, Lourinhã Formation, Lusitanian Basin. The attribution of the specimens to *Hybodus cf. reticulatus*, was based on the presence of the following most striking characteristics: a reticulated, spongy root, perpendicular to the crown; a completely to almost completely straight main cusp; several straight, well-defined, and parallel ridges that run from the base of the crown to about half of the height of the main cusp; and flat, well-defined cutting edges.

Keywords: Hybodontiformes, *Hybodus cf. reticulatus*, Upper Jurassic, Lusitanian Basin, Torres Vedras.

Resumo: No presente trabalho, fez-se a descrição e a classificação de um conjunto de espécimes de dentes fósseis de tubarão, do Kimmeridgiano superior-Tithoniano inferior (Jurássico Superior) de Torres Vedras. O material, atualmente sediado na coleção paleontológica da Sociedade de História Natural, foi colhido à superfície nos depósitos marinhos do topo do Membro da Praia Azul, Formação da Lourinhã, Bacia Lusitaniana. A atribuição dos espécimes a *Hybodus cf. reticulatus*, baseou-se na presença das seguintes características mais marcantes: raiz reticulada, esponjosa e perpendicular à coroa; cúspide principal totalmente ou quase totalmente estreita; várias pregas estreitas, bem definidas e paralelas entre si, que surgem desde a base da coroa até aproximadamente metade da altura da cúspide principal; e bordo cortante liso e bem definido.

Palavras-chave: Hybodontiformes, *Hybodus cf. reticulatus*, Jurássico Superior, Bacia Lusitaniana, Torres Vedras.

1. Introduction

The hybodontiforms were a group of sharks that first appeared in the latest Devonian (c. 360 Myr) and went extinct right at the end of the Cretaceous (c. 66 Myr) (Ginter *et al.*, 2002; Rees and Underwood, 2005; Stumpf and Kriwet, 2019; Stumpf *et al.*, 2021). Hybodontiformes is the supposed sister group of Neoselachii, i. e. the true modern selachians (sharks, skates and rays) (Kriwet, 2000; Maisey, 2012; Cuny *et al.*, 2017; Stumpf and Kriwet, 2019). Hybodonts thrived and were very abundant in the Mesozoic, especially between the Triassic and Jurassic, when they were vastly present in both marine and continental aquatic environments (Carrillo-Briceño *et al.*, 2016; Stumpf *et al.*, 2021). However, their numbers declined, starting in the Late Jurassic and continuing throughout the Cretaceous, probably due to competition and niche overlapping with neoselachians (Rees and Underwood, 2005, 2008), which were undergoing a rapid increase in diversity, starting in the late Early Jurassic onwards (Underwood, 2006; Stumpf *et al.*, 2021). This resulted in hybodonts gradually occupying more restricted marine and, especially, freshwater environments (Rees and Underwood, 2008; Carrillo-Briceño *et al.*, 2016). Their dentition is characterized by an array of different morphologies and adaptations, including tearing, grinding, clutching, crushing, and cutting types (Cappetta, 1987; Stumpf *et al.*, 2021). Despite the increasing progress on identifying and classifying hybodonts in recent times, there is still much to solve about their paleodiversity, systematics, taxonomy and phylogenetic relationships, in Portugal and worldwide (Kriwet, 2004; Stumpf *et al.*, 2021). This great uncertainty is mainly due to the lack of cohesive and reliable identification of synapomorphies, since most species are based solely on isolated teeth and spines, which can produce much ambiguity and/or erroneous interpretations (Rees and Underwood, 2005, 2008; Stumpf *et al.*, 2021).

1.1. State of the art of fossil hybodonts in Portugal

The hybodont fossil record in Portugal has been poorly documented. Choffat (1885, in Sauvage, 1897-98), was the first researcher to publish the occurrence of Hybodontiformes in Portugal, by reporting the genus *Strophodus* sp., from Mexilhoeira (Valanginian) and Bellas (Hauterivian). Afterwards, Sauvage

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(1897-1898) described a single tooth, with no photographic record, collected in Santa Cruz (Torres Vedras), dating the Late Jurassic ["Malm supérieur" in Sauvage (1897-98)], that was attributed to the species *Hybodus polyprion* Agassiz, 1843 [= "*Hybodus aff. polyprion*, Ag." Sauvage (1897-1898: 10)]. Also, material of *Strophodus* sp. from the "Infravalanginien" [in Sauvage (1897-98)], Valanginian, and Hauterivian of Brouco was recorded. About a century later came other discoveries: one isolated tooth of *Asteracanthus* sp., from the Fonte Quente limestone quarry, dating the Toarcian age, late Early Jurassic (Antunes, 1967); *Hybodus lusitanicus* Kriwet, 2004 [= *Hybodus* sp. Kriwet (1998, p. 245, pl. 1, figs. 2-3); *Polyacrodus* sp. Kriwet (1998, p. 245, pl. 1, figs 5-6; 2000, p. 42, figs. 6.2a-6.2b, p. 43, fig. 6.3)], *Asteracanthus biformatus* Kriwet, 1995, *Hybodus* sp. (teeth), and *Hybodontoida* indet. (placoid scales) from the Guimarota coal mine, Leiria (Kriwet, 1998, 2000, 2004); *Hybodus* cf. *reticulatus* Buckland, 1836 [= *Hybodus* cf. *reticulatus* Agassiz, 1837, in Balbino (2003)], from Peralta and Porto das Barcas, Lourinhã (Balbino, 2003); and lastly, additional material of *H. lusitanicus* collected from Porto das Barcas, Lourinhã (Guillaume, 2018). With this work, the research regarding the diversity and occurrences of fossil selachians is continued and will hopefully add more knowledge to the hybodontiforms of the Upper Jurassic of Portugal.

2. Geological and stratigraphic framework

In the central-western section of Portugal lies the Lusitanian Basin (Fig. 1), the largest on the country (Kullberg *et al.*, 2006; Martinius and Gowland, 2010; Taylor *et al.*, 2013). The deposits range from Upper Triassic (probably Carnian) to Lower Cretaceous (upper Aptian) in age (Leinfelder, 1987; Hill, 1989a; Kullberg *et al.*, 2006; Mateus *et al.*, 2013), and it witnessed the formation of the North Atlantic Ocean in the early Mesozoic (Leinfelder, 1987; Kullberg *et al.*, 2006; Taylor *et al.*, 2013). The fossiliferous material from this study came, more specifically, from the marine deposits of the top of the Praia Azul Member, Lourinhã Formation (following Hill, 1989b) (Fig. 1, black star). The Praia Azul Member lies directly above the Praia da Amoreira-Porto Novo Member (Hill, 1989b; Taylor *et al.*, 2013). It crops out south to Areia Branca syncline near Santa Cruz, and from Porto Dinheiro to Paimogo localities (Hill, 1989b; Taylor *et al.*, 2013). Further, it crops out in Vale Frades and Vale Pombas, in a northward direction, in respect to Areia Branca syncline (Taylor *et al.*, 2013). The Praia Azul Member is characterized mainly by meandering fluvial channels and calcrete-bearing paleosoils, composed by ~75 to 88% of marls and mudstones, and ~12 to 25% of sandstones, although the percentage of the latter rises from south to north (Hill, 1989b; Mateus *et al.*, 2013; Taylor *et al.*, 2013). Some sandstones display abundant carbonaceous material, defined by brackish-marine bay-fill sediments, with numerous occurrences of shelly organisms (Mateus *et al.*, 2013; Taylor *et al.*, 2013). Fürsich (1981) recognized the type section as being represented by a sequence of grey mudstones cut by lenticular, cross-bedded sand channels, and also reddish mudstones that bear calcareous nodules (paleosoils). The base of the Praia Azul Member is defined by an initial transgressive surface that overlies the first shelly unit (Taylor *et al.*, 2013); and its upper boundary is delimited by the top of the third and final unit that contains numerous shell remains (Martinius and Gowland, 2010; Taylor *et al.*, 2013). Thus, the interval of Praia Azul Member is defined by the presence of three distinct, laterally extensive shelly units that develop in thick successions of floodplain muddy deposits (Martinius and Gowland, 2010; Mateus *et al.*, 2013; Taylor *et al.*, 2013). Overall, the sections that include the Praia Azul Member represent a change from fluvial or floodplain environments to marginal marine or

brackish bays, sometimes very shallow, and protected lagoons, with deltaic influence (Fürsich, 1981). Although reliable biostratigraphic markers are generally scarce, based on the combination of shelly biota, spores, dinocysts, algae, forams, and ostracods (e. g. *Cetacella armata* Martin, 1958), the age of the Praia Azul Member has been attributed from between uppermost Kimmeridgian and lowermost Tithonian (Fürsich, 1981; Mateus *et al.*, 2013; Taylor *et al.*, 2013). A reliable numeric age is still yet to be established for this unit.

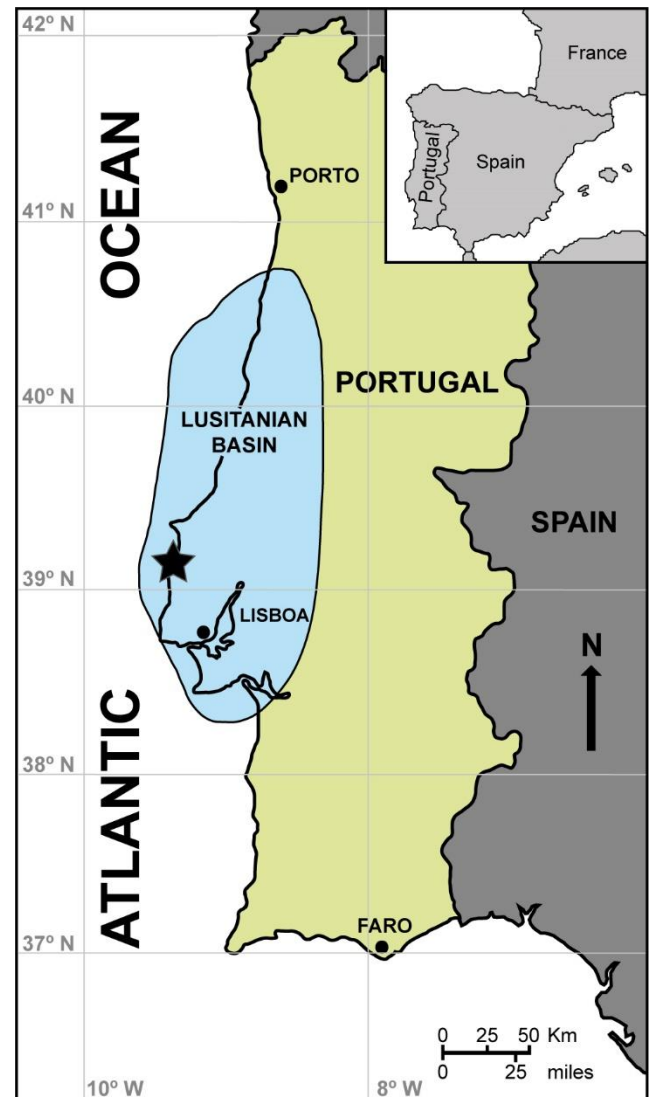


Figure 1. Lusitanian Basin. The black star indicates the approximate location where the specimens under study came from. Adapted from Taylor *et al.* (2013).

Figura 1. Bacia Lusitaniana. A estrela negra indica o local aproximado de onde provieram os espécimes deste estudo. Adaptado de Taylor *et al.* (2013).

3. Materials and Methods

The fossil material discussed in this study was collected in Praia Azul by José Joaquim dos Santos, a local collector. This material is now housed in the paleontological collection of CI2Paleo at the Sociedade de História Natural, Torres Vedras, by which the majority of such collection was gathered and donated by José Joaquim dos Santos. Unfortunately, since the present specimens were collected without any detailed designation of the locality where they were found, it is not possible to provide any detailed

information concerning the exact location of the sites or horizons, in Praia Azul. Digital photographs presented in the plates were obtained with a Canon EOS 550D digital camera, with 18-55 mm lens kit.

4. Systematic paleontology

Remarks. The descriptive dental terminology follows Cappetta (1987). Authorship follows Pollerspöck and Straube (2021).

Class CHONDRICHTHYES Huxley, 1880
 Subclass ELASMOBRANCHII Bonaparte, 1838
 Cohort EUSELACHII Hay, 1902
 Order HYBODONTIFORMES Maisey, 1975
 Superfamily HYBODONTOIDEA Owen, 1846
 Family HYBODONTIDAE Owen 1846
 Subfamily HYBODONTINAE Owen, 1846
 Genus *HYBODUS* Agassiz, 1836
 (Fig. 2)

Type species. *Hybodus reticulatus* Buckland, 1836 from the Sinemurian (Lower Jurassic) of Lyme Regis, southern England.

HYBODUS CF. *RETICULATUS* Buckland, 1836
 (Pl. I, Fig. 1-9; Pl. II, Fig. 1-4)

Locality. Praia Azul, Torres Vedras, Portugal.

Horizon. Unknown.

Age. late Kimmeridgian-early Tithonian, Late Jurassic.

Material. 30 incomplete teeth [SHN.(JJS).584-613]. Plates I and II.

Description. The studied specimens are represented by incomplete tooth crowns, lacking or having poorly preserved roots. The isolated teeth are small - 4-10 mm in crown height; 4-7 mm in length (mesiodistally); 2-4 mm in crown width. The ratio of the crown height and crown length is roughly 1.5:1, making it higher than wider. The crown is rather high and slender. The orientation of the main cusp varies between slightly distally inclined to straight, in labial view. The cutting edges are smooth, extending from the mesial and distal margins of the crown, although they generally present some degree of erosion. All specimens present longitudinal, parallel, irregularly alternated ridges on the base of the crown, on both faces. The ornamentation reaches from 1/3 to half the total height of the main cusp, on the labial face, and from half to near-total height of the main cusp on the lingual face. There are no lateral cusplets preserved, however, there seems to be some remnants, though they are eroded (Pl I, Fig. 7). The root, when perceptible, is perpendicular to the crown and exhibit a reticulated, spongy aspect, with many foramina, being most evident at the junction between the crown and the root.

Discussion. The lack of lateral cusplets, assuming they were present, and well-preserved root, makes the task of a more specific classification harder. The taxa below-mentioned were used to compare with the specimens from this study, mainly due to overall similarity in shape. When comparing with the late Kimmeridgian *Planohybodus* Rees and Underwood, 2008, figured by Leuzinger *et al.* (2017, Fig. 6, A-Q), the ornamentation of the enameloid of *Planohybodus* is delicate and weaker than the specimens under study, and the main cusp is wider. Teeth of *Egertonodus* Maisey, 1987, figured by Rees and Underwood (2008, Pl. 1, Fig. 13-17; Pl. 2, Fig. 4-10; more specifically to *Egertonodus duffini* Rees and Underwood, 2008), are not comparable by their weak, often bifurcating ridges on the enameloid, and slimmer main cusp that is

sigmoidally curved in mesio-distal views. By comparing with *Hybodus cuspidatus* Agassiz, 1843 and *H. sublaevis* Agassiz, 1843, figured by Agassiz (1833-1843, Vol. 3, Tab. 22a, Fig. 5-7; Tab. 22a, Fig. 2-4, respectively), the ridges in the enameloid of *H. cuspidatus* are much more prominent, and they reach the apex, unlike every specimen under study. Additionally, the main cusp is notably inclined backwards. The ridges on the tooth enameloid of *H. sublaevis* are extremely delicate, to a point that the surface appears smooth, which does not correspond with any specimen herein. Comparing with *Parhybodus plicatilis* (Hogard, 1837) [= "*Hybodus plicatilis*" in Agassiz (1843), Balbino (2003), and Manzanares *et al.* (2019)], figured by Manzanares *et al.* (2019, Fig. 2, A-D), the root of its teeth is less porous than the teeth under study, and the main cusp is thinner and slimmer. The studied specimens do not resemble, in most part, those of *Hybodus lusitanicus* Kriwet, 2004, figured by Kriwet (2004, Fig. 2, a-q; Fig. 3, a-m), from lower Kimmeridgian of Guimarota, central Portugal. For instance, the latter are distinguished by their low crowns; different vertical ridge patterns on both faces of the crown; the labial face of the main cusp forms a bulge that overhangs the root; and different root morphology overall. The closest similarities can be traced, however, by comparing the specimens under study with the teeth figured by Balbino (2003, Pl. 1, Fig. 1-2; Pl. 2, Fig. 1-4), attributed to *Hybodus* cf. *reticulatus* Buckland, 1836. For instance, both have completely to near completely straight main cusps; several parallel, well-defined, straight ridges that run from the base of the crown to about half the total height of the main cusp; well-defined, smooth cutting edges; and the root is reticulated, spongy, rather perpendicular to the crown, and presents many foramina. After Agassiz (1833-1843, Vol. 3, Tab. 22a, Fig. 22-23; Tab. 24, Fig. 26), it is possible to correlate the root morphology, and the particularly pronounced ridges on the base of the main cusp. Furthermore, the teeth described and figured by Stumpf and Kriwet (2019, Fig. 2a-f), attributed to *Hybodus reticulatus* Agassiz, 1837?, is also consistent with the ones described in this work. Thus, as a result of the description, comparisons made, and lack of more definitive characters, the current specimens will be attributed to *H. cf. reticulatus*.

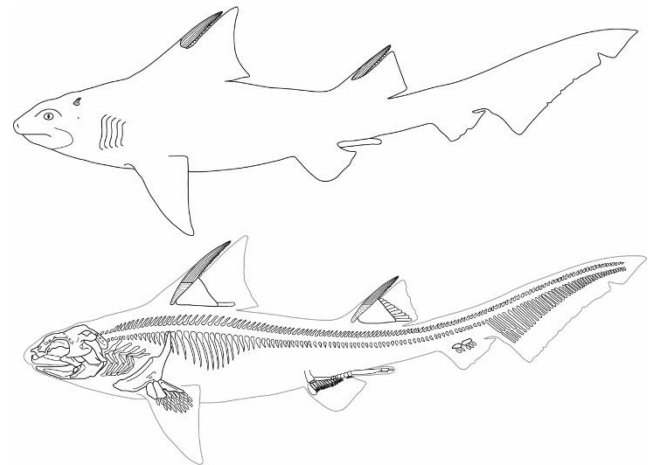


Figure 2. Reconstitution of *Hybodus* sp. (adapted from Maisey, 1982).

Figura 2. Reconstituição de *Hybodus* sp. (adaptado de Maisey, 1982).

5. Conclusion

As a typical Early Jurassic species, *H. reticulatus* is known from several European localities, from both isolated teeth and disarticulated skeletal material, ranging from the middle Hettangian to the late Pliensbachian (Stumpf and Kriwet, 2019). With this work, the presence of *H. cf. reticulatus* in the Upper

Jurassic Portuguese record is confirmed, thus extending this species stratigraphic range to the Late Jurassic. Additionally, it adds more knowledge to the diversity and occurrences of fossil sharks in Portugal, as well as more insight into the aquatic vertebrate paleobiodiversity from the Upper Jurassic of the Lusitanian Basin. More prospection in Praia Azul is necessary, as it may prove to be a locality full of ichthyological material, including fossil shark material.

Acknowledgements

We would like to greatly thank the reviewers for providing constructive comments to help improve the manuscript.

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