Universidade de Évora - Escola de Ciências e Tecnologia Universidade
Nova de Lisboa - Faculdade de Ciências e Tecnologias

Mestrado em Paleontologia

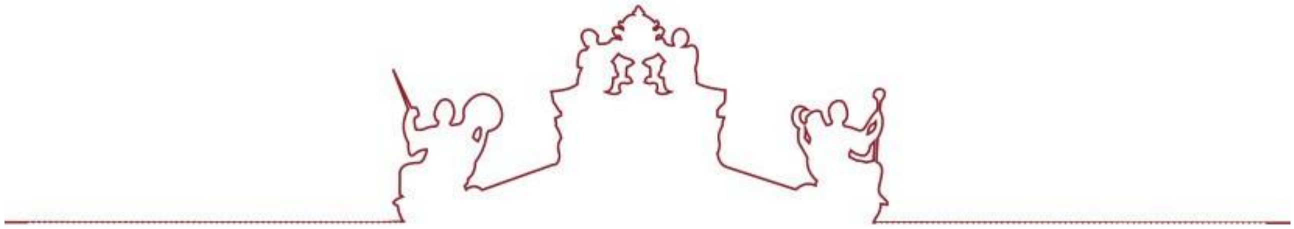
Dissertação

Fishes from the Upper Jurassic of Torres Vedras, Portugal

Bruno Leite Pereira Costa

Orientador(es) | Ausenda Cáceres Balbino

Évora 2022



Universidade de Évora - Escola de Ciências e Tecnologia Universidade
Nova de Lisboa - Faculdade de Ciências e Tecnologias

Mestrado em Paleontologia

Dissertação

Fishes from the Upper Jurassic of Torres Vedras, Portugal

Bruno Leite Pereira Costa

Orientador(es) | Ausenda Cáceres Balbino

Évora 2022

A dissertação foi objeto de apreciação e discussão pública pelo seguinte júri nomeado pelo Diretor da Escola de Ciências e Tecnologia:

Presidente	|	Carlos Alexandre Ribeiro (Universidade de Évora)
Vogais	|	Ausenda Cáceres Balbino (Universidade de Évora) (Orientador)
		Pedro Miguel Callapez Tonicher (Universidade de Coimbra) (Arguente)

Évora 2022

Acknowledgements

Firstly, I would like to thank my advisor, Professor Ausenda Balbino, for all the support she has given me throughout my entire Master's and my academic path in general, and for encouraging me to be involved in the researcher's world. I would also like to thank my co-advisor, Professor Miguel Telles Antunes, for all of his constructive comments for the improvement of my thesis, and for encouraging me to pursue and study the field of Paleontology, with both passion and hard work.

I want to greatly thank Pedro Fialho for being an awesome mentor and friend, by helping me figure the right choices, for always being present, and for lending his vote of confidence in me, by inviting me to join and work on his projects and other endeavors.

I am very grateful and I thank the entire team of Sociedade de História Natural: Bruno Camilo Silva, for his mentorship, for providing the specimens for this study and helping me with the development of my Thesis, and for his hospitality, by letting me stay in the facilities of SHN; Pedro Bonifácio, for his support, help and advice on photographing the specimens and materials, and for guiding me on the CI2Paleo lab work; Remmert Schouten, for his advice, support, and for teaching me useful and important conservation and storage techniques; and Magda Samborska and Dagmara Skiba, for their support, for helping me with the practical work, and for guiding me through the CI2Paleo lab. I want to greatly thank every member of the SHN team that helped me during fieldwork and practical work, such as washing and cleaning sediments, and picking of microfossils. I am really thankful for the incredible parties, hangouts, lunches, dinners, drinks, games, and many other good memories that we had, with the entire team, including, of course, Isaak Eijkelboom, Jean-Pierre Mayen, and the good friend Ângela Duarte Inácio. You are all incredible!

I immensely thank Miguel Marx and Maciej Ruciński, for being spectacular friends and roommates, for all the support they have given me, for all the Catan games in the Caparica PaleoHouse, and for all the good moments and memories we shared during our stay in Monte de Caparica. I want to thank Miguel Marx for his mentorship, specifically on the preparation lab, *Laboratório de MacroPaleontologia Prof. Miguel Telles Antunes*, of the Earth Sciences Department, FCT-NOVA, where he taught me how to prepare blocks with fossils, and the tools to use. Further, I am grateful for his vote of confidence on letting me help him to prepare his plesiosaur specimens, that he would later describe on his Thesis. I also greatly thank Maciej Ruciński for his helpfulness and support, specifically on his constructive comments for the development of my thesis.

Last but not least, I want to thank my family, for all the love and support they have given, and for letting me pursue my dream: to be a Paleontologist.

Abstract

In this study, fossil hybodontiform and neopterygian specimens from the Upper Jurassic of Torres Vedras are reported. Material was collected on the surface of the marine deposits at the top of Praia Azul Member, Lourinhã Formation, dating between upper Kimmeridgian-lower Tithonian; and on the surface of the transitional deposits of Cambelas fossil site, Freixial Formation, dating between middle-upper Tithonian, Upper Jurassic. Fossils are housed in the CI2Paleo of Sociedade de História Natural, in Torres Vedras. Hybodontiforms are represented by 30 isolated teeth, which are attributed to *Hybodus* cf. *reticulatus*, as per diagnostic evidences on the main cusp, cutting-edges, and, especially, the root. Neopterygians are represented by 29 isolated or partially associated body scale specimens, diagnosed as cf. Ginglymodi; and 64 isolated and partially articulated prearticular and vomerine teeth referred to Pycnodontiformes indet. This work hopefully improves our understanding about the fish diversity and occurrences of the Upper Jurassic of Portugal.

Keywords: Hybodontiformes, Neopterygii, Late Jurassic, Torres Vedras, Portugal

Resumo

Neste estudo são reportados exemplares fósseis de hybodontiformes e neopterígios do Jurássico Superior de Torres Vedras. Este material foi recolhido à superfície dos depósitos marinhos no topo do Membro da Praia Azul, Formação da Lourinhã, datando o Kimmeridgiano superior-Tithoniano inferior; e à superfície dos depósitos transicionais da jazida fóssil de Cambelas, Formação do Freixial, datando o Tithoniano médio-superior, Jurássico Superior. Os fósseis estão alojados no CI2Paleo da Sociedade de História Natural, em Torres Vedras. Os hybodontiformes são representados por 30 dentes isolados, atribuídos a *Hybodus* cf. *reticulatus*, conforme evidências diagnósticas na cúspide principal, bordo cortante e, especialmente, a raiz. Os neopterígios são representados por 29 espécimes de escamas corporais isoladas ou parcialmente associadas, diagnosticadas como cf. Ginglymodi; e 64 dentes pré-articulares e vomerinos isolados e parcialmente articulados, atribuídos a Pycnodontiformes indet. Esperançosamente, este trabalho aprimora a nossa compreensão acerca da diversidade e ocorrências dos peixes do Jurássico Superior de Portugal.

Palavras-chave: Hybodontiformes, Neopterygii, Jurássico Superior, Torres Vedras, Portugal

Table of Contents

Table of Figures

Table Index

List of Abbreviations

SCE – single crystallite enameloid

SLE – shiny-layered enameloid

PBE – parallel-bounded enameloid

TBE – tangle-bundled enameloid

K-Pg – Cretaceous-Paleogene mass extinction

SHN – Sociedade de História Natural

CI2Paleo – Centro de Investigação de Paleobiologia e Paleoecologia

H_2O_2 – hydrogen peroxide

1. Introduction

The present work concerns fossil remains of elasmobranchs and neopterygians from the Upper Jurassic of Torres Vedras, Portugal.

Hybodontiforms are chondrichthyans, and the latter are characterized by their entirely cartilaginous skeletons, by which the endoskeletal cartilage is subjected to a prismatic type of calcification (Kardong, 2012, 2018), *i. e.* the cartilages are superficially supported by a coat of calcified prismatic plates, that provides strength and consistency. This, however, does not happen in the vertebral centra. Instead, a bone-like tissue is present (Cappetta, 1987; Helfman, et al., 2009).

Hybodontiforms are an extinct group of sharks that lived from the middle Paleozoic to the end of the Mesozoic Era (Cuny, Guinot, & Enault, 2017; Stumpf & Kriwet, 2019). They first appeared in the Late Devonian (*ca.* 360 Myr), surviving two (Permian-Triassic and Triassic-Jurassic) of the “Big Five” mass extinctions of the Phanerozoic Eon, and went extinct at the end of the Cretaceous (*ca.* 66 Myr) (Rees & Underwood, 2005; Hodnett, Elliott, & Olson, 2013; Cuny et al., 2017; Stumpf & Kriwet, 2019; Stumpf et al., 2021). They were the most diverse and widely distributed elasmobranchs from the Paleozoic to early Mesozoic (Triassic) (Kriwet, 2000; Klug et al., 2010; Fischer, 2012). Hybodont shark remains occur in the Mesozoic units of Europe and North America with facies typical of fully marine, offshore to coastal, brackish and freshwater paleoenvironments. Although in other regions of the world, such as Asia, the hybodont fossil record is not as rich (Klug et al., 2010). More recently, however, there has been made descriptions of more hybodont material, as in the case of India and China (see Bhat, Ray, & Datta, 2017; Klug et al., 2010, see Table 1). Hybodontiformes is the supposed sister group of Neoselachii [= “elasmobranchs” *sensu* Stumpf et al. (2021)], *i. e.* the true modern selachians (sharks, skates, and rays) (Kriwet, 2000, 2004; Kriwet & Klug, 2008; Klug et al., 2010; Fischer, 2012; Maisey, 2012; Cuny et al., 2017; Stumpf & Kriwet, 2019; Stumpf et al., 2021). Although it is substantially difficult to determine which morphological characters are basal and which ones are derived in fossil and current elasmobranchs, hybodonts are characterized as being plesiomorphic, when compared to the more derived neoselachians (Cappetta, 1987). For instance, the primitive hybodontid tooth histology is orthodont, with single crystallite enameloid (SCE), while neoselachians possess the more derived triple-layered enameloid [however, not all Hybodontiformes possessed a single SCE layer, and not all neoselachians possessed the triple-layered enameloid, following Cuny, Rieppel, & Sander (2001) and Andreev & Cuny (2012)] (Maisey, 1987; Cuny et al., 2001; Guinot & Cappetta, 2011; Andreev & Cuny, 2012; Hoffman, Hageman & Claycomb, 2016).

Before the hybodonts went extinct at the end of the Cretaceous, they were subjected to competition with neoselachians, which underwent a first major radiation event in the Toarcian age, Early Jurassic (*ca.* 180 Myr) (Kriwet et al., 2009; Maisey, 2012; Stumpf & Kriwet, 2019; Stumpf et al., 2021). The niche overlap between these two taxa further increased during the Middle to Late Jurassic, resulting from the strong diversification of the neoselachians during this geological timespan (Kriwet, 2004; Kriwet & Klug, 2008; Kriwet, Kiessling, & Klug, 2009; Leuzinger et al., 2017). Moreover, stem-neoselachians, belonging to the order Synechodontiformes, were the group of modern sharks with the highest diversity during the Jurassic, therefore increasing even more the ecological pressures upon the hybodonts (Klug et al., 2010). The continuous rise and dominance of neoselachians likely prompted the decline in diversity of the Hybodontiformes. This process was gradually taking place in the Late Jurassic and continuing throughout the Cretaceous (Kriwet, 2004; Rees & Underwood, 2005, 2008; Kriwet & Klug, 2008; Stumpf et al., 2021). Marine hybodontiforms were gradually replaced by neoselachians, as exemplified by Upper Jurassic record of Europe (Leuzinger et al., 2017). However, during the earliest Early Cretaceous a greatly increased diversification event occurred amongst brackish and fluvial hybodont species, allowing these non-marine hybodonts to persist until the K-Pg mass extinction (Kriwet, 2000; Kriwet & Klug, 2008; Rees & Underwood, 2008; Leuzinger et al., 2017).

Hybodonts are known worldwide mostly from isolated teeth and spines, but also from skin impressions and, more importantly, complete skeletons (Fig. 1). Their dentition is characterized by an array of different morphologies and adaptations, including tearing, grinding, clutching, crushing, and cutting tooth 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 (Kriwet, 2004; Stumpf et al., 2021). This great uncertainty is mainly due to the lack of cohesive and reliable identification of synapomorphies, since the classification of most hybodont species is heavily based on isolated teeth and spines (Rees & Underwood, 2005, 2008; Stumpf et al., 2021). Moreover, due to the occurrence of heterodonty, different tooth wear patterns, and the fact that dental morphologies, especially concerning the crown, are particularly prone to homoplasy, the taxonomy based solely on teeth may be especially susceptible to ambiguous and/or erroneous interpretations (Rees & Underwood, 2005, 2008; Stumpf et al., 2021).

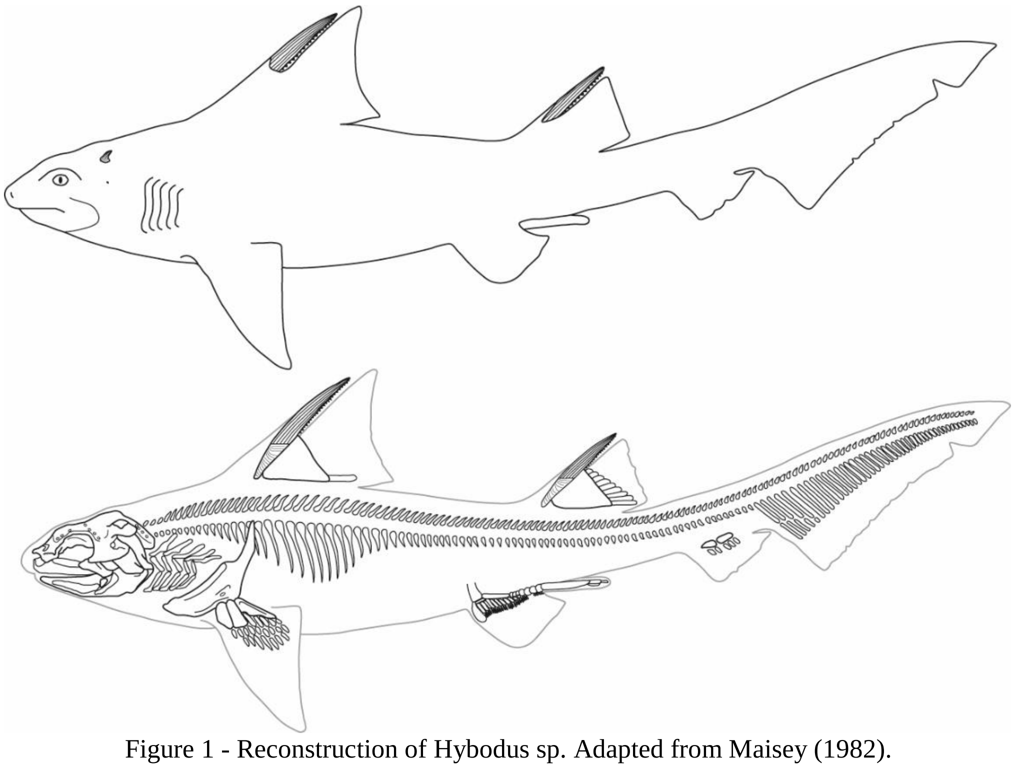


Figure 1 - Reconstruction of Hybodus sp. Adapted from Maisey (1982).

Actinopterygians, *i. e.* the ray-finned-fishes, are a group of bony fishes that are distinguished by their stiff bony spines, or fin rays, that support their fins (Long, 2011).

Today, actinopterygians are the most diversified vertebrates on Earth (Diogo, 2007; Helfman et al., 2009; Long, 2011; Hughes et al., 2018). They comprise at least *ca.* 28. 000 species, and new species still keep being discovered (Diogo, 2007; Long, 2011). Throughout their history, they underwent various radiations, leading to the evolution of various clades (Fig. 2): Palaeonisciformes, and Acipenseriformes (= Chondrostei; *e. g.* sturgeons and paddlefishes; Helfman et al., 2009; Kardong, 2012), basal and more derived Neopterygii, formerly divided into Holostei (*e. g.* gars and Bowfin) and Teleostei (Helfman *et al.*, 2009).

Neopterygii, meaning "new fins" (Helfman et al., 2009; Cawley et al., 2021), is a group of actinopterygian fishes that first appeared in the fossil record during the Late Permian (Fig. 2) (Helfman et al., 2009; Kardong, 2018).

Since their appearance in Paleozoic, their morphological variability and taxonomic diversity has been increasing (Helfman et al., 2009; Kardong, 2018). Neopterygians started replacing the Palaeonisciformes - a group of primitive ray-finned fishes - as the most dominant group of bony fishes during the early Mesozoic (Helfman et al., 2009; Kardong, 2012, 2018), in the aftermath of two major radiation events. First, it took place during the Triassic and Jurassic, and second in the Late Cretaceous (Helfman et al., 2009). In fact, many of the orders of modern teleostean fishes (the most dominant group of modern bony fishes) originated in the radiation event of the late Mesozoic (Helfman et al., 2009), in which *ca.* half of the 40 recognized living orders of teleosts have a fossil record that can be traced back into the Cretaceous period, and only about seven orders are younger than the Eocene epoch, *i. e.* are younger than *ca.* 50 Myr old (Helfman et al., 2009).

Following Helfman et al. (2009), non-teleostean neopterygians are characterized by seven orders, five of which are now extinct:

1. Macrosemiiformes; Semionotiformes; Pycnodontiformes; Aspidorhynchiformes; and Pachycormiformes.
2. Extant non-teleostean neopterygians include: ginglymodian lepisosteiform gars and the halecomorph amiiform bowfin (Helfman et al., 2009; Long, 2011; Kardong, 2012; Cawley et al., 2021).

Both Ginglymodi and Halecomorphi form the clade Holostei, which comprises only eight modern species (seven species of gars, and the bowfin) (Grande, 2010; López-Arbarello & Sferco, 2018; Cawley et al., 2021). Both gars and bowfin were traditionally recognized as being part of their own, separate division: Holostei, the sister group to Teleostei (Helfman et al., 2009; Kardong, 2012). However, more recent works have concluded that holosteans were paraphyletic. Thus, gars have been considered to be the most primitive and were added to their own separate group, Ginglymodi (Helfman et al., 2009). The bowfin is generally considered more derived than gars, and it is part of its own taxon, called Halecomorphi, which is considered by other authors as the sister group to Teleostei (Halecomorphi + Teleostei = Halecostomi) (Helfman et al., 2009; Long, 2011).

Nowadays, Neopterygii includes three monophyletic clades: Ginglymodi, Halecomorphi and Teleostei (Diogo, 2007; Helfman et al., 2009; Long, 2011; Cawley et al., 2021), with teleosts being, by far, the most diverse, abundant, and successful of all the neopterygians, with a total of around 32. 000 living species, which is more species than all other vertebrate classes combined (Diogo, 2007; Helfman et al., 2009; Romano et al., 2014; López-Arbarello & Sferco, 2018).

Unlike chondrichthyans, *i. e.* cartilaginous fishes, actinopterygians are much better represented in the fossil record, due to the fact that their skeletons are made up of calcified bone, which greatly facilitates fossilization processes, given the right taphonomical conditions (Helfman et al., 2009; Long, 2011). Moreover, although just as ancient as other gnathostome groups, there are, comparably, several more well-preserved whole-body fossils of pre-historic ray-finned fishes, many of them relatively similar in shape and size to modern species (Helfman et al., 2009; Long, 2011). Thus, it is much easier to trace back the ancestry of neopterygians, as well as compare the form and possibly even function between both living and fossil neopterygian taxa (Helfman et al., 2009).

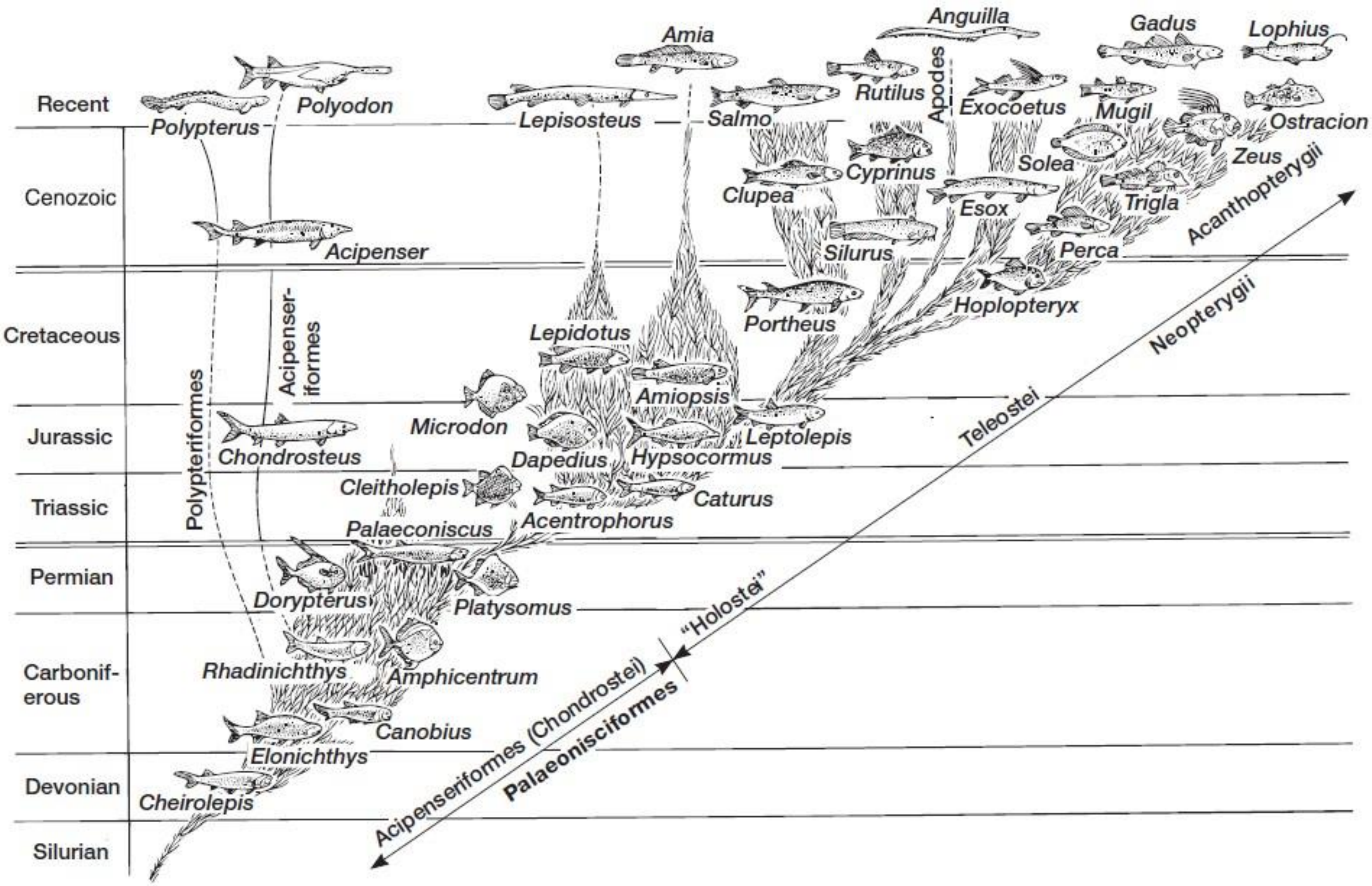


Figure 2 - Phylogeny of actinopterygians. Fig. 3.16 from Kardong (2012).

2. State of the art of Mesozoic hybodonts and neopterygians in Portugal

The hybodont fossil record in Portugal has been poorly documented (Table 1). Choffat [1885, in Sauvage (1897-98)], was the first researcher to publish the occurrence of Hybodontiformes in the country, by reporting the genus *Strophodus* sp., from Mexilhoeira (Valanginian, Lower Cretaceous) and Belas (Hauterivian, Lower Cretaceous). Afterwards, Sauvage (1897-98) described a single tooth, with no photographic record, collected in Santa Cruz (Torres Vedras), dating the Upper Jurassic [= "Malm supérieur" in Sauvage (1897-98)], that was attributed to the species *Hybodus polyprion* Agassiz, 1843 [= "*Hybodus* aff. *polyprion*, Ag." in 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 (close by the Tomar to Pedreira road, ca. 2 Km from the latter), dating the Toarcian age, upper Lower 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 Hybodontoidea indet. (placoid scales) from the Guimarota coal mine, Leiria (Kriwet, 1998, 2000, 2004); *Hybodus* cf. *reticulatus* Buckland, 1836 [authorship follows Pollerspöck & Straube (2021)], from Peralta and Porto das Barcas, Lourinhã (Balbino, 2003); and lastly, additional material of *H. lusitanicus* was collected from Porto das Barcas, Lourinhã (Guillaume, 2018).

Table 1 - List of occurrences of hybodontiform sharks previously documented from the Mesozoic of Portugal.

Taxon	**Age**	**Locality**	**Reference**
Strophodus sp.	Valanginian	Mexilhoeira	Choffat [1885, in Sauvage (1897-98)]
Strophodus sp.	Hauterivian	Belas	Choffat [1885, in Sauvage (1897-98)]
Hybodus polyprion	Late Jurassic	Santa Cruz (Torres Vedras)	Sauvage (1897-98)
Strophodus sp.	"*Infravalanginien*"[1]	Brouco	Sauvage (1897-98)
Strophodus sp.	Valanginian	Brouco	Sauvage (1897-98)
Strophodus sp.	Hauterivian	Brouco	Sauvage (1897-98)
Asteracanthus sp.	Toarcian	Fonte Quente limestone quarry	Antunes (1967)
Hybodus lusitanicus	early Kimmeridgian	Guimarota coalmine	Kriwet (1998, 2000, 2004)
Asteracanthus biformatus	early Kimmeridgian	Guimarota coalmine	Kriwet (1995)
Hybodus sp.	Late Jurassic	Guimarota coalmine	Kriwet (2004)
Hybodontoidea indet.	Late Jurassic	Guimarota coalmine	Kriwet (2004)
Hybodus cf. *reticulatus*	Late Jurassic	Peralta	Balbino (2003)
Hybodus cf. *reticulatus*	Late Jurassic	Porto das Barcas	Balbino (2003)
Hybodus lusitanicus	Late Jurassic	Porto das Barcas	Guillaume (2018)

According to Parker (1958): [1]Berriasian.

Mesozoic fossil neopterygians, although much more diverse than hybodonts in the Portuguese record (Table 2), are often not possible to determine on a specific and even generic level, due to their overall poor preservation (Kriwet, 2000). They are mainly represented by isolated or partially articulated scales and teeth, partially to fully articulated bones, namely jaw elements, and sometimes indeterminable bones (*e. g.* Kriwet, 2000; Malafaia et al., 2010), and rare complete, but poorly preserved full-bodied specimens (*e. g.* Callapez et al., 2014).

Choffat [1885, in Sauvage (1897-98)] reported the presence of fossil neopterygians in Portugal, namely: *Pycnodus* sp., from the "*Infravalanginien*" [in Sauvage (1897-98)] of Murches, Brouco, Algueirão, and Mata, from the Valanginian of Mexilhoeira and Algueirão, from the Hauterivian of Mexilhoeira, and from the "*Urgonien*" [in Sauvage (1897-98)] of Belas and Sintra [= "Cintra" in Sauvage (1897-98)]; and '*Lepidotus*' sp. from the Valanginian of Mexilhoeira and "*Urgonien*" of Belas. The most diverse Mesozoic fossil neopterygian material in Portugal was described by Sauvage (1897-98), with the mentioning of the following taxa: (1) *Tetragonolepis* sp., dating the "*Charmouthien*" (= Pliensbachian) and Toarcian (Early Jurassic) of Pentelheira (near S. Pedro de Moel); (2) *Scheenstia laevis* (Agassiz, 1837) [= "*Lepidotus laevis*, Ag." in Sauvage (1897-98)], and '*Lepidotes*' *lusitanicus* Sauvage, 1897 [= "*Lepidotus lusitanicus*" in Sauvage (1897-98)], from the "*Lusitanien*" (= part of Oxfordian and Kimmeridgian, Late Jurassic) [= "Malm inférieur" in Sauvage (1897-98)] of Alcobaça (Leiria); (3) *Macromesodon gigas* (Agassiz, 1832) [= "*Mesodon* aff. *gigas*, Ag." in Sauvage (1897-98)] from the *Lima alternicosta* beds and "*Ptérocérien inférieur*" (= lower Pterocerian) from Santa Cruz, *Eomesodon granulatus* (Münster, 1846) [= "*Mesodon granulatus*, Mstr." in Sauvage (1897-98)] from Cabecinhas mill, in Arrábida (Freixial beds), *Proscinetes hugii* (Agassiz, 1839) [= "*Microdon hugii*, Ag." in Sauvage (1897-98)], and *S. laevis*, the last two from the "*Ptérocérien supérieur*" (= upper Pterocerian), from Santa Cruz. All are dated between Kimmeridgian-Tithonian, Late Jurassic [= "Malm supérieur" in Sauvage (1897-98)]; (4) '*Lepidotus*' sp. and "*Anomoeodus* aff. *complanatus*, Ag." from the Valanginian of Forte da Guia (near Cascais); (5) '*Lepidotus*' sp. from the "*Urgonien*" of Belas; (6) *Mesodon limai* Sauvage, 1898, *Coelodus cuneiformis* Sauvage, 1898, *Coelodus choffati* Sauvage, 1898, *Coelodus delgadoi* Sauvage, 1898, *Coelodus bocagei* Sauvage, 1898, *Clupea* sp., and '*Lepidotus*' sp., dating the "*Bellasien*", from the *Ostrea pseudoafricana* level, Pendão hill, near Belas; (7) *Coelodus ribeiroi* Sauvage, 1898, from the upper Cenomanian of Sargento-Mor; (8) *C. bocagei* and *Anomoeodus woodwardi* Sauvage, 1897, from the upper Cenomanian of Figueira da Foz; (9) "*Mesodon* aff. *ricordeaui*, Svg.", "*Pycnodonte* ind.", *Clupea* sp., *Sardinoides*? sp., *Osmeroides*? sp., '*Lepidotus*'? sp., *Kymatolepis*? sp., and *Berycopsis*? sp. [= *Platycormus*?, in Sauvage (1897-98)], dating the upper Cenomanian (Late Cretaceous) of Alcântara; (10) '*Lepidotus*' sp. from the upper Cenomanian (Late Cretaceous) of the *Ostrea pseudoafricana* level, Pendão hill; (11) *C. bocagei* from the upper Cenomanian of Sargento-Mor; (12) *C. bocagei* dating the upper Cenomanian of the 1st level of *Pterocera incerta* of Nazaré, and the *Ostrea pseudoafricana* level, Pendão hill; (13) *Clupea gomesei* Sauvage, 1897, from the upper Cenomanian of Alcântara; (14) and finally, *Clupea arazedi* Sauvage, 1898, and *Pycnodus* sp., dating the "*Garumnien*" of Vizo (Arazede, Coimbra).

Kriwet (1998) disclosed the ichthyofauna of Guimarota coal mine, Leiria, dating the early Kimmeridgian (Late Jurassic). Part of the material comprised a disarticulated skull of Caturidae indet. [later to be attributed to Amioidea indet. by Kriwet (2005a)], and isolated teeth, jaw, cranial and postcranial elements that were attributed to Semionotiformes ["*Lepidotes*", belonging to Lepisosteiformes, according to López-Arbarello & Sferco (2018)], Pycnodontiformes [Pycnodontidae indet. (cf. *Coelodus* or *Proscinetes*)], Macrosemiidae indet., Ionoscopidae indet., Amiiformes (Amiidae indet.), Pachycormiformes (*Sauropsis*), and Actinopterygii indet. (Kriwet, 1998), all of which, excluding the last, belong to Neopterygii

(López-Arbarello & Sferco, 2018, see Fig. 8; Dobson et al., 2019; Cawley et al., 2021). Kriwet (2000) reported that the clade of fishes that is most common in the Guimarota coal mine is Semionotiformes. However, the former stated that this group, as well as the genus *Lepidotes*, were not monophyletic, and are in great need of revision. Recent studies, however, have been solving the phylogenetic relationships of both *Lepidotes* and its closest relatives (López-Arbarello, 2012). Further material from the Guimarota coal mine was later reported, which was attributed to the pycnodontids *Macromesodon* sp. and *Anomoeodus* sp. (Kriwet, 2002). A fragmentary left prearticular dentition, belonging to Pycnodontiformes indet., dating the Berriasian (Early Cretaceous) of Porto das Barcas, was briefly figured (Kriwet, 2005b, see Fig. 39). An individual *Lepidotes*-like lepisosteiform [= semionotiform, in Malafaia et al. (2010)], from the Andrés quarry, Bombarral Formation, dating the upper? Kimmeridgian-Tithonian [*sensu* Malafaia et al. (2010)], in Pombal, was mentioned, as it is one of the rare occasions of articulated bony fish remains reported from the Portuguese fossil record (Malafaia et al., 2010). Callapez et al. (2014) reported bony fish remains from the Nazaré fossil-site, dating the middle Cenomanian (Late Cretaceous). The referred material was said to belong to *Coelodus* sp., cf. *Enchodus*, and Teleostei indet., with the latter presenting, in one of its specimens, an almost complete individual (Callapez et al., 2014).

With this work, the research regarding the diversity and occurrences of fossil selachians and actinopterygians is continued, and will hopefully add more knowledge to both hybodontiforms and neopterygians of the Upper Jurassic of Portugal, more specifically from Praia Azul (Praia Azul Member, Lourinhã Formation) and Praia de Cambelas (Freixial Formation), Torres Vedras.

Table 2 - List of occurrences of Mesozoic fossil neopterygians previously documented from Portugal.

Taxon	**Age**	**Locality**	**Reference**
Pycnodus sp.	“*Infravalanginien*”[1]	Foraminifera layers of Murches and Brouco; *Cyprina infravalanginiensis* layers of Brouco, Algueirão, and Mata	Choffat [1885, in Sauvage (1897-98)]
Pycnodus sp.	Valanginian	Mexilhoeira and Algueirão	Choffat [1885, in Sauvage (1897-98)]
Pycnodus sp.	Hauterivian	*Ostrea couloni* layers of Mexilhoeira	Choffat [1885, in Sauvage (1897-98)]
Pycnodus sp.	“*Urgonien*”[2]	Belas and Sintra	Choffat [1885, in Sauvage (1897-98)]
‘*Lepidotus*’ sp.	Valanginian	Mexilhoeira	Choffat [1885, in Sauvage (1897-98)]
‘*Lepidotus*’ sp.	“*Urgonien*”[2]	Belas	Choffat [1885, in Sauvage (1897-98)]
Tetragonolepis sp.	“*Charmoutien*”[3]	Pentelheira (near S. Pedro de Moel); *Schlotheimia jamesoni* layers	Sauvage (1897-98)

Tetragonolepis sp.	Toarcian	Pentelheira (near S. Pedro de Moel); *Schlotheimia jamesoni* layers	Sauvage (1897-98)
Scheenstia laevis	“*Lusitanien*”[4]	Alcobaça (Leiria)	Sauvage (1897-98)
‘*Lepidotes*’ lusitanicus	“*Lusitanien*”[4]	Alcobaça (Leiria)	Sauvage (1897-98)
Macromesodon gigas	“*Malm supérieur*”[5]	Santa Cruz	Sauvage (1897-98)
Eomesodon granulatus	“*Malm supérieur*”[5]	Cabecinhas mill, Arrábida (Freixial beds)	Sauvage (1897-98)
Proscinetes hugii	“*Malm supérieur*”[5]	Santa Cruz	Sauvage (1897-98)
Scheenstia laevis	“*Malm supérieur*”[5]	Santa Cruz	Sauvage (1897-98)
‘*Lepidotus*’ sp.	Valanginian	Forte da Guia (near Cascais)	Sauvage (1897-98)
“*Anomoeodus* aff. *complanatus*”	Valanginian	Forte da Guia (near Cascais)	Sauvage (1897-98)
‘*Lepidotus*’ sp.	“*Urgonien*”[2]	Belas	Sauvage (1897-98)
Mesodon limai	“*Bellasien*”[6]	*Ostrea pseudoafricana* level, Pendão hill, near Belas	Sauvage (1897-98)
Coelodus cuneiformis	“*Bellasien*”[6]	*Ostrea pseudoafricana* level, Pendão hill, near Belas	Sauvage (1897-98)
Coelodus choffati	“*Bellasien*”[6]	*Ostrea pseudoafricana* level, Pendão hill, near Belas	Sauvage (1897-98)
Coelodus delgadoi	“*Bellasien*”[6]	*Ostrea pseudoafricana* level, Pendão hill, near Belas	Sauvage (1897-98)
Coelodus bocagei	“*Bellasien*”[6]	*Ostrea pseudoafricana* level, Pendão hill, near Belas	Sauvage (1897-98)
Clupea sp.	“*Bellasien*”[6]	*Ostrea pseudoafricana* level, Pendão hill, near Belas	Sauvage (1897-98)
‘*Lepidotus*’ sp.	“*Bellasien*”[6]	*Ostrea pseudoafricana* level, Pendão hill, near Belas	Sauvage (1897-98)

Coelodus ribeiroi	late Cenomanian	Sargento-Mor	Sauvage (1897-98)
Coelodus bocagei	late Cenomanian	Figueira da Foz and Sargento-Mor	Sauvage (1897-98)
Anomoeodus woodwardi	late Cenomanian	Figueira da Foz	Sauvage (1897-98)
“*Mesodon* aff. *ricordeaui*”	late Cenomanian	Alcântara	Sauvage (1897-98)
Sardinoides? sp.	late Cenomanian	Alcântara	Sauvage (1897-98)
Osmeroides? sp.	late Cenomanian	Alcântara	Sauvage (1897-98)
‘*Lepidotus*’? sp.	late Cenomanian	Alcântara	Sauvage (1897-98)
Kymatolepis? sp.	late Cenomanian	Alcântara	Sauvage (1897-98)
Berycopsis? sp.	late Cenomanian	Alcântara	Sauvage (1897-98)
“*Pycnodonte* ind.”	late Cenomanian	Alcântara	Sauvage (1897-98)
Clupea sp.	late Cenomanian	Alcântara	Sauvage (1897-98)
‘*Lepidotus*’ sp.	late Cenomanian	*Ostrea pseudoafricana* level, Pendão hill, near Belas	Sauvage (1897-98)
Coelodus bocagei	late Cenomanian	Sargento-Mor	Sauvage (1897-98)
Coelodus bocagei	late Cenomanian	1st level of *Pterocera incerta* of Nazaré	Sauvage (1897-98)
Coelodus bocagei	late Cenomanian	*Ostrea pseudoafricana* level, Pendão hill, near Belas	Sauvage (1897-98)
Clupea gomesei	late Cenomanian	Alcântara	Sauvage (1897-98)
Clupea arazedi	“*Garumnien*”[7]	Vizo (Arazede, Coimbra)	Sauvage (1897-98)
Pycnodus sp.	“*Garumnien*”[7]	Vizo (Arazede, Coimbra)	Sauvage (1897-98)
Lepisosteus sp.	Campanian-Maastrichtian	Taveiro (Coimbra)	Antunes & Pais (1978)

Amia sp.	Campanian-Maastrichtian	Taveiro (Coimbra)	Antunes & Pais (1978)
Teleostei indet.	Campanian-Maastrichtian	Taveiro (Coimbra)	Antunes & Pais (1978)
Enchodus sp.	late Campanian	Mira (Coimbra)	Antunes (1979)
Coelodus sp.	late Campanian	Mira (Coimbra)	Antunes (1979)
Pycnodus sp.	late Campanian	Mira (Coimbra)	Antunes (1979)
Clupeiformes indet.	Late Cretaceous	Diapiro de Soure (Coimbra)	Antunes (1979)
Amioidea indet.	early Kimmeridgian	Guimarota coal mine, Leiria	Kriwet (1998)
‘*Lepidotes*’ sp.	early Kimmeridgian	Guimarota coal mine, Leiria	Kriwet (1998)
Pycnodontidae indet. (cf. *Coelodus* or *Proscinetes*)	early Kimmeridgian	Guimarota coal mine, Leiria	Kriwet (1998)
Macrosemiidae indet.	early Kimmeridgian	Guimarota coal mine, Leiria	Kriwet (1998)
Ionoscopidae indet.	early Kimmeridgian	Guimarota coal mine, Leiria	Kriwet (1998)
Amiidae indet.	early Kimmeridgian	Guimarota coal mine, Leiria	Kriwet (1998)
Sauropsis indet.	early Kimmeridgian	Guimarota coal mine, Leiria	Kriwet (1998)
Macromesodon sp.	early Kimmeridgian	Guimarota coal mine, Leiria	Kriwet (2002)
Anomoeodus sp.	early Kimmeridgian	Guimarota coal mine, Leiria	Kriwet (2002)
Pycnodontiformes indet.	Berriasian	Porto das Barcas	Kriwet (2005b)
Lepidotes-like lepisosteiform	late? Kimmeridgian-Tithonian	Andrés quarry, Bombarral Formation, Pombal	Malafaia et al. (2010)
Coelodus sp.	middle Cenomanian	Nazaré fossil-site	Callapez et al. (2014)
cf. *Enchodus*	middle Cenomanian	Nazaré fossil-site	Callapez et al. (2014)

Teleostei indet.	middle Cenomanian	Nazaré fossil-site	Callapez et al. (2014)

According to Parker (1958): ^{1}Berriasian; According to Moureau & Brace (2000): ^{2}lower Barremian to lower Aptian, ^{3}Pliensbachian, ^{4}part of the Oxfordian and the Kimmeridgian, ^{5}Tithonian, ^{6}reef limestone of Cenomanian age, from Belas, Portugal, ^{7}European lacustrine facies in the terminal Cretaceous.

3. Chondrichthyan general anatomy and morphology

Most chondrichthyans swim by the lateral motion of their caudal fins. Others swing their entire posterior region of the body to swim (Cappetta, 1987; Kardong, 2012, 2018). Their many vertebrae are amphicoelus, and the centra have the shape of bobbins (Cappetta, 1987). Male individuals possess a characteristic paired intromittent organ that results from the modification of the pelvic fins, that serves for reproduction - the claspers (Compagno, 1990; Helfman et al., 2009; Kardong, 2012, 2018). Chondrichthyans mate by internal fertilization; display a spiral valve intestine; and their skulls are sutureless (Compagno, 1990; Helfman et al., 2009; Kardong, 2012, 2018). As cartilaginous fish are denser than water, they lack swim bladders and lungs, but use instead their heavily oiled, sometimes very large liver for buoyancy (Compagno, 1990; Helfman et al., 2009; Kardong, 2012, 2018). The development is direct, without any larval stage in between. The fin rays are soft, unsegmented ceratotrichia (Compagno, 1990; Helfman et al., 2009).

3.1 Elasmobranchii

Elasmobranchs, meaning “plate or strap gills”, are a group that compose a set of characteristics that make them unique among chondrichthyans. A notable one is the branchial basket that expands posteriorly, making it lie mostly behind the neurocranium (Cappetta, 1987). The gill arches are spaced between them (Cappetta, 1987; Maisey, 2012). Additionally, the gill pouches have their openings separately to the exterior (Cappetta, 1987; Helfman et al., 2009; Kardong, 2018). The scapulacoracoids are positioned well behind the occiput; the pectoral fins are part of the axial skeleton; their skin is covered with placoid scales (dermal denticles) (Cappetta, 1987; Helfman et al., 2009; Kardong, 2012, 2018); the palatoquadrate (upper jaw) is never fused to the neurocranium, but the first can be supported either by the hyomandibula (hyostylic suspension) or secured to the skull by the palatobasal and otic processes (amphistylic suspension), and this provides a protrusible upper jaw (Cappetta; 1987) (Fig. 3). The dentition is polyphyodont, meaning that throughout their lives the dentition is continuously being replaced, and the teeth are not fused to the jaw cartilages, but instead are embedded in the connective tissue (Cappetta, 1987; Helfman et al., 2009; Kardong, 2012, 2018). The nasal openings are partially divided by a flap and are ventral. The mouth can be ventral, subterminal or terminal (Cappetta, 1987; Helfman et al., 2009).

Specifically concerning sharks, they occupy several habitats in marine environments, and some species are also known to penetrate deeply into tropical and warm-temperate rivers and lakes. However, most modern sharks occur in the oceans worldwide (Compagno, 1990; Helfman et al., 2009; Kardong, 2012, 2018).

Their body shape can vary greatly, depending on the specific environment: (1) pelagic, nectic species present larger pectoral fins, which are much larger than the pelvic fins (Cappetta, 1987); a fusiform, streamlined body with pointy snouts (Cappetta, 1987); powerful caudal fins, normally with a heterocercal format (Cappetta, 1987); more or less high, triangular-shaped dorsal fins (Cappetta, 1987); small-sized anal fins, which in some groups is missing (Squaliformes, Pristiophoriformes) (Cappetta, 1987). For (2) species that live closer to the bottom, their pectoral fins are smaller (Cappetta, 1987); the lower lobe of the caudal fin is reduced and the anal fin is more developed (Cappetta, 1987); normally, sharks present 5 pairs of gill slits (as well as skates and rays), however some species acquire 6 or 7 pairs of gill slits (Hexanchiformes) (Cappetta, 1987; Kardong, 2012, 2018); the dorsal fins are much more posteriorly placed, when compared to pelagic species (Cappetta, 1987); some individuals have developed a flattened body shape (Squatiniformes), making them resemble skates (Cappetta, 1987). In all sharks, the pectoral and pelvic girdles (Fig. 4) are totally independent from the axial skeleton, and the pelvic girdle is rather simple (Cappetta, 1987).

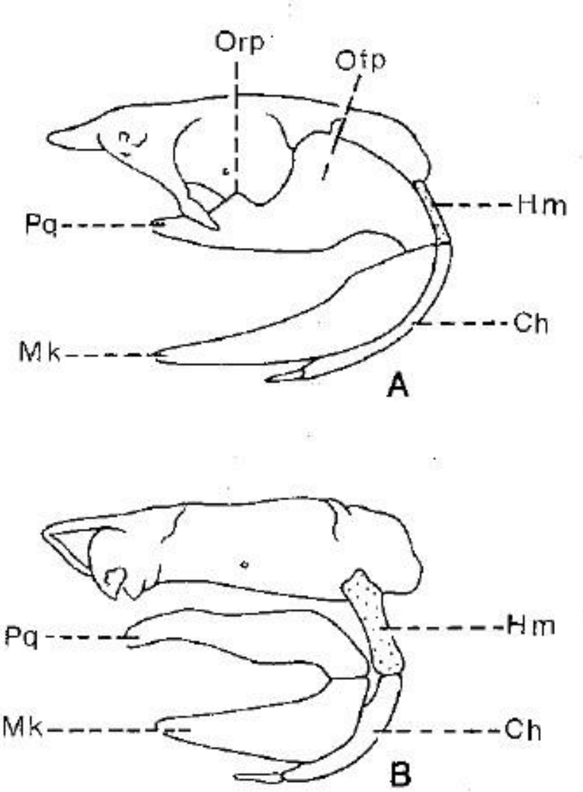


Figure 3 - Jaw (palatoquadrate) suspension in selachians: A, amphistylic (*Hexanchus*); B, hyostylic (*Carcharhinus*). Legend: Pq, palatoquadrate; Mk, Meckel's cartilage; Hm, hyomandibula; Orp, orbital process; Otp, otic process; Ch, ceratohyal. Fig. 6 from Cappetta (1987).

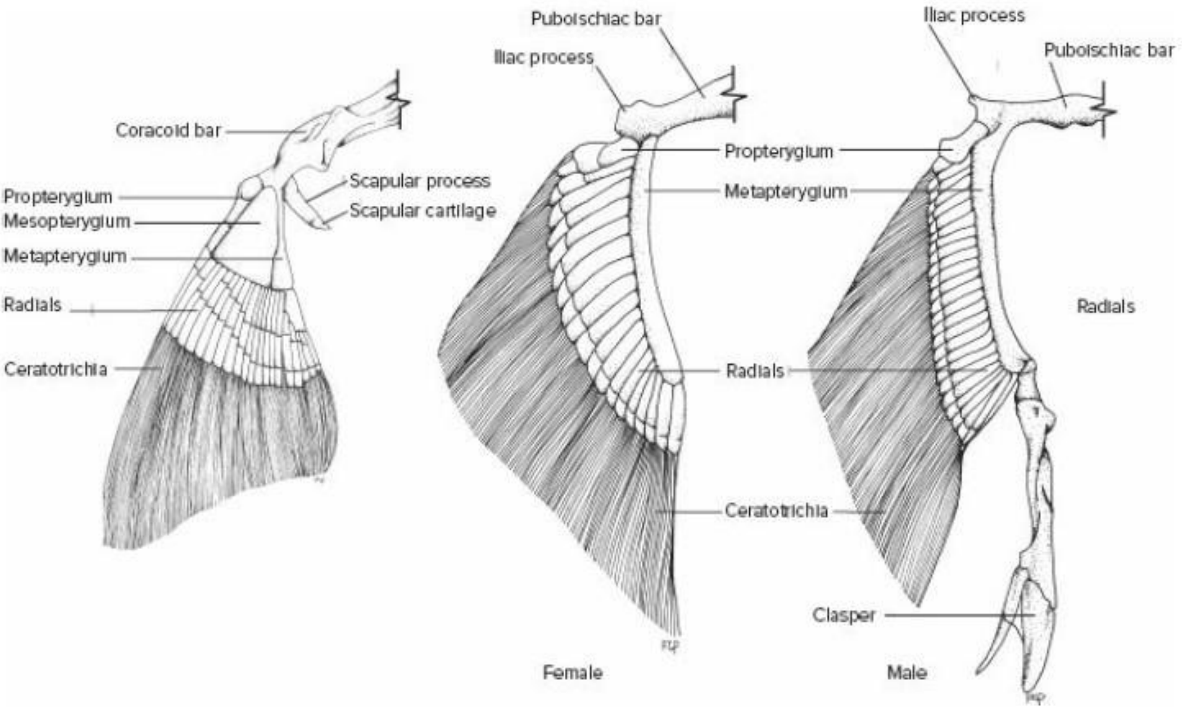


Figure 4 - Pectoral (left) and pelvic fins and girdles (middle and right) of the modern *Squalus* shark, highlighting the appendicular elements. The ceratotrichia are structures composed of keratin that radiate out like vanes in a fan, serving as internal support to the fins of chondrichthyans. Fig. 9.11 from Kardong (2018).

3.2 Euselachii

Euselachians, meaning "true selachians", are a group of elasmobranchs that includes the true sharks, skates and rays. They possess a set of characters that distinguish them from the other shark-like elasmobranchs. Taking into account the Paleozoic euselachians, at least, following Cappetta (1987), such characters include the possession of two dorsal fins, each housing spines of neoselachian morphology, in this case meaning that the spines are covered by a coat of orthodentine (Maisey, 1975; Cappetta, 1987). Zangerl (1981) had considered that Euselachii was a monophyletic group, composed by Ctenacanthoidea, Hybodontoidea, and Neoselachii, due to the fact that there were no other Paleozoic sharks that owned such dorsal fin spines. Thus, the three previously mentioned taxa were grouped together also due to the similarity on the composition of their dorsal fin spines (Cappetta, 1987).

3.3 Hybodontiformes

One of the synapomorphies that sets Hybodontoidea apart from other elasmobranchs, is the abundant presence of cephalic spines (Cappetta, 1987). Other synapomorphies, according to Cappetta (1987), include: the lack of calcified vertebral centra, but possessing calcified neurapophyses, haemapophyses and ribs; occurrence of recurved fin spines with longitudinally-arranged, posteriorly-directed denticles, at both anterior and posterior sides of the spines; the fin spines present a trabecular trunk outer layer, accompanied by a set of anteriorly longitudinal canals; and finally, the spines present an oval shape in cross section. Hybodontiformes also retained a terminal mouth, while neoselachians later evolved the subterminal and ventral mouths (Helfman et al., 2009). Compared to other Paleozoic taxa, hybodonts developed a highly derived heterocercal caudal fin, which increased their maneuverability (Helfman et al., 2009).

3.4 Dental terminology and characters

The terminology and characters used for selachian teeth follows Cappetta (1987). The tooth is composed by a crown, with a more or less sharp tip, *i. e.* the cusp, and a well-developed root on the base (Cappetta, 1987).

The crown is made up of enameloid, and it can be smooth or puckered. The presence of ridges/folds on the enameloid can occur either on the labial face (external) or lingual face (internal) only, or both of them (Cappetta, 1987). The teeth are limited by more or less sharp cutting edges (Cappetta, 1987). The cutting edges in selachian teeth may possess variable morphologies, ranging from different kinds of serrations to being smooth, facilitating the acquisition of diverse diets among the members of that group (Cappetta, 1987). The main cusp can be, or not, accompanied by one or several pairs of more or less developed lateral cusplets, that protrude on each side of the main cusp (Cappetta, 1987). The lateral cusplets can be either smooth or folded (Cappetta, 1987). Only the base of the main cusp may also bear more or less developed vertical folds. The root can possess long, well-separated lobes, or it could possess a flat basal face of cordiform outline (Cappetta, 1987).

3.5 Heterodonty

Numerous selachian taxa present heterodonty (except some particular families, such as Rhincodontidae and Cetorhinidae, that have secondary homodonty; homodonty = teeth with the same morphology) (Cappetta, 1987).

Following Cappetta (1987), there are three types of heterodonty: the monognathic type, in which the teeth in one jaw have different morphologies; the dignathic type (Fig. 5), where the teeth in the upper and lower jaw have different morphologies; and the gynandric type (Fig. 6), in which the differences in teeth are related to sexual dimorphism. The most common type is dignathic heterodonty (Cappetta, 1987).

One of these types of heterodonty can occur in a species, or even both of them at the same time, as seen in Hexanchidae (Cappetta, 1987). This morphological differentiation of the teeth is a great problematic when attempting to classify fossil taxa, as the teeth under study may not belong to a new species, but rather belong to a different position of the jaw of an already known species (Cappetta, 1987). In addition to that, young selachians normally present a different set of teeth, as their prey items differ from those during adulthood. These are the main reasons why there are so many fossil “species” of selachians (Cappetta, 1987).

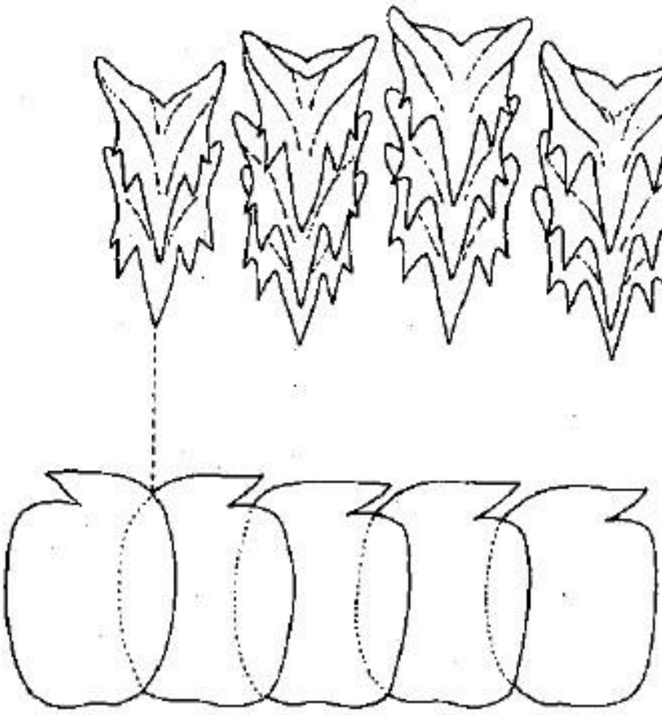


Figure 5 - Dignathic heterodonty for the species *Etmopterus hillianus*. Fig. 17 from Cappetta (1987).

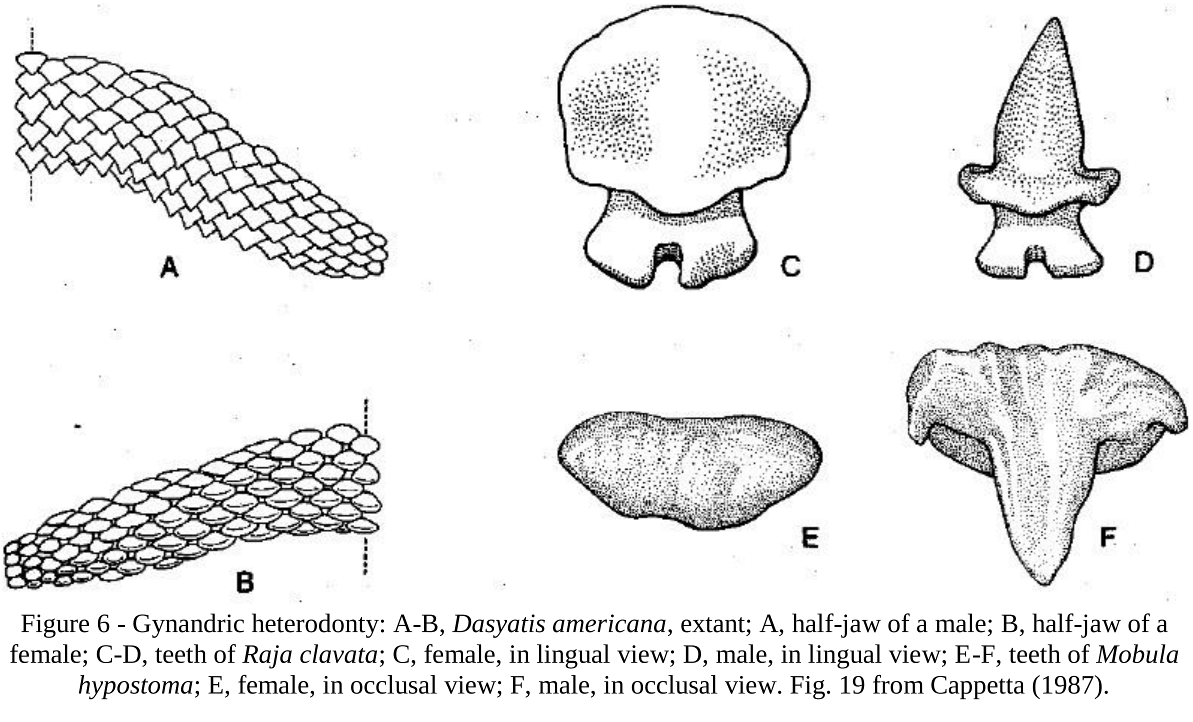


Figure 6 - Gynandric heterodonty: A-B, *Dasyatis americana*, extant; A, half-jaw of a male; B, half-jaw of a female; C-D, teeth of *Raja clavata*; C, female, in lingual view; D, male, in lingual view; E-F, teeth of *Mobula hypostoma*; E, female, in occlusal view; F, male, in occlusal view. Fig. 19 from Cappetta (1987).

3.6 Crown vs Root

The crown-root junction morphology constitutes another important morphological aspect considered in fossil selachian taxonomy (Cappetta, 1987). The crown is much more susceptible to homoplasy, since distinct phyletic taxa might develop similar crown shapes to deal with similar kinds of prey in a given environment – an example of convergent evolution (Cappetta, 1987). It is because of the external similarities between the teeth of fossil and recent taxa that lead to believe that many fossil teeth belonged to modern selachian genera, which now proves to be faulty (Cappetta, 1987). The root, on the other hand, is less susceptible to homoplasy, and therefore it can be used more accurately in teeth identification.

Casier (1947a, b, c) studied and defined four structural stages of the root, based on the evolution of the vascularization of the root and the disposition of the foramina: the anaulacorhize, hemi- and holaulacorhize, and polyaulacorhize stages (Fig. 7).

The anaulacorhize stage is characteristic of more primitive taxa, such as Hybodontiformes, and in modern forms, exclusively within Hexanchiformes; the hemi- and holaulacorhize stages occur from Jurassic neoselachians (*i. e.* sharks and rays) to the present day; and the polyaulacorhize stage appears on the most derived batoids (Myliobatoidea and Mobuloidea) (Cappetta, 1987).

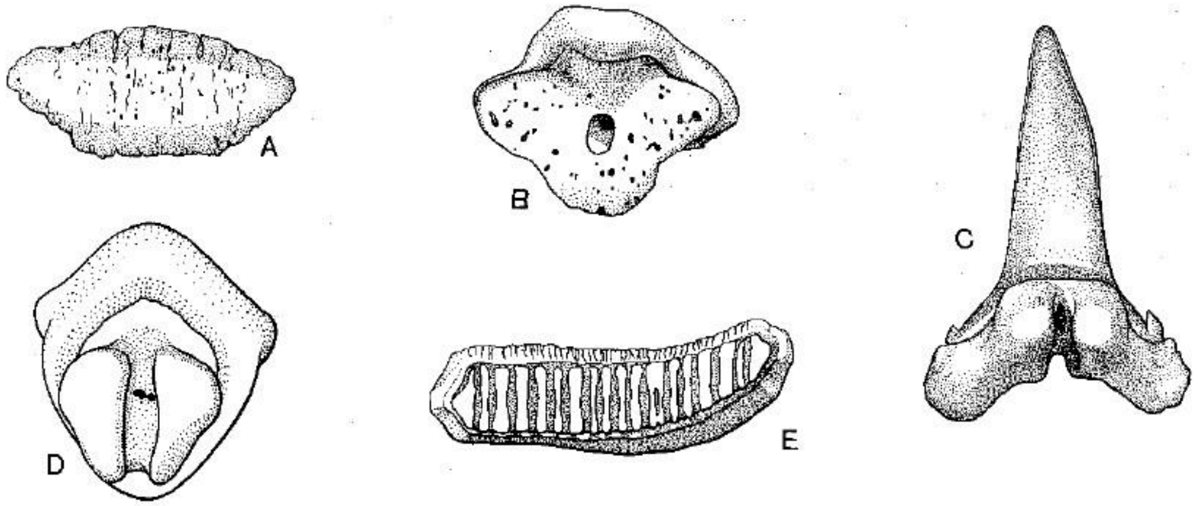


Figure 7 - Root vascularization stages in selachians: A, anaulacorhize stage (*Sphenodus*); B, hemiaulacorhize stage (*Nebrius*); C, holaulacorhize stage (*Chaenogaleus*); D, holaulacorhize stage (*Raja*); E, polyaulacorhize stage (*Igdabatis*). Fig. 21 from Cappetta (1987).

4. Actinopterygian general anatomy and morphology

The ray-finned fishes are grouped together according to some general morphological features, that serve to support this group's monophyly. These characters are the unique arrangement of their scales (Diogo, 2007); the presence of one single dorsal fin (Diogo, 2007); the enlargement of the basal elements of the pectoral fin (Diogo, 2007); and, finally, the interlocking mechanism (Diogo, 2007). Actinopterygians are commonly called "ray-finned" fishes, due to the uniqueness of their fins.

Similar to cartilaginous fishes, bony fish are denser than water. To solve this problem, most bony fishes possess a gas-filled swim bladder to achieve neutral buoyancy (Kardong, 2012, 2018). The amount of gas that fills the swim bladder varies depending whether the animal needs to swim up or down the water column (Kardong, 2018).

4.1 Neopterygii

Neopterygians have attained a set of morphological and anatomical features that gave them the upper hand against their competition. (Kardong, 2012, 2018). The morphological traits that helped neopterygians acquire crucial advantages over their counterparts can be analyzed in their external bodies and skeletons (Kardong, 2012, 2018). For instance, their skulls have been evolving in a trend of acquiring additional attachment sites for feeding muscles, thus increasing jaw mobility and feeding efficiency (Kardong, 2012, 2018). Furthermore, their upper jawbones are fused in the midline and possess well-developed pharyngeal tooth plates, well-suited for grinding up food (Long, 2011). Scales became thinner and rounder, which granted neopterygians more mobility, flexibility and maneuverability (Kardong, 2018). Probably as a result of the reduced surface scalation, neopterygians developed faster swimming (Kardong, 2018). A homocercal tail promoted a faster swimming capability, as well as the increasingly calcified vertebrae, that were replacing the notochord (Kardong, 2018). Additionally, the presence of an ossified symplectic and the rays in both dorsal and anal fins got equal in number to the endoskeletal supports (Diogo, 2007; Long, 2011).

4.2 Fins

Their fins possess numerous slender, endoskeletal rays, called lepidotrichia (Fig. 8), that serve to support the fins internally (Kardong, 2012, 2018). These fish can control their fin movements, and the muscles to do so are located within the body wall (Kardong, 2018).

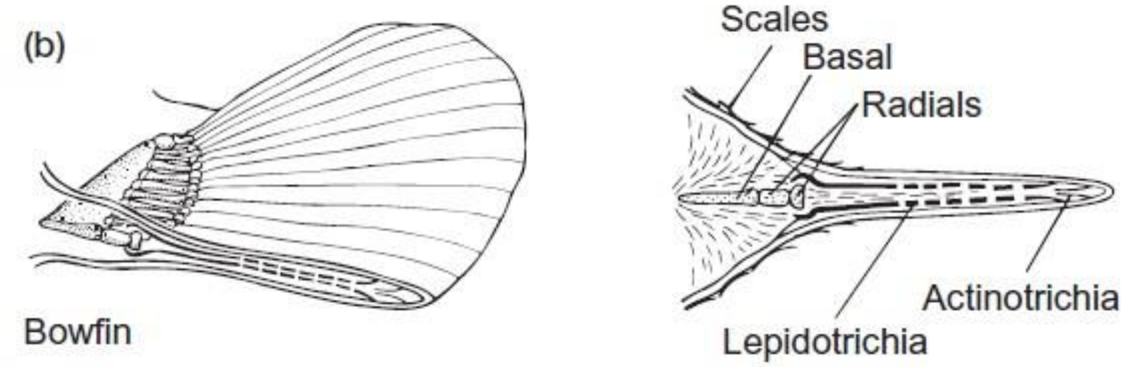


Figure 8 - Fin rays in a bowfin. (b), Lepidotrichia can be cartilaginous or ossified, providing support within fins of actinopterygians. Modified Fig. 9.1 from Kardong (2012).

4.3 Scales

Bony fishes in general have evolved different scale morphologies. The recognized types of scales are: the cosmoid scale [Fig. 9, (a)], which has a thick, well-develpod layer of dentin (cosmine) beneath a thinner layer of enamel (seen in basal sarcopterygians) (Kardong, 2018); the ganoid scale [Fig. 9, (b)], which is shiny, overlapping and interlocking, and presents a thick surface coat of enamel (ganoin), with no layer of dentin beneath (seen especially in modern polypteriforms, gars, palaeoniscoids) (Kardong, 2018); and the elasmoid scale [Fig. 9, (c)], which is divided in (1) cycloid scale [Fig. 9, (d)] and (2) ctenoid scale (Fig.

9, (d)]. Both of these types lack enamel, dentin, and vascular bone layer, and only lamellar bone is present, which is acellular and practically non-calcified (Kardong, 2018).

The (1) cycloid scale is composed of several concentric rings, also called circuli, that are laid down when the teleost fish is growing, similar to the growth rings of a tree; and the (2) ctenoid scale has a fringe of projections allocated along the posterior margin of the scale (Kardong, 2018).

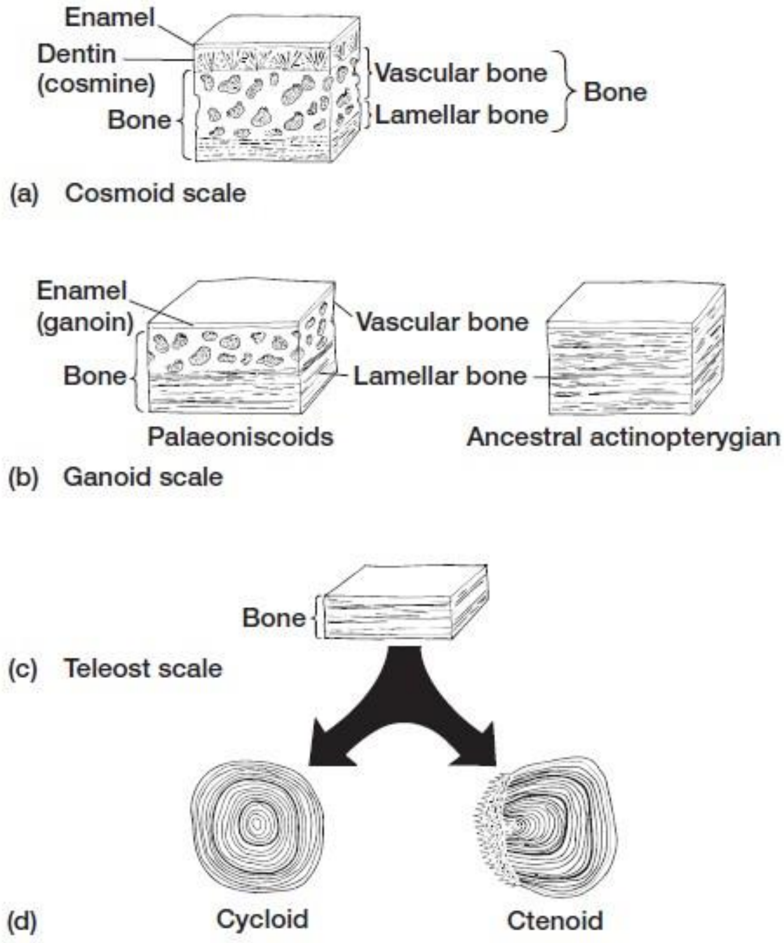


Figure 9 - Scale types in bony fishes, showing a cosmoid scale(a), ganoid scale (b), and a teleost scale (c), divided into cycloid and ctenoid scales (d), both of which are in surface view. Fig. 6.11 from Kardong (2018).

4.4 Dentition

Actinopterygians have developed a wide range of different dental types. They can either possess a unique kind of dentition, or a mixture of some (Helfman et al., 2009). The dental morphologies and types in species can differ greatly even within families (Helfman et al., 2009). For the case of piscivores and other soft-bodied prey eaters, such as squid, and following the concept of Helfman et al. (2009), they can display five basic patterns of oral (= jaw) teeth:

1. Long, slender, sharp teeth, useful to grab hold slippery prey (seen in moray eels, deep-sea viperfishes, lancetfishes, anglerfishes, goosefishes). In some groups, such as goosefishes, anglerfishes, and esocid pikes, there is even repeated elongated dentition

along the palatine or vomerine bones. These latter teeth are often pointed backwards, so that prey are moved towards the throat of the predator, preventing it to escape;

2. Villiform teeth, characterized for being numerous, small and needle-like, occur in surface-dwelling, elongate predators, such as gars and needlefishes, and also occur in benthic species, like lizardfishes and lionfishes;
3. Flat-bladed, pointed, triangular teeth, useful to cut through prey, as seen in piranhas, barracudas, and large Spanish mackerels;
4. Recurved, conical, large caniniform teeth, with sharp points, very practical for grasping and holding prey, well-suited for species such as Bowfin, snappers, cod, and some seabasses, all of which are piscivores;
5. Cardiform teeth, presenting a rough sandpaper texture and consisting various, short, fine, pointed teeth, arranged as in a wool card, as seen in large seabasses, Largemouth Bass, snook, and billfishes.

As for the fishes that prey on hard-bodied prey, including crustaceans, echinoderms, and mollusks, they display strong, conical teeth, especially on the anterior part of the mouth, to pluck mollusks from surfaces (Helfman et al., 2009). Moving posteriorly from the tip of the mouth, the teeth become flat and round. These durophagous, molariform teeth are located posteriorly in marginal or pharyngeal jaws (Helfman et al., 2009).

Pharyngeal teeth can also be present, and are especially well-developed in teleostean neopterygians, such as cichlids, parrotfishes, minnows, and suckers (Helfman et al., 2009).

4.5 Vertebrae

The vertebrae are divided, normally, into precaudal and caudal vertebrae (Fig. 10; Helfman et al., 2009). The precaudal vertebrae are positioned anteriorly and extend posteriorly to the end of the body and bearing ribs; the caudal vertebrae are positioned posteriorly, beginning with the first vertebra that holds an elongate haemal spine. This haemal spine surrounds the haemal canal through which the caudal artery enters (Helfman et al., 2009).

Vertebrae may possess various types of bony elements the project from the centrum. To enumerate some, there is: the neural spine, that projects dorsally, housing the neural arch, through which the spinal cord passes (Helfman et al., 2009); the parapophyses, that sits ventrally and extends ventrolaterally, to which the ribs attach (Helfman et al., 2009); the haemal canal, to which the dorsal aorta (the main artery of the body) enters, via the precaudal vertebrae (Helfman et al., 2009); the neural prezygapophyses and postzygapophyses, that sit dorsolaterally on the margins of the vertebrae, and the haemal prezygapophyses and postzygapophyses, that sit on the ventrolateral margins (Helfman et al. 2009).

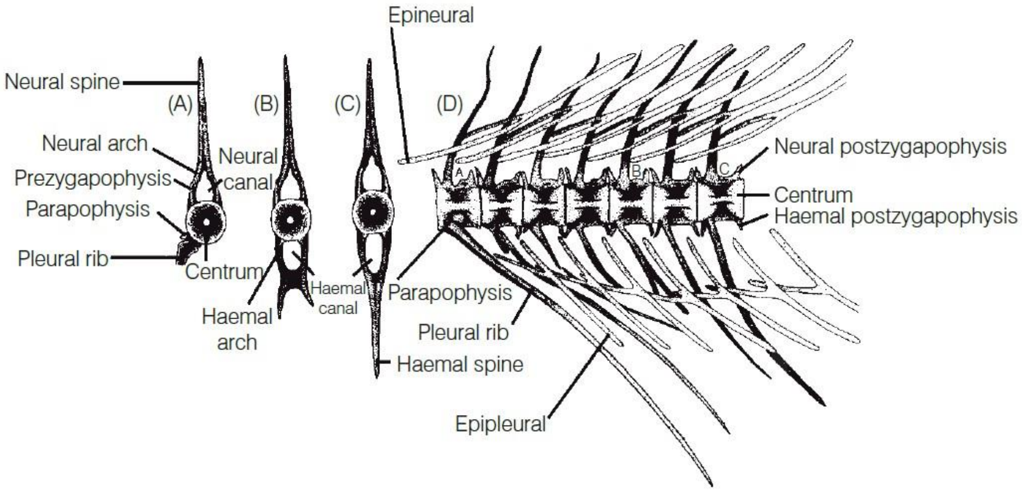


Figure 10 - Precaudal and caudal vertebrae of a characin (*Brycon meeki*). (A), anterior view of the 20th precaudal vertebra; (B), anterior view of the 24th precaudal vertebra; (C), anterior view of the 2nd caudal vertebra; (D), lateral view of the succession from 20th precaudal through the 2nd caudal vertebrae. Figure 3.13 from Helfman et al. (2009).

5. Geological and stratigraphic framework

The Lusitanian Basin stretches in the central-western section of Portugal, which represents the largest Basin in the country (Kullberg et al., 2006; Martinius & Gowland, 2010; Taylor et al., 2013). The basin extends approximately 200 km in a NNW-SSE direction, and more than 70 km E-W, even extending offshore (Fig. 11), with a combined area of about 22 000 km^2 (Kullberg et al., 2006; Martinius & Gowland, 2010; Taylor et al., 2013). The eastern boundary of the Lusitanian Basin is marked by Hercynian basement rocks of the Iberian Meseta, and the western boundary is delimited by a structural relief, the Berlenga *horst* (Hill, 1989a; Kullberg et al., 2006), which constitutes fault-bounded blocks that form the Berlenga and Farilhões Islands (Hill, 1989a). The deposits range from Upper Triassic (probably Carnian) to upper Lower Cretaceous (upper Aptian) in age (Leinfelder, 1987; Hill, 1989a; Kullberg et al., 2006; Mateus, Dinis, & Cunha, 2013). Starting from the early Mesozoic (Late Triassic), the area of the Lusitanian Basin was involved in the formation of the North Atlantic Ocean by crustal extension (Leinfelder, 1987; Kullberg et al., 2006; Taylor et al., 2013).

The events that played the biggest role in the genesis of the Lusitanian Basin were episodes of premature transitional tectonic inversion and diapirism (Kullberg et al., 2006), that were responsible by paleotopography and increased the complexity of the lithostratigraphy. Additionally, these processes were accompanied by smaller scale events, such as the contemporaneous magmatism and volcanism (Kullberg et al., 2006). Generally, its development was made in a divergent regime, due to the opening of the North Atlantic Ocean (Kullberg et al., 2006). The basin is, nowadays, characterized as a fault-bounded half-graben to graben structure (Leinfelder, 1987; Kullberg et al., 2006), separated into three distinct sectors, the northern, central and southern Lusitanian Basin, due to reactivated late major Hercynian faults that follow a NE-SW trend (Nazaré and Tagus faults) (Leinfelder, 1987; Kullberg et al., 2006; Schneider, Fürsich, & Werner, 2009; Martinius & Gowland, 2010), and characterized by several sub-basins.

The Lusitanian Basin witnessed major rifting episodes. Some authors consider a total of three, others consider four (Kullberg et al., 2006; Martinius & Gowland, 2010). Here in this work, it will be considered four, as proposed by Kullberg, Mouterde, and Rocha (1997), Kullberg (2000), Kullberg et al. (2006), Rasmussen et al. (1998), Alves et al. (2002), Martinius & Gowland (2010), and Taylor et al. (2013). The fill of the Lusitanian Basin registers a major phase of sea-floor spreading, linked to the opening of the North Atlantic Ocean (Kullberg et al., 2006; Martinius & Gowland, 2010; Taylor et al., 2013), and four rifting episodes, each being characterized by a particular set of sediments, rate of subsidence and tectonic activity, which spanned from the Late Triassic to late Early Cretaceous (Martinius & Gowland, 2010; Taylor et al., 2013).

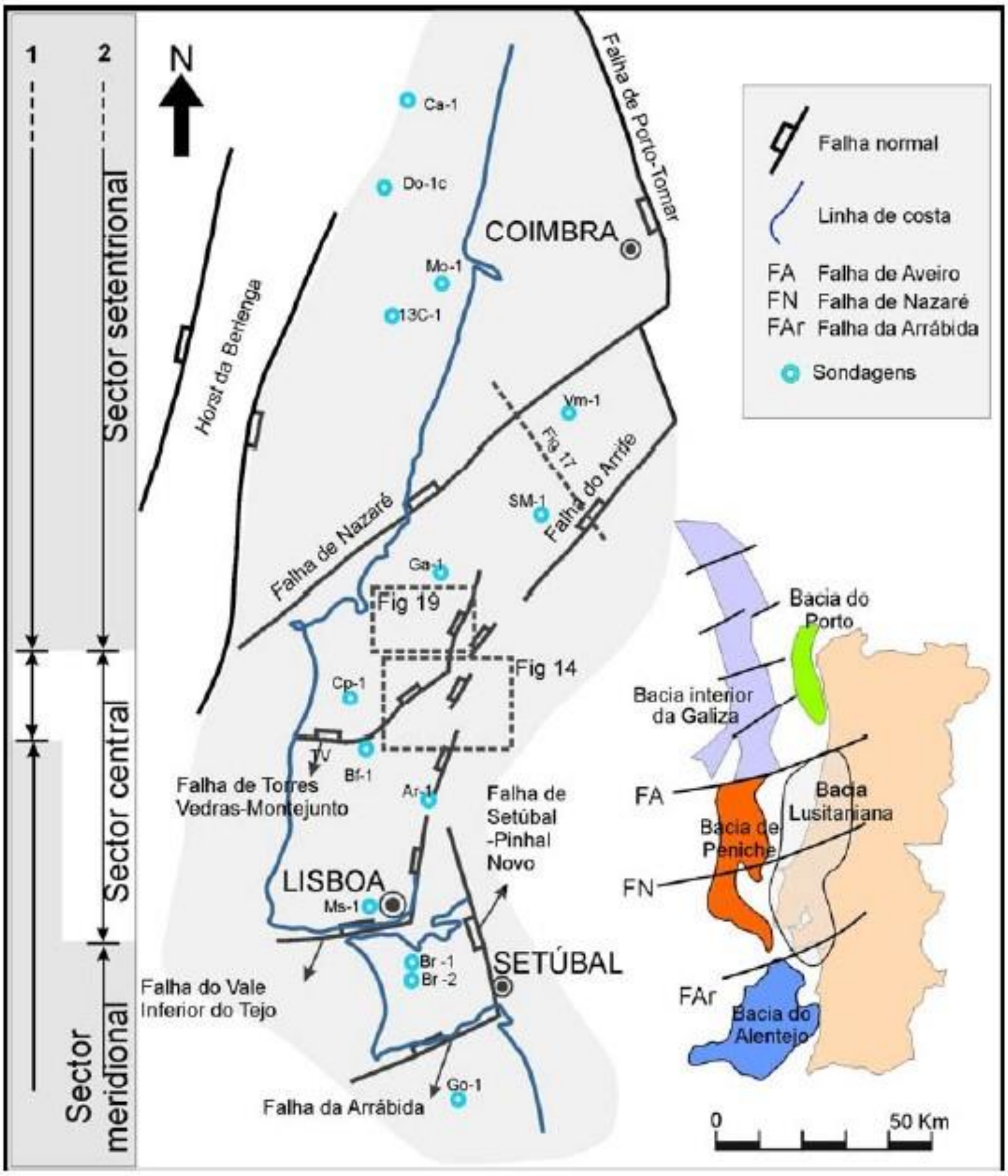


Figure 11 - Geographical and tectonic framework of the Lusitanian Basin, as well as other basins from the Western Iberian Margin. Probes: Ca - Carapau, Do - Dourada, Mo - Moreia, Vm - Vermoil, Sm - S. Mamede, Ga - Gaiteiros, Cp - Campelos, Ar - Arruda, Ms - Monsanto, Br - Barreiro, Go - Golfinho. Fig. 1 from Kullberg et al. (2006).

5.1 Lithostratigraphical definitions and proposals

The definition, nomenclature and composition of the different geological units of the Lusitanian Basin have been changing throughout the decades (Table 3). Different authors have presented conflicting interpretations, and no fully accepted proposal of lithostratigraphic division exists, resulting in synonyms or different correspondences of specific geological units (Leinfelder, 1987; Kullberg et al., 2006; Mateus et al., 2013). A detailed analysis of this basin is arduous and confusing also due to the lack of reliable biostratigraphic markers, and to the great differentiation in the development of facies, which resulted from the different sedimentation patterns (Leinfelder, 1987; Schneider et al., 2009; Taylor et al., 2013). Additionally, the existing literature mixes lithostratigraphic and biostratigraphic terminology (Wilson, 1979). This was a result from the wide variety of facies of the Lusitanian Basin in general, and maybe from the similarly wide variety of nationalities of geologists that have studied this area (Wilson, 1979; Leinfelder, 1987; Schneider et al., 2009; Taylor et al., 2013).

Most of the literature assumes that there are at least three Sub-basins within the central-western section of the Lusitanian Basin, all confined by the Fault of Torres Vedras-Montejunto (FTVM): Arruda, Bombarral-Alcobaça, and Turcifal (Alves et al., 2003; Martinius & Gowland, 2010; Mateus et al., 2013; Taylor et al., 2013). More recently, it has been added a fourth Sub-basin, initially suggested by Taylor et al. (2013), the Consolação Sub-basin, among the other three. Afterwards, some authors began considering and mentioning four Sub-basins within the central section of the Lusitanian Basin, instead of just three, for instance Malafaia et al. (2018) and Castanera et al. (2020a, 2020b). Martinius & Gowland (2010), however, have only mentioned the Consolação Sub-basin, but did not integrate the latter with the three other known Sub-basins. Even a fifth one, named Lower Tagus Sub-basin, was proposed by Mateus et al. (2013) to join the previously mentioned four. Mocho, Royo-Torres, and Ortega (2017) proposed the joining of the Bombarral-Alcobaça and Consolação Sub-basins to form the Bombarral Sub-basin. Kullberg et al. (2006) and Schneider et al. (2009) also consider the Bombarral Sub-basin, instead of Bombarral-Alcobaça Sub-basin.

The Freixial Formation belongs to the Turcifal Sub-Basin (Kullberg et al., 2006; Castanera et al., 2020a, 2020b). It was described in detail as a geological Formation by Leinfelder (1986). However, it was previously known as “Freixialien”, according to Choffat [1901, in Mouterde et al., (1972)], and as the Freixial beds, sitting within the Farta Pão Formation, following Leinfelder (1993). It was also considered as the Lourinhã Formation *pars* Leinfelder & Wilson (1989). Schneider et al. (2009) admitted this geological site as a Member, thus being the Freixial Member, whose outcrops were limited to the southern Arruda Sub-Basin.

The Praia Azul Member in encompassed within the Lourinhã Formation [following Hill (1989b)]. It was first described by Fürsich (1981) and named as Praia Azul Member by Hill (1989b). It was previously mentioned as: Porto das Barcas Member according to Martinius & Gowland (2010) (= Porto de Barcas Member) and Taylor et al. (2013) (= misspelled Porto de Barças), both being part of the Lourinhã Formation. It also corresponds to the Sobral unit according to Manuppella et al. (1999). Additionally, it corresponds to the Arranhó I Member and part of the Arranhó II Member, to the south, both within the Farta Pão Formation, according to Schneider et al. (2009). In Zbyszewski, Almeida, and Assunção (1955), Praia Azul is not highlighted, but instead Praia da Areia ou Formosa is, in the same area.

In this work, the geological site of Praia Azul will be considered as Praia Azul Member, being part of the Lourinhã Formation [following Hill (1989b)], and the Cambelas fossil site (Praia de Cambelas) will be considered as part of the Freixial Formation, which is included in the Turcifal Sub-Basin [the same case for the Praia Azul Member; according to Kullberg et al. (2006)].

Table 3 - List of different lithostratigraphical definitions and proposals of different geological units of the Lusitanian Basin of Portugal.

Geological objects	Definition	Reference
Lusitanian Basin (central-western section)	Composed by: Arruda, Bombarral-Alcobaça, and Turcifal Sub-basins	Alves et al. (2003), Martinius & Gowland (2010), Mateus et al. (2013)
	Composed by: Arruda, Bombarral-Alcobaça, Turcifal Sub-basins, with the addition of a fourth Consolação Sub-basin	Taylor et al. (2013), Malafaia et al. (2018), Castanera et al. (2020a, 2020b)
	Composed by: Arruda, Bombarral-Alcobaça, Turcifal, Consolação Sub-basins, with the addition of a fifth Lower Tagus Sub-basin	Mateus et al. (2013)
	Bombarral Sub-basin unified, instead of Bombarral-Alcobaça Sub-basin	Kullberg et al. (2006), Schneider et al. (2009), Mocho et al., (2017)
Freixial Formation	“Freixialien”	Choffat [1901, in Mouterde et al., (1972)]
	Lourinhã Formation	Leinfelder & Wilson (1989)
	Freixial beds, sitting within the Farta Pão Formation	Leinfelder (1993)
	Within the Turcifal Sub-basin	Kullberg et al. (2006), Castanera et al. (2020a, 2020b)
	Freixial Member, whose outcrops were limited to the southern Arruda Sub-Basin.	Schneider et al. (2009)
Praia Azul Member	Within the Lourinhã Formation	Hill (1989b)
	Sobral unit	Manuppella et al. (1999)
	Arranhó I Member and part of the Arranhó II Member, to the south, both within the Farta Pão Formation	Schneider et al. (2009)
	Porto das Barcas Member, part of the Lourinhã Formation	Martinius & Gowland (2010), Taylor et al. (2013)
Cambelas fossil site	Part of the Freixial Formation, which is included in the Turcifal Sub-basin	Kullberg et al. (2006)

5.2 Praia Azul Member

The Praia Azul Member lies directly above the Praia da Amoreira-Porto Novo Member. It crops out South to Praia da Areia Branca syncline near Santa Cruz, and from Porto Dinheiro to Paimogo localities (Taylor et al., 2013). Additionally, in a northward direction, in respect to the Praia da Areia Branca syncline, the Praia Azul Member crops out in Vale Frades and Vale Pombas localities (Taylor et al., 2013).

This unit is characterized mainly by meandering fluvial channels and calcrete-bearing paleosoils, composed of 75 to 88% of marls and mudstones (Taylor et al., 2013; Mateus et al., 2013), and rare occurrences of sandstones (around between 12 and 25% of sand, although the percentage rises from south to north), with some displaying abundant carbonaceous material (Taylor et al., 2013; Mateus et al., 2013), defined by brackish-marine bay-fill sediments, with numerous occurrences of shell-bearing organisms (Taylor et al., 2013; Mateus 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 thickness of this Member is about 110-123 m (Taylor et al., 2013). Its base is defined by an initial transgressive surface, that overlies the first shelly unit (Taylor et al., 2013) and its upper boundary is delimited on the top of the third and final unit that contains various shell remains (Martinius & 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 & Gowland, 2010; Taylor et al., 2013; Mateus et al., 2013). The meandering deposits, frequently containing abundant carbonaceous material, are especially noted on the base of the member, while the rarer, thin sandy layers are attributed to mouth-bars and sandy bay shorelines, than can be found locally (Martinius & Gowland, 2010; Taylor et al., 2013). Carbonates are very rare in this Member, and they are confined by very thin sections of shelly micrite, with variable concentrations of quartz sand (Fürsich, 1981). Large amounts of plant matter, such as wood from trees and lignitic debris, also occur, suggesting that in some parts there was dense vegetation (Fürsich, 1981).

Overall, the sections of Praia Azul Member characterize a change from fluvial or floodplain environments to marginal marine or brackish bays, sometimes very shallow. In some sections, the possible lagoonal deposits, with deltaic influence, occur (Fürsich, 1981). If these lagoons existed, being possibly separated physically by barrier islands, and being influenced by river and marine waters, then the environment would be subjectable to great salinity fluctuations. Therefore, it would reflect the specific structure of benthic faunas that lived there (Fürsich, 1981).

Although reliable biostratigraphic markers are generally scarce, the age of Praia Azul Member has been attributed from uppermost Kimmeridgian to lowermost Tithonian (Schneider et al., 2009; Mateus et al., 2013). Fürsich (1981) has dated the deposits from this Member as upper Kimmeridgian (*sensu gallico*) to lower Tithonian, based on the presence of the ostracod *Cetacella armata* Martin, 1958, present in the middle of the unit. Based on the combination of shelly biota, spores, dinocysts, algae, foraminifera, and ostracods, Taylor et al. (2013) has given the age of uppermost Kimmeridgian to lowermost Tithonian to this unit. Overall, the Praia Azul Member possesses a decent biostratigraphical content, with the most diverse assemblages being associated with the shelly associations (Taylor et al., 2013).

The shell-rich sections of the Praia Azul Member comprise sandy bioclastic limestones, micritic limestones and laminated mudstones with high organic content (Taylor et al., 2013). Shelled species that can be found plenty in this Member are: *Isognomon lusitanicum* Solander, 1768; *Liostrea* sp., *Praeexogyra pustulosa* (Sharpe, 1850); *Eomiodon securiformis* (Sharpe, 1850); *Nanogyra (Nanogyra) nana* (Sowerby, 1822) (= *Nanogyra nana*, *sensu* Taylor et al., 2013); *Myophorella (Myophorella) lusitanica* (Sharpe, 1900) (= *Myophorella lusitanica*, *sensu* Taylor et al., 2013); *Jurassicorbula edwardi* (Sharpe, 1850); and *Juranomia calcibyssata* Fürsich & Werner, 1989 (= *Placunopsis suprajurensis*, *sensu* Taylor et al., 2013). Dinocysts, spores, algae, ostracods and foraminifera are also dominant and very diverse in this unit (Taylor et al., 2013). Additionally, algal material, echinoid spines, serpulids and rare terebratulid brachiopods can be found too (Taylor et al., 2013).

The stratigraphic log presented herein (Fig. 12) represents the studied locality near Praia Azul, Torres Vedras, (part of Praia Azul Member) where the excavations and prospection took place. The observed column is approximately 9 m thick, and it is composed entirely of siliciclastic sediments. The observed layers can be divided as follows:

- Massive sandstone bed - 70 cm;
- Conglomerate bed - 20 cm;
- Sandstone bed with load casts at the base of the bed, transitioning into ripple cross-bedding - 60 cm;
- Sandstone bed containing gravel-sized grains and plant material, with erosional surface at the top - 30 cm;
- Siltstone bed containing vertebrate fossil remains - 1 m;
- Mudstone bed with horizontal lamination, containing horizontal burrows and bivalve shells at the top - 1,80 m;
- Massive siltstone bed - 75 cm;
- Horizontally laminated mudstone bed - 1 m;
- Bed of thinning upwards sequence composed of siltstone and mudstone - 1 m;
- Bed of thinning upwards sequence composed of siltstone and mudstone - 1,80 m.

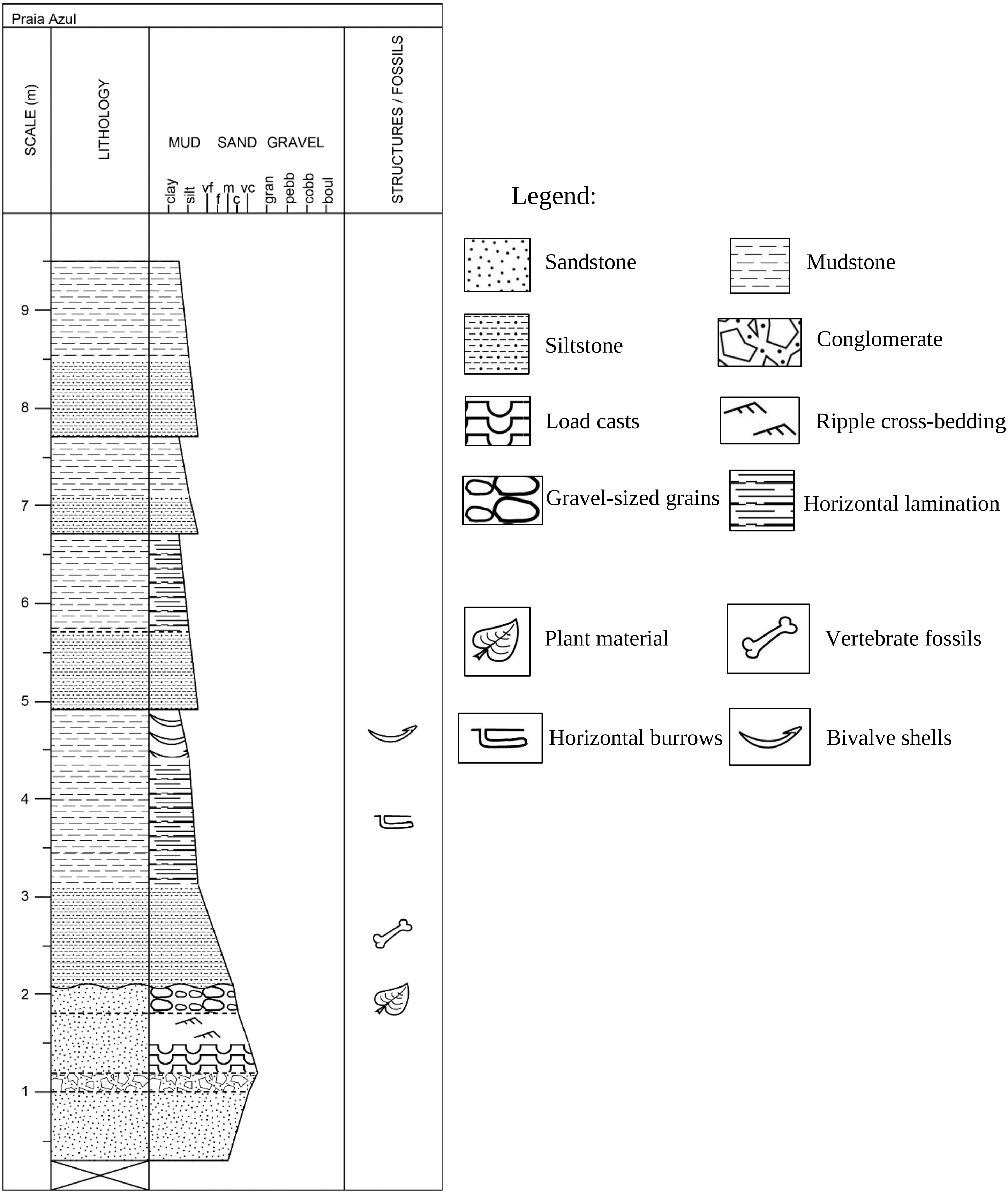


Figure 12 - Stratigraphic column of the studied locality near Praia Azul, Torres Vedras (part of Praia Azul Member)

5.3 Freixial Formation (Cambelas fossil site)

The Freixial Formation is not well-defined, mostly due to the poor observational conditions that do not allow good visibility of the outcrops (Kullberg et al., 2006). However, it is known that it represents an interchange between limestones, marls, and siliciclastic material (Leinfelder, 1993; Kullberg et al., 2006; Schneider et al., 2009), overlapping southwards the Arranhó unit (Leinfelder, 1993; Kullberg et al., 2006). In this specific site, the bivalve *Trigonia freixialensis* Choffat, 1885, is common, and it indicates the Tithonian age (Kullberg et al., 2006; Schneider et al., 2009). The depositional environment corresponds to a shallow marine slope, deepening towards the south, with water of mixed salinity (Leinfelder, 1993; Kullberg et al., 2006). The red terrestrial siliciclastic material shows various (at least three) episodes of progradation from North and Northwest to South (Leinfelder, 1993; Kullberg et al., 2006). However, it is not clear, in the field, the interdigitation between this unit and the Lourinhã Formation admitted by Leinfelder (1993) (Kullberg et al., 2006).

Within the Freixial Formation, lies the Cambelas fossil site, which corresponds to Praia de Cambelas. The Cambelas fossil site consists of strata representing a sequence of thick red mudstones with numerous levels of well-developed caliche, intercalated by cross-bedded sandstones (Leinfelder, 1993; Kullberg et al., 2006; Malafaia et al., 2018). In the area of Cambelas, the Freixial Formation is interpreted as possessing deposits of coastal delta plains and distal fluvial environments (Hill, 1989b).

The age of the Cambelas fossil site was interpreted based on foraminifera and dasycladaceans, and it was dated as upper Tithonian (Leinfelder, 1993; Kullberg et al., 2006; Schneider et al., 2009).

6. Material and Methods

The fossil material discussed in this work was collected by José Joaquim dos Santos, a local collector. On one hand, the shark specimens were collected in the marine deposits of the top layers of Praia Azul (marked with a red rectangle in Fig. 13) (Praia Azul Member, Lourinhã Formation), in Santa Cruz, Torres Vedras. On the other hand, the neopterygian specimens were collected in the marine deposits of both the Cambelas fossil site, in Praia de Cambelas (marked with a blue rectangle in Fig. 13) (Freixial Formation), in Torres Vedras, and the top layers of Praia Azul (Fig. 13). All specimens from this study were collected by surface picking.

The material from this work is housed in the paleontological collection of CI2Paleo at Sociedade de História Natural (SHN), Torres Vedras. This material, as well as the majority of the paleontological collection of SHN, was collected throughout the last 20-25 years by José Joaquim dos Santos, which he later donated to this entity.

For the case of the Cambelas neopterygian specimens, they were inserted in two separate protective foams, inside a box, to provide protection and safety (Fig. 14, 15). These are 29 specimens, with at least three of them representing fin parts, while the others represent scales, some of which are articulated. This material can be utilized for different purposes hereafter.

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. Digital photographs presented in the figures (see "Systematic Paleontology" section) were obtained with a Canon EOS 550D, 18-55mm lens kit digital camera.

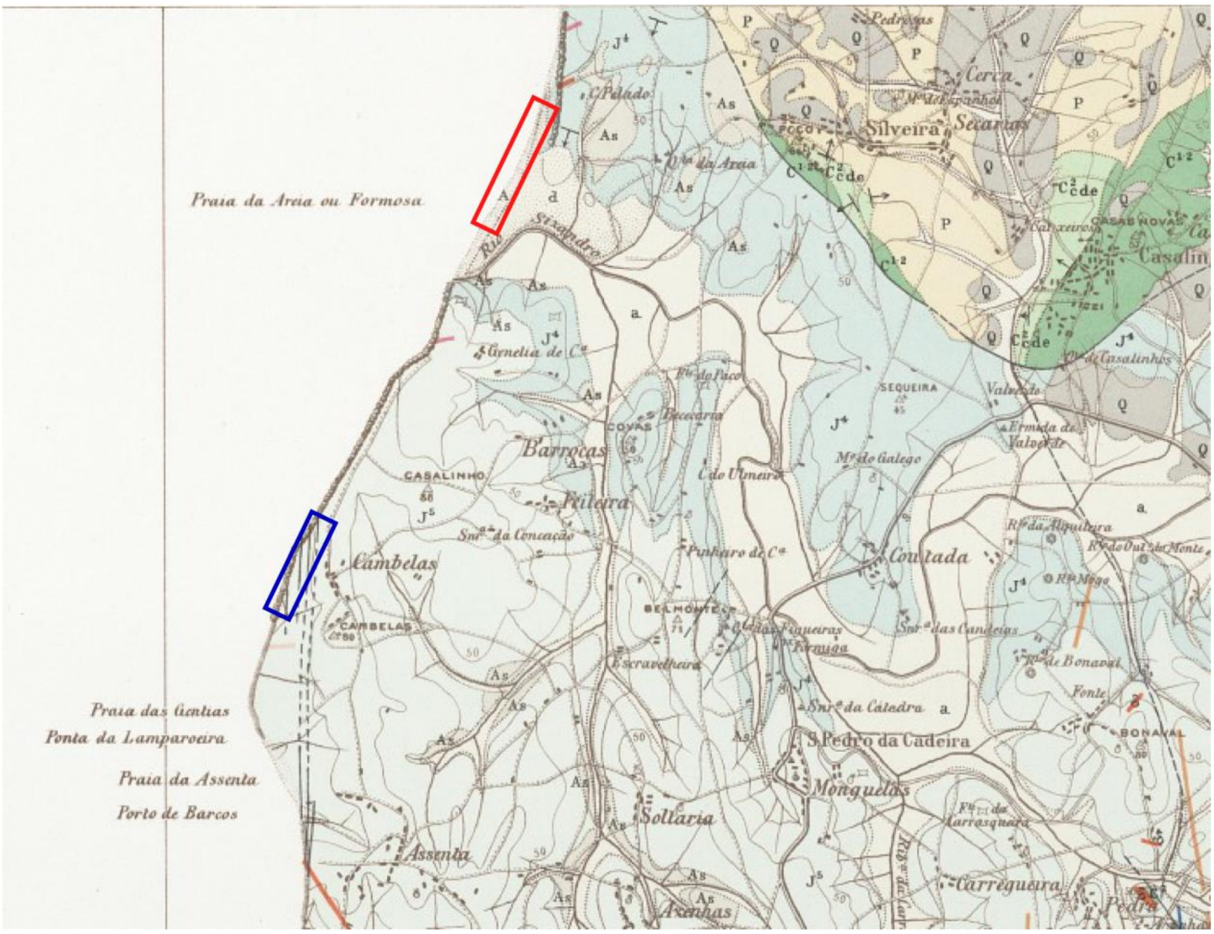


Figure 13 - Excerpt from the Geological Map of Portugal, 30-C Torres Vedras, scale 1:50000, highlighting the approximate location of Praia Azul (red rectangle) and Praia de Cambelas (blue rectangle). Modified from Zbyszewski et al. (1955).

Figure 14 - Upper protective foam lodging a set of fossil neopterygian samples, from Praia de Cambelas, Cambelas fossil site, Freixial Formation. Preservation and conservation techniques were properly applied, in order to keep the samples the safest possible. Picture taken by Bruno Costa.

Figure 15 - Lower protective foam lodging the other set of fossil neopterygian samples, from Praia de Cambelas, Cambelas fossil site, Freixial Formation. Picture taken by Bruno Costa.

6.1 Fieldwork samples

In order to enrich the fossil collection and obtain geological/stratigraphic context of fossil chondrichthyans and actinopterygians, fieldwork was performed.

Thus, it was made an accord with the SHN team in order to do prospection in the coastal region of Torres Vedras. Three trips were made, in October and November of 2019, and July of 2020. The targeted location was the top of the cliff of Praia Azul, Torres Vedras, with deposits dating between upper Kimmeridgian and lower Tithonian (Upper Jurassic).

On the first trip to the top of Praia Azul cliff, eight different levels were previously chosen by Bruno Camilo Silva, Director of SHN, to then proceed to the prospection. From these different levels, equal-weighting, heavy samples of the sediment were obtained, which would later be placed inside different sample bags (Fig. 16).

Figure 16 - Top of the cliff of Praia Azul. Sediment being collected for posterior analysis in search of fossils. Sample labeled as (level) “7”. Picture taken by Bruno Costa.

In order to acquire the fossils from the sediment, it was necessary to apply screen-washing. First, a certain amount of sediment from each sample was subjected to a bath with a mix of water and hydrogen peroxide (H_2O_2), in order to fractionate the slightly carbonated muddy sediment (Fig. 17). This procedure lasted for one day.

Figure 17 - Eight buckets containing a portion of sediment from each respective sample bag. Water and hydrogen peroxide were added to these buckets with sediment. Every bucket and respective sample bag is labeled based on the levels in which the sediment was collected. From left to right: level 1, 2.1, 2.2, 3, 4, 5, 6, and 7. Picture taken by Bruno Costa.

The next procedure was to retrieve the processed material from each bucket and sieve it, to separate the eventual fossils from the soft sediments (Fig. 18). The sieves utilized had three different meshes, including: 1.70 and 1.40 mm, and smaller mesh-sized sieves of 500 micra (0.5 mm). After the separation of the rock samples into fractions (Fig. 19), the respective portions of sediment were analyzed under a Wild M7 binocular magnifying glass, in order to extract any fossil remains (Fig. 20).

Figure 18 - Sieving process. Picture taken by Pedro Bonifácio.

Figure 19 - Drying process, after sieving. Picture taken by Bruno Costa.

Figure 20 - Picking process, using a binocular magnifying glass, metal plates, and pincers, to search for fossils. Picture taken by Bruno Costa.

On the second trip, the objective was to perform surface picking, on the same cliff as the previous trip (Fig. 21). This time around, the picking process was undertaken across a wider area, instead of specific localized portions, attempting to cover as much surface on the different levels as possible.

Figure 21 - Top layers of the Praia Azul cliff, in Santa Cruz, Torres Vedras. Picture taken by Maciej Ruciński.

On the third and final trip, another prospection was made on the surface of the top of the cliff of Praia Azul, with the main objective of determining the exact location where the hybodont and neopterygian material was collected. Unfortunately, the provenance of the mentioned material could not have been uncontestably determined.

6.2 Outcome of the fieldwork

Unfortunately, despite all the fieldwork made at the top of the cliff of Praia Azul, it was not possible to find any shark and/or neopterygian material. Additionally, no fossil material was found at the time of the screen-washing.

More prospection and picking is required in the rather poorly explored layers of the top of Praia Azul. Additionally, the reason behind this absence or scarcity of fossil shark and neopterygian remains can definitely be related to the lack of any stratigraphic record, right after the specimens were discovered.

The specimens from this study were collected throughout the last 20-25 years, by surface picking. This timespan contributes to the lack of available information. Moreover, since this fossil assemblage was gathered with no geographical information devices that could provide the finding location, and since there are no scientific publications that mention this topic, specifically concerning fossil sharks and neopterygians from Praia Azul, it makes the procedure of determining the exact location much more arduous.

7. Systematic Paleontology

In this section of the work, the descriptive dental terminology for the shark specimens follows Cappetta (1987), and the taxonomy for the neopterygian specimens follows Helfman et al. (2009) and Callapez et al. (2014).

Class Chondrichthyes Huxley, 1880
Subclass Elasmobranchii Bonaparte, 1838
Cohort Euselachii Hay, 1902
Order Hybodontiformes Patterson, 1966
Superfamily Hybodontoidea Zangerl, 1981
Family Hybodontidae Owen, 1846
Subfamily Hybodontinae Owen, 1846
Genus *Hybodus* Agassiz, 1836

Type-species: *Hybodus reticulatus* Buckland, 1836 from Sinemurian (Lower Jurassic) of Lyme Regis, southern England, although, due to the preservation of the specimen, it is more likely that it comes from near Hastings, Sussex, southern England.

Hybodus cf. *reticulatus* Buckland, 1836
Fig. 22a-r; Fig. 23a-h

Locality: Praia Azul, Torres Vedras, Portugal.
Horizon: Unknown.
Age: late Kimmeridgian-early Tithonian, Late Jurassic.
Material: 30 incomplete teeth [SHN.(JJS).584-613]. Figs. 22 and 23.
Remarks: Over the past decades, *Hybodus* has been used to include large amounts of species that possessed similar tooth morphologies, ranging from the Paleozoic to the end of the Mesozoic. However, many of such species might be erroneously classified and the genus *Hybodus* should be thoroughly revised, before the generic diversity can be assessed. Nonetheless, better interpretations of *Hybodus* teeth need to be established.

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 preserved crowns are composed of one cusp (representing the main cusp). The crown is labio-lingually compressed. Near the base of the main cusp, the crown expands mesiodistally, resembling an inverted T-shape. However, the prominence of that feature depends on the state of preservation of the specimens. One specimen with a more complete crown base possesses remnants of a lateral cusplet, located at the mentioned transversal termination (Fig. 22m-n). The lateral cusplet is highly eroded and it is only represented by its base. Within the collected material, two general tooth crown types can be distinguished. The first one, with triangular, narrow, slender, and slightly distally curved to straight cusp (Fig. 22a-d, i-j, m-n). The second type is characterized by a triangular, broad, straight, and massive cusp (Fig. 22e-h, k-l, o-r). Due to the incompleteness of some specimens (Fig. 23), some teeth present transitional morphologies between the mentioned types. All specimens present smooth cutting edges that extend from the mesial and distal margins of the crown, starting from the base and reaching the apex of the crown. In case of some specimens, the cutting edges are abraded, resulting in the occurrence of small notches cutting in the margins of the crown. All specimens present longitudinal, parallel, irregularly-alternated ridges on the base of the crown, on both faces. Two general patterns of ridge ornamentation can be distinguished, (1) with straight ridges perpendicular to the crown base (Fig. 22a-b, e-h, k-p; Fig. 23a-b, e-f), and (2) with coarser ornamentation with the ridges curved medially, and their base located more laterally compared to their apical parts (Fig. 22c-d, i-j, q-r; Fig. 23c-d, g-h). The ridges do not bifurcate and do not connect each other, in any specimen. The density of the ridges is irregular throughout their extent on the crown, in both faces. The height of the ridges is variable, which pertains to different extend of the ridges in different crown specimens, the height of the ridges on the lingual and labial faces of the crown, and the height of the ridges within one side of the crown. The ornamentation reaches from 1/3 to half of the total height of the crown, on the labial face. On the lingual face, the ridges reach half to near-total height of the main cusp. 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 general tooth morphology and features seen in the discussed assemblage can be similar to other taxonomically distinct groups. Different groups possess a form of slightly distally curved to straight main cusp (present within neoselachians and other hybodontiforms, for instance; *e. g.* Case et al., 2017; Leuzinger et al., 2017), well-developed smooth cutting edges (present within ctenacanthiforms, stem-neoselachians, and other hybodontiforms, for example; *e. g.* Rees & Underwood, 2008; Guinot et al., 2013; Leuzinger et al., 2017; Stumpf & Kriwet, 2019), longitudinal, more or less parallel ridges, forming on the base of the crown, on both faces (present in other hybodontiform and stem-neoselachians, for instance; *e. g.* Rees & Underwood, 2008; Stumpf & Kriwet, 2019), and a porous root (present, for example, in other hybodontiforms; *e. g.* Rees & Underwood, 2008). The taxa below-mentioned were hereby used to compare with the specimens from this study, mainly due to overall similarity in shape, with both the teeth from this work and other Mesozoic selachian material from Portugal. In some cases, however, taking into account that the teeth from this study are incomplete, the similarities are of such order, that the process of distinguishing and classifying the assemblage from this work becomes very arduous.

The teeth from this study can be excluded from Ctenacanthiformes, mainly due to differences in crown morphology. For instance, ctenacanthids such as *Glikmanius* and other ctenacanthiform representatives, such as *Heslerodus*, and ‘*Ctenacanthus*’ *costellatus*, possess teeth with a flat labial crown face, and a medio-labial depression at the base of the crown (Guinot et al., 2013). These features not being present in the teeth from this study imply that, at least, these above-mentioned taxa can be excluded.

When distinguishing hybodonts from neoselachians, for the case of this study, it is extremely arduous the make the difference. The predominant reason is due to the type of material here discussed and its state of preservation. Over the past 40 years, the analyses of the tooth enameloid microstructure has been thoroughly studied for distinguishing fossil and extant selachian groups (Enault et al., 2015). Furthermore, this type of analyses was more extensively studied in neoselachians and hybodonts, but more among the first (Cuny et al., 2017). For instance, it has been largely accepted, since the work of Reif (1973), that neoselachians possess a triple-layered enameloid: an external layer of made up of individual hydroxyfluorapatite crystallites [shiny-layered enameloid (SLE)], an intermediary layer made up of parallel bundles of crystallites [parallel-bounded enameloid (PBE)], and lastly, an internal layer composed by randomly oriented bundles of crystallites [tangle-bundled enameloid (TBE)] (Guinot & Cappetta, 2011; Enault et al., 2015). Moreover, hybodonts were largely considered to possess a simple single-layered enameloid [single crystallite enameloid (SCE)], lacking any notable microstructural differentiation (Enault et al., 2015). Thus, enameloid microstructure was vastly considered as a reliable method to distinguish hybodonts from neoselachians and vice-versa. However, more recent studies have challenged and questioned this method, and it might not be as reliable as thought before, since different enameloid microstructures are actually more taxonomically widespread within chondrichthyans (Cuny et al., 2001; Guinot & Cappetta, 2011; Andreev & Cuny, 2012; Enault et al., 2015; Cuny et al., 2017). Nevertheless, the enameloid microstructure would not be discussed here for distinguishing the teeth under study from neoselachians, since this type of analyses was not accomplished.

When comparing with the late Kimmeridgian *Planohybodus* Rees & 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 & Underwood (2008, Plate 1, figures 13-17; Plate 2, figures 4-10; more specifically to *Egertonodus duffini* Rees & 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), and *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 ridges in the enameloid of *H. cuspidatus* are coarser, and they reach the apex, unlike every specimen under study. Additionally, the main cusp is notably inclined lingually. 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. Finally, the root of the teeth of *P. plicatilis* is less porous than the teeth under study, and the main cusp is thinner and slimmer.

The specimens here mentioned 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), which were 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. By comparing with 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 & Kriwet (2019, Fig. 2a-f), attributed to *Hybodus reticulatus* Buckland, 1836, is also very consistent with the ones described in this work.

Thus, as a result of the description and comparisons made, the current specimens will be attributed to *Hybodus* cf. *reticulatus* Buckland, 1836, due to the following morphological characters: a reticulated, spongy root, perpendicular to the crown; a completely to almost completely straight main cusp; several vertical, more or less coarse, and parallel enameloid ridges that are present in the base of the crown, on both faces; and well-defined smooth cutting edges.

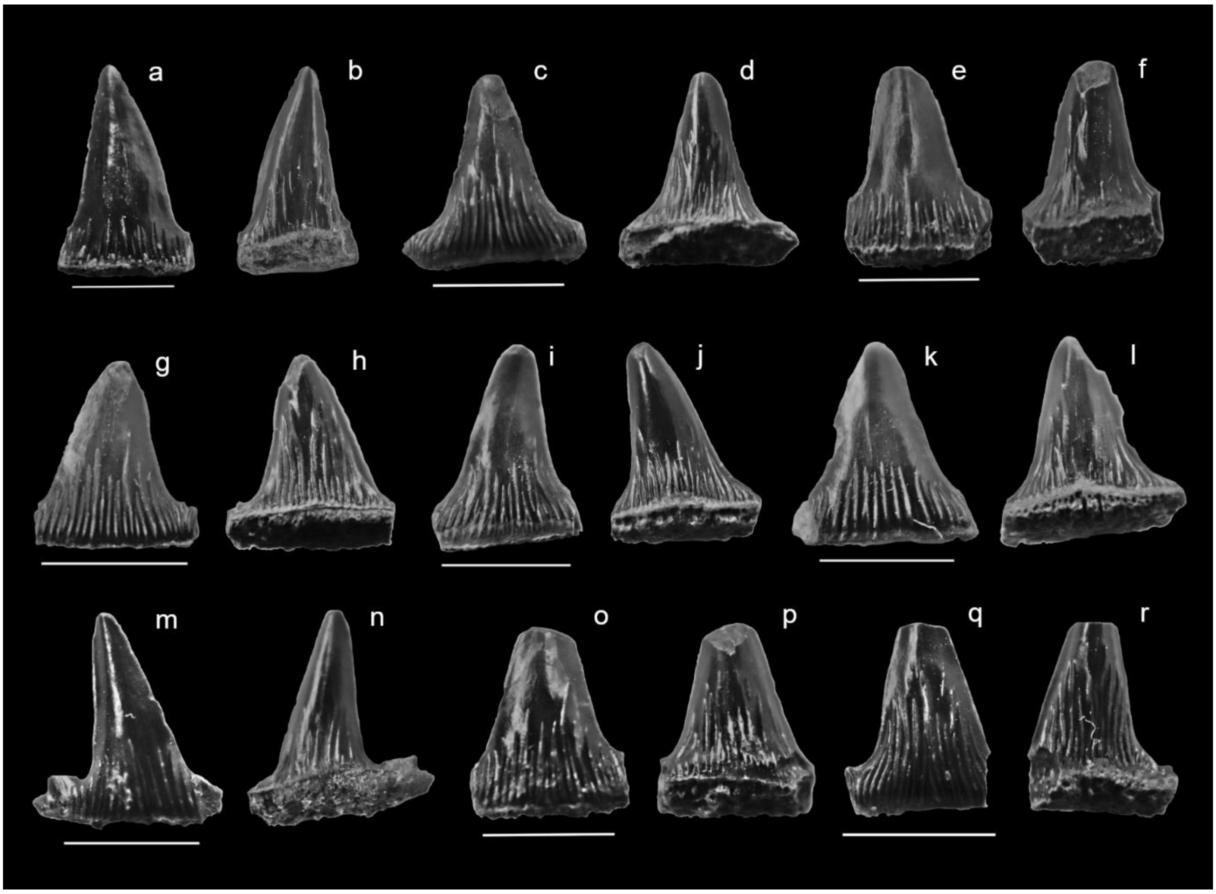


Figure 22 - Fossil tooth specimens of *Hybodus* cf. *reticulatus* Buckland, 1836, from upper Kimmeridgian-lower Tithonian of Praia Azul (Torres Vedras, Central-Western Portugal). **a, b** [SHN.(JJS).584] in labial (**a**) and (**b**) lingual views; **c, d** [SHN.(JJS).586] in labial (**c**) and (**d**) lingual views; **e, f** [SHN.(JJS).587] in labial (**e**) and (**f**) lingual views; **g, h** [SHN.(JJS).588] in labial (**g**) and (**h**) lingual views; **i, j** [SHN.(JJS).589] in labial (**i**) and (**j**) lingual views; **k, l** [SHN.(JJS).590] in labial (**k**) and (**l**) lingual views; **m, n** [SHN.(JJS).591] in labial (**m**) and (**n**) lingual views; **o, p** [SHN.(JJS).592] in labial (**o**) and (**p**) lingual views; **q, r** [SHN.(JJS).595] in labial (**q**) and (**r**) lingual views. Scale = 5 mm.

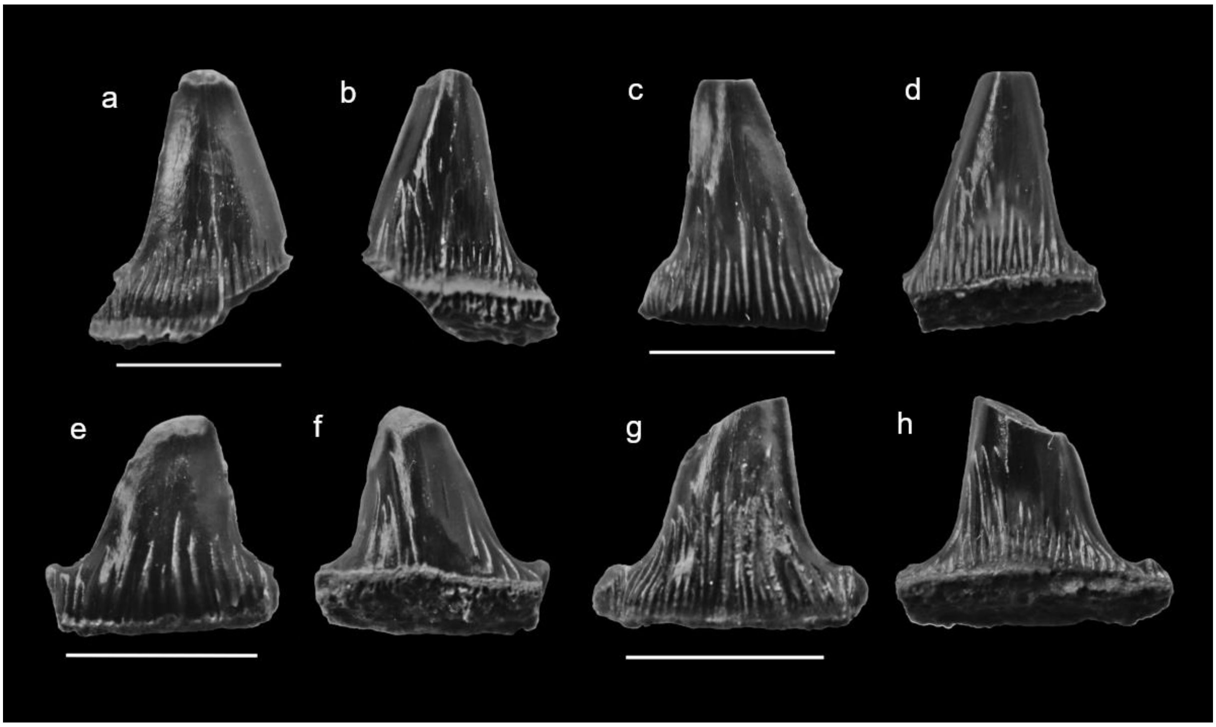


Figure 23 - Fossil tooth specimens of *Hybodus* cf. *reticulatus* Buckland, 1836, from upper Kimmeridgian-lower Tithonian of Praia Azul (Torres Vedras, Central-Western Portugal). **a, b** [SHN.(JJS).596] in labial (**a**) and (**b**) lingual views; **c, d** [SHN.(JJS).597] in labial (**c**) and (**d**) lingual views; **e, f** [SHN.(JJS).600] in labial (**e**) and (**f**) lingual views; **g, h** [SHN.(JJS).603] in labial (**g**) and (**h**) lingual views. Scales = 5 mm.

Superclass Osteichthyes Huxley, 1880
Class Actinopterygii Cope, 1887
Subclass Neopterygii Regan 1923

cf. Ginglymodi
Fig. 24a-j; Fig. 25a-c

Locality: Praia de Cambelas, São Pedro da Cadeira, Torres Vedras, Portugal.
Horizon: Unknown.
Age: middle-late Tithonian, Late Jurassic.
Material: 29 specimens, three of which may represent fin parts, while the others represent scales (some articulated) [SHN.(JJS).021]. Figs. 24 and 25.
Remarks: All specimens are partially wrapped in marly mudstone, which hampers any further preparation methods upon them. All specimens present certain amounts of bony elements that are superficially visible, although the possibility that at least some specimens present hidden bony elements is not discarded.

Description: The specimens are small-to-moderately-sized - 70 mm max. length; 30 mm max. width. Four specimens comprise articulated scales, at least partially (Fig. 24a-h), while the others are taphonomically displaced. The scales from all specimens are not entirely uncovered, as the surrounding sediment is strongly attached and partially covers them. Nonetheless, some anatomical characters are discernible. The surface of the scales is smooth and covered with ganoine. Their shape varies among the specimens and it is not very perceptible due to the covering sediment and scale fragmentation. However, in better-preserved specimens (Fig. 24c-d, g-h), the scale shape ranges from rectangular-oblong to rhomboidal-like forms. The rhomboidal-like scales in these specimens are characterized as ganoid scales. In the rectangular-oblong scales, the posterior margin is smooth and straight, within the most of its extension, with one or two small bow-shaped notches cutting into the scales in their middle to upper posterior margin (Fig. 24c). The exact position and size of the notches varies among the specimens. These notches might be evidence of a kind of dorsal peg, for transversal articulation, and, therefore, evidence of peg-and-socket articulation. They can be, at least, embedded in the sediment, however. The incision development differs between the specimens, with some forming an angle, and others forming a round-like (concave) cut. Dorsal and ventral processes on the scales, for longitudinal articulation, seems to be absent or, at least, hidden within the sediment. Although it is not very perceptible, due to sediment coverage in the specimens, the scales seem to overlap each other (Fig. 24a, c, e, g). Apart from the most well-preserved scales of the specimens from this study, there are numerous poorly-preserved ones. In fact, the majority of the scales are not well-preserved enough to distinguish its most relevant characteristics. This hampers any further analyses for classification of the material. Three particular specimens (Fig. 25a-c) are composed of fin parts. These fin parts were found associated with the scale specimens. Thus, we assume that could have come from the same individual/taxon. One of the specimens (Fig. 25a) is composed of, at least, 10 visible fin rays; another (Fig. 25b) composed of 8 visible fin rays; and the third specimen (Fig. 25c) comprising, at least, 15 visible fin rays, although it is difficult to determine the original number of fin rays, due to partial covering of sediment in every specimen.

Discussion: Due to the lack of more complete and well-preserved material, it is not possible to determine in which section of the body these specimens would belong to.

For the case of the other specimens that contain scales and are not figured here, their incompleteness and lack of characteristic features impedes any further taxonomical classification.

The better-preserved specimens (Fig. 24a-j) present oblong-rectangular to rhomboidal-like scales. These specimens are, therefore, characterized here by possessing rhomboid scales, and more specifically, ganoid scales. Ganoid scales are known to occur since basal actinopterygians, evolving independently various times throughout actinopterygian history (*e. g.* Palaeonisciformes, Pycnodontiformes, Ginglymodi, Pachycormidae, Semionotidae, Macrosemiidae, Ophiopsidae, Caturidae, Aspidorhynchidae, Pleuropholidae, and Pholidophoridae; Schultze, 1996, 2018; Helfman et al., 2009).

The specimens seem to present some notches on the posterior margin of the scales (Fig. 24c) which most likely characterizes the peg-and-socket articulation. The latter enables longitudinal articulation of the scale. This is another morphological feature that is present in other actinopterygian taxa, namely in Cheirolepididae (*e. g.* Giles et al., 2015), Palaeoniscidae (*e. g.* Dias, Vega & Canhete, 2010), Guildayichthyiformes (*e. g.* Lund, 2000), Halecomorphi (*e. g.* Wen et al., 2012), Teleosteomorpha, stem and more advanced teleosts (*e. g.* Giordano, Arratia & Schultze, 2016). The peg-and-socket articulation is, thus, a primitive morphological character in actinopterygians, tracing back to the Devonian (Giles et al., 2015).

The surface of the scales of these specimens is covered with ganoine. Since ganoine is characteristic for its microtubercles, forming multilayered packages and occurring on the surface of ganoine (Schultze, 2018), it is possible to discard the possibility that these scales are cosmoid. The latter possess a hexagonal design, in result of the imprint of basal epidermal cells, displayed by the true enamel of cosmoid scales (Schultze, 2018). The scale specimens from this study do not resemble those of teleosts, since the specimens do not present the typical and unique round shape of the ctenoid and cycloid scales of teleosts. Thus, the Teleostei group can be discarded, regarding to the classification of the material from this study.

The presence of both ganoid scales and peg-and-socket articulation is a common feature of ginglymodian neopterygians (Giordano et al., 2016). Among all the clades mentioned above, the discussed specimens seem to be attributable to cf. Ginglymodi, due to the overall morphology of the scales. Moreover, scales with rather similar morphology to the ones discussed in this work were previously attributed to Lepisosteiformes and Semionotiformes (*e. g.* Heckert, 2004; Antczak & Bodzioch, 2018; Kovalchuk & Anfimova, 2020), with both groups being nested within Ginglymodi (Brito, Alvarado-Ortega, & Meunier, 2017; López-Arbarello & Sferco, 2018). The classification will be maintained as cf. Ginglymodi, due to its overall features occurring commonly in different actinopterygian groups, which hampers any further specific assignation. Additionally, as there is great morphological variability of scales depending on the position in the body (Giordano et al., 2016), the precise taxonomic classification of the studied specimens is precluded. Thus, the studied material will be classified as cf. Ginglymodi, due to the following characters: rectangular-oblong to rhomboidal-like ganoid scales, with smooth surface, covered with ganoine; rectangular-oblong scales with smooth and straight posterior margin, within the most of its extension; presence (probably) of some kind of dorsal pegs, for transversal articulation, and, therefore, evidence of peg-and-socket articulation; scales seemingly overlapping each other.

There is no possibility in to classifying the fin part specimens (Fig. 25a-c) to a more specific taxonomical rank, since these are isolated from the rest of the body and there are no specific diagnostic characters that would assign them to a more specific taxonomy. Since the fin parts were found together in association with the scale specimens, they will be attributed and classified to the same taxon.

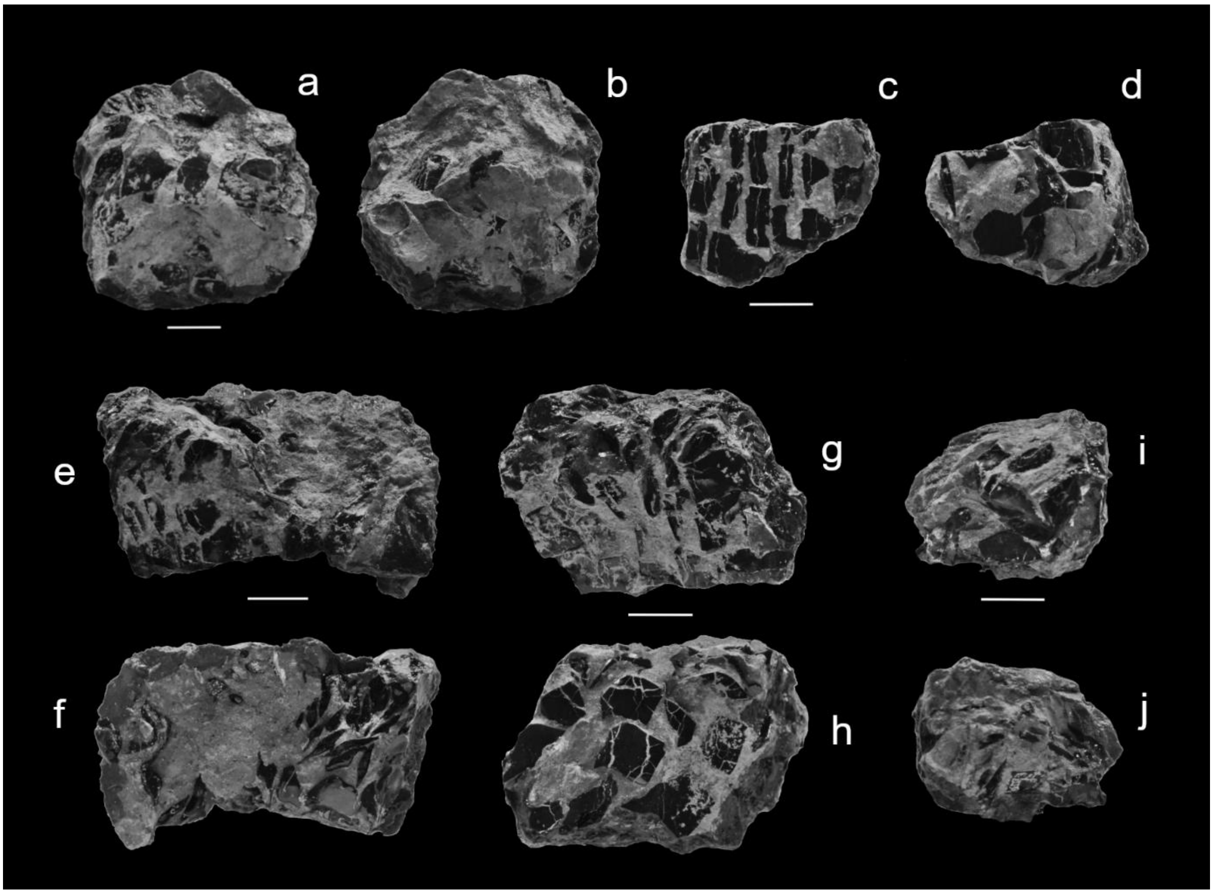


Figure 24 - Partially articulated scale specimens of cf. Ginglymodi, from middle-upper Tithonian of Cambelas fossil site (Torres Vedras, Central-Western Portugal), [SHN.(JJS).021], in left (**a**), (**c**), (**e**), (**g**), (**i**) and (**b**), (**d**), (**f**), (**h**), (**j**) right? lateral views. Scales = 10 mm.

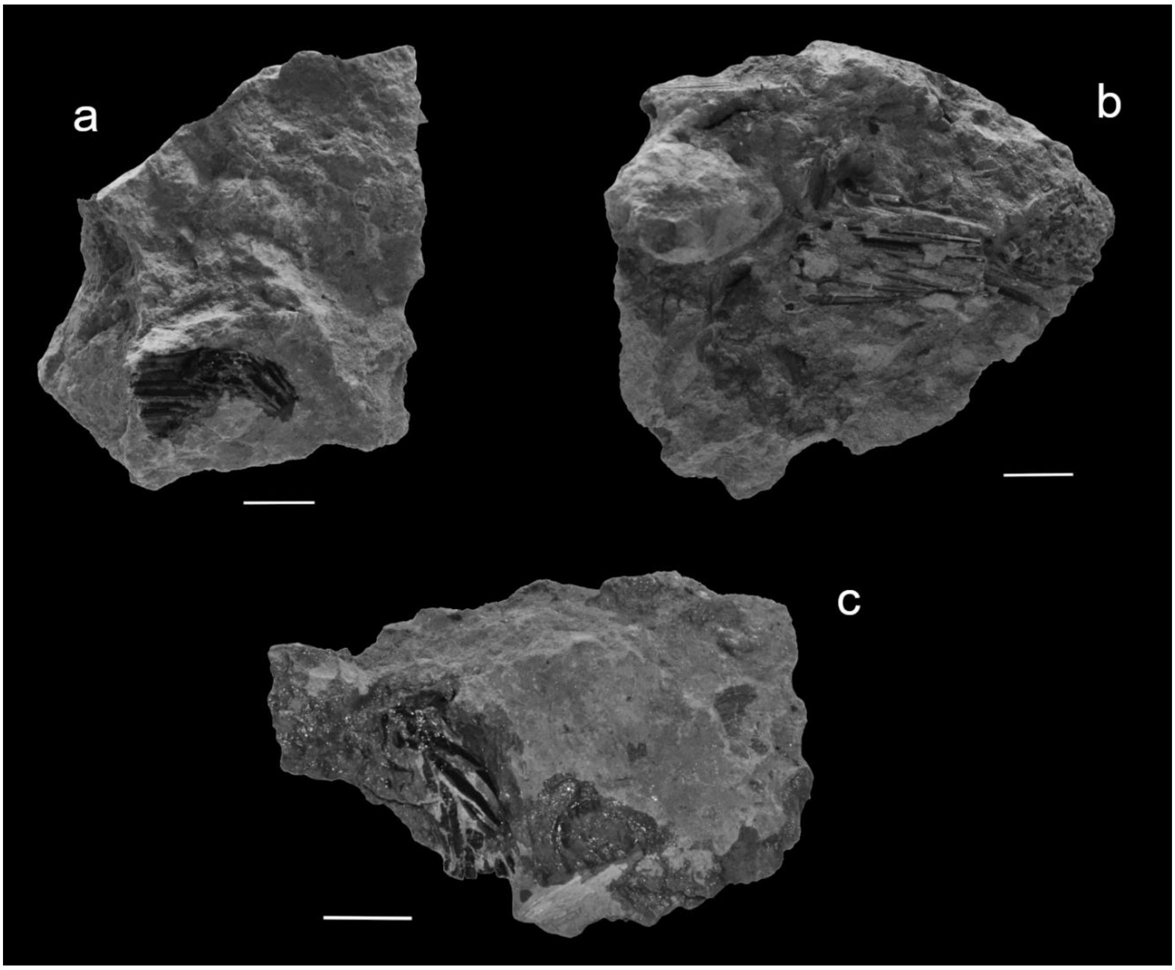


Figure 25 - Fin specimens of cf. Ginglymodi, from middle-upper Tithonian of Cambelas fossil site (Torres Vedras, Central-Western Portugal), [SHN.(JJS).021], in (**a**), (**b**), (**c**) lateral? views. Scales = 10 mm.

Pycnodontiformes indet.
Fig. 26a-n

Locality: Praia Azul, Torres Vedras, Portugal.
Horizon: Unknown.
Age: late Kimmeridgian-early Tithonian, Late Jurassic.
Material: 16 isolated durophagous teeth, and 8 sets of partially articulated durophagous teeth (48 teeth in total, for the latter), at least 3 of which represent fragmentary prearticular or vomerine dentitions. A total of 64 molariform teeth. Fig. 26.
Remarks: For the case of the partially articulated tooth sets, all of them, from this assemblage, are incomplete, *i. e.* none of them represent the entire tooth set and apparatus. Nonetheless, it is possible to determine, to some extent and with caution, from which mouth parts these partially articulated teeth come from. As for the isolated teeth, the admeasurement has to be even more cautious. However, these teeth are quite similar to the partially articulated ones, hence their classification being the same here.

Description: The molariform teeth are small - 7 mm max. length; 2 mm max. width. The ratio of the tooth length and tooth width, for the case of the transversally elongated teeth, is 2:1 in average, but it can reach 3.5:1, making them longer than wider. There are two morphotypes that can be distinguished: one represents teeth that possess a transversally elongated morphology, and are characterized by a more or less pillow-shape (Fig. 26b-d, i-n); the second represents teeth that are circular-shaped (Fig. 26a, e-h). All of the tooth specimens present a smooth convex occlusal surface (Fig. 26a-n). Some tooth arrangements (Fig. 26b-d) seem to have been part of a longitudinal row, forming a more or less dense pavement. The latter are characterized as fragmentary prearticular or vomerine teeth. In these particular specimens (Fig. 26b-d), there is a row of large teeth, that are part of the main row, flanked by smaller teeth, part of the marginal row. The other material (Fig. 26a, e-n) can also be characterized as being part of a prearticular or vomerine dentition, due to the similarities observed in every specimen.

Discussion: Durophagy is well-distributed throughout different actinopterygian clades. These teeth are mainly used to crush hard-bodied or hard-shelled prey, with a rigid exoskeleton (Kriwet, 2000). Durophagous molariform teeth can be found in semionotid and lepidotid ginglymodians, advanced teleosts, such as trigger- and parrotfishes, which present crushing dentitions (Kriwet, 2000). During the Late Jurassic, however, both trigger- and parrotfishes had yet to evolve, only appearing near the end of the Mesozoic Era (Hughes et al., 2018).

The highly specialized and diverse heterodont crushing dentition of pycnodonts has been regarded, for a long time, as a main character to identifying pycnodont species (Kriwet, 2005). In fact, most pycnodonts were classified based entirely on the characteristics of their prearticular and/or vomerine dentitions (Kriwet, 2005).

Unfortunately, due to the fragmentary nature of the specimens (Fig. 26a-f), it is not possible to determine the complete number of tooth rows, both medial and lateral, which would be useful for more specific taxonomic classification. A more specific classification is, thus, not possible with the discussed material, mainly due to the incompleteness of all these specimens, and due to the great intra- and interspecific variations in tooth morphology of neopterygians.

The discussed specimens will be attributed, in open nomenclature, to Pycnodontiformes indet., due to following characteristics: fragmentary prearticular or vomerine teeth with transversally elongated to circular morphology, with the first presenting a more or less pillow-shape; a smooth convex occlusal surface; tooth arrangements forming a longitudinal row; a main row composing the larger, elongated teeth, and a marginal row composing smaller, more circular teeth.

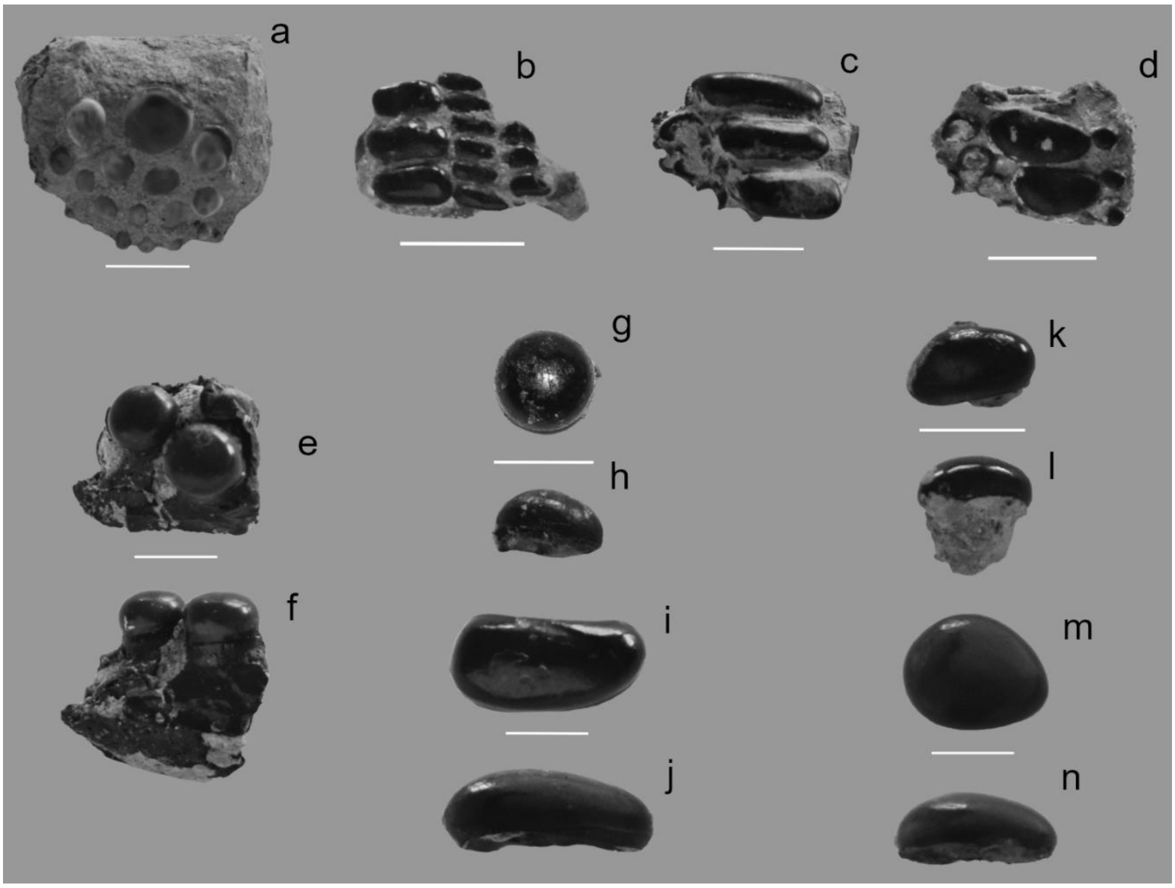


Figure 26 - Isolated and partially articulated durophagous teeth of Pycnodontiformes indet., from upper Kimmeridgian-lower Tithonian of Praia Azul (Torres Vedras, Central-Western Portugal). **a-f**, fragmentary prearticular or vomerine dentitions in occlusal (**a-e**) and (**f**) lateral views; **g-n**, isolated molariform teeth in occlusal (**g**), (**i**), (**k**), (**m**) and (**h**), (**j**), (**l**), (**n**) lateral views. Scales = 5 mm.

8. Results and Discussion

In this work, a set of material was studied and identified: a total of 30 isolated hybodontiform teeth, being attributed to *Hybodus* cf. *reticulatus* Buckland, 1836; 29 ginglymodian specimens, three of which may represent fin parts, while the others represent scales (some articulated), all of which are assigned to cf. Ginglymodi; and 16 isolated durophagous teeth, and 8 sets of partially articulated durophagous teeth (48 teeth in total, for the latter), at least three of which represent fragmentary prearticular or vomerine dentitions, all of which are attributed to Pycnodontiformes indet.

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 (Maisey, 1987; Duffin, 1993; Stumpf & 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.

It is crucial to note the great disparity in bibliographical publications, as well as diversity of occurrences between hybodontiform sharks and neopterygians. One very plausible explanation concerns the success rate of fossilization in these taxa (Helfman et al., 2009; Long, 2011). Actinopterygians, with their calcified bony skeletons, are more prone to fossilize, given the optimal taphonomical conditions, whereas chondrichthyans, with their cartilaginous skeletons, are scarcer in the fossil record (excluding their teeth; Helfman et al., 2009; Long, 2011).

8.1 Paleoecological considerations

Taking into account that the Lusitanian Basin beholds fossil remains of various distinct aquatic vertebrates and invertebrates (Fürsich, 1981; Kriwet, 1998, 2000), it is possible to infer that, particularly during the Late Jurassic, it corresponds to a rather diverse paleobiodiversity (Kriwet, 1998).

Elasmobranch and actinopterygian teeth are crucial to interpret ecological niches, as they provide significant adaptive features related to diet preferences (Stumpf & Kriwet, 2019). However, tooth morphology alone is not enough to provide a clear picture of the diet and biological role (Stumpf & Kriwet, 2019). Therefore, the predator-prey interactions and diet preferences listed here should be treated cautiously, since, on one hand, there are no direct evidences of predator-prey interactions in these specimens, and on the other hand, prey ranges and diversity were probably more diverse than expected, when considering tooth morphology alone.

The teeth of *Hybodus reticulatus* are regarded to correspond to the clutching-type (Stumpf & Kriwet, 2019), which infers a diet predominantly of cephalopods, but also fish (Stumpf & Kriwet, 2019). Based on the morphology of the teeth of *Hybodus* cf. *reticulatus* from this study, it is possible to infer that its diet preferences were probably towards fish and cephalopods. However, since the material from this study is fragmentary and incomplete, this approach is more limited and has to be taken more carefully. The pycnodontiform durophagous teeth from this work are characteristic of a crushing dentition, which they utilized, predominantly, to crush hard-shelled invertebrates. Although, pycnodontiforms are known to have possessed a highly specialized heterodonty (Kriwet, 2000).

During the Upper Jurassic of the Lusitanian Basin, more specifically in what is now the Praia Azul Member of the Lourinhã Formation, the ecosystem varied between fluvial or floodplain environments to marginal marine or brackish bays, with some sections possibly representing lagoonal deposits with deltaic influence (Fürsich, 1981). Additionally, in what is now the Freixial Formation, during the same geochronological epoch in the Lusitanian Basin, it corresponded to a shallow marine slope, deepening towards the south, with water of mixed salinity (Leinfelder, 1993; Kullberg et al., 2006). Specifically, in Cambelas, coastal delta plains and distal fluvial environments were present (Hill, 1989b). Following these lithostratigraphical interpretations, the changing environmental conditions and inconstant water salinity, correlates with the fact that the organisms living in these ecosystems were most likely euryhaline, *i. e.* these organisms were able to tolerate and adapt to a wide range of water salinity.

As evidenced by the shell-rich fossil biota present in Praia Azul (Fürsich, 1981; Taylor et al., 2013), it can be inferred that the pycnodonts were probably preying upon these shelly invertebrates, thus taking advantage on this source of food. Above in the trophic level, the hybodont sharks were probably preying upon the neopterygians, such as pycnodonts, that were present in the same environment. For the case of the ginglymodians, since there are no fossil oral parts or teeth preserved, it is not possible to infer the diet preferences and ecological niche of these particular specimens.

9. Conclusions

The current study provides more knowledge about the diversity and occurrences of fossil Mesozoic hybodonts and neopterygians from the Upper Jurassic of Portugal. Thus far, the hybodont fossil record in Portugal has been poorly documented. Material from this taxonomic group in the country is composed predominantly by isolated teeth, as well as fin and cephalic spines, all of which are frequently incomplete. This hampers any further specific classification of such specimens. Additionally, since the classification of most hybodont species is heavily biased towards isolated teeth, the identification of the hybodont material from this study, for instance, is by no means completely certain and truthful. Until now, there is no record of partially or completely preserved hybodont skeletons in Portugal.

The Mesozoic neopterygian fossil record in Portugal, although much better documented, more diverse and abundant than hybodonts, it comprises mostly incomplete specimens, which are not possible to classify on a specific and even generic level, mainly due to their overall poor preservation and lack of diagnostic characters. Mesozoic neopterygian material is more often composed by isolated or partially articulated scales and teeth, partially to fully articulated bones, namely jaw elements, with some bones being indeterminable, and rare occasions of complete, but poorly preserved full-bodied specimens.

More prospection is required in the future, specifically in the cliffs and deposits of Praia Azul, since this and nearby geological sites may bear important fossil remains of elasmobranchs and actinopterygians. There is a great need to develop more studies on the ichthyofauna of the Lusitanian Basin. With the discovery and documentation of more fossil ichthyological material, it will certainly enhance our understanding about the fossil fish diversity of the Upper Jurassic of Portugal, as well as our understanding of the paleoecology and paleoenvironment of these deposits.

10. References

Alves, T. M., Gawthorpe, R. L., Hunt, D. W., & Monteiro, J. H. (2002). Jurassic tectono-sedimentary evolution of the Northern Lusitanian Basin (offshore Portugal). *Marine and Petroleum Geology, 19*(6), 727-754. doi: 10.1016/S0264-8172(02)00036-3

Alves, T. M., Manuppella, G., Gawthorpe, R. L., Hunt, D. W., & Monteiro, J. H. (2003). The depositional evolution of diapir-and fault-bounded rift basins: examples from the Lusitanian Basin of West Iberia. *Sedimentary Geology, 162*(3), 273-303. doi: 10.1016/S0037-0738(03)00155-6

Andreev, P. S., & Cuny, G. (2012). New Triassic stem selachimorphs (Chondrichthyes, Elasmobranchii) and their bearing on the evolution of dental enameloid in Neoselachii. *Journal of Vertebrate Paleontology, 32*(2), 255-266. doi: 10.1080/02724634.2012.644646

Antczak, M., & Bodzioch, A. (2018). Diversity of fish scales in Late Triassic deposits of Krasiejów (SW Poland). *Paleontological Research, 22*(1), 91-100. doi: 10.2517/2017PR012

Antunes, M. T. (1967). Um Mesosuquiano do Liásico de Tomar (Portugal): considerações sobre a origem dos crocodilos. In M. T. Antunes (Ed.), *Memórias dos Serviços*

Geológicos de Portugal, Serviços Geológicos de Portugal, Lisboa, 13, 66 (Nova Série).

Antunes, M. T. (1979). Ensaio de síntese crítica acerca do Cretácico terminal e do Paleogénico de Portugal. *Ciências da Terra, 5*, 145-174.

Antunes, M. T., & Pais, J. (1978). Notas sobre depósitos de Taveiro. Estratigrafia, paleontologia, idade, paleoecologia. *Ciências da Terra, 4*, 109-128.

Balbino, A. C. (2003). Upper Jurassic Hybodontidae (Selachii) from Lourinhã, Portugal. *Ciências da Terra (UNL), 15*, 45-52.

Bhat, M. S., Ray, S., & Datta, P. M. (2017). A new hybodont shark (Chondrichthyes, Elasmobranchii) from the Upper Triassic Tiki Formation of India with remarks on its dental histology and biostratigraphy. *Journal of Paleontology, 92*(2), 221-239. doi: 10.1017/jpa.2017.63

Brito, P. M., Alvarado-Ortega, J., & Meunier, F. J. (2017). Earliest known lepisosteoid extends the range of anatomically modern gars to the Late Jurassic. *Scientific Reports, 7*(1), 1-8. doi: 10.1038/s41598-017-17984-w

Callapez, P. M., Barroso-Barcenilla, F., Cambra-Moo, O., Ortega, F., Pérez-García, A., Segura, M., & Torices, A. (2014). Fossil assemblages and palaeoenvironments in the Cenomanian vertebrate site of Nazaré (West Central Portugal). *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen, 273*(2), 179-195. doi: 10.1127/0077-7749/2014/0422

Cappetta, H. (1987). Chondrichthyes II: Mesozoic and Cenozoic Elasmobranchii. In H. -P. Schultze (Ed.), *Handbook of Paleoichthyology* (Vol. 3B, 193 p.). Stuttgart: Verlag Dr. Friedrich Pfeil.

Case, G. R., Cook, T. D., Saford, E. M., & Shannon, K. R. (2016). A late Maastrichtian selachian assemblage from the Peedee Formation of North Carolina, USA. *Vertebrate Anatomy Morphology Palaeontology, 3*, 63-80. doi: 10.18435/B5T88N

Castanera, D., Malafaia, E., Silva, B. C., Santos, V. F., & Belvedere, M. (2020a). New dinosaur, crocodylomorph and swim tracks from the Late Jurassic of the Lusitanian Basin: implications for ichnodiversity. *Lethaia*, *54*(2), 271-287. doi: 10.1111/let.12402

Castanera, D., Silva, B. C., Santos, V. F., Malafaia, E., & Belvedere, M. (2020b). Tracking Late Jurassic ornithopods in the Lusitanian Basin of Portugal: ichnotaxonomic implications. *Acta Palaeontologica Polonica*, *65*(2). doi: 10.4202/app.00707.2019

Cawley, J. J., Marramà, G., Carnevale, G., Villafaña, J. A., López-Romero, F. A., & Kriwet, J. (2021). Rise and fall of †Pycnodontiformes: Diversity, competition and extinction of a successful fish clade. *Ecology and Evolution*, *11*(4), 1769-1796. doi: 10.1002/ece3.7168

Cuny, G., Guinot, G., & Enault, S. (2017). Hybodont Sharks. In G. Cuny, G. Guinot & S. Enault (Eds.), *Evolution of Dental Tissues and Paleobiology in Selachians* (33-45). London: ISTE Press - Elsevier.

Cuny, G., Rieppel, O., & Sander, P. M. (2001). The shark fauna from the Middle Triassic (Anisian) of north-western Nevada. *Zoological Journal of the Linnean Society*, *133*(3), 285-301. doi: 10.1006/zjls.2000.0273

Dias, E. V., Vega, C. S., & Canhete, M. V. U. (2010). Microstructure of paleoniscid fish scales from Irati Formation, Permian (Cisuralian) of Paraná Basin, Brazil. *Gaea - Journal of Geoscience*, *6*(2), 69-75. doi: 10.4013/gaea.2010.62.03

Diogo, R. (Ed.). (2007). *The Origin of Higher Clades: Osteology, Myology, Phylogeny and Evolution of Bony Fishes and the Rise of Tetrapods* (First Edition). Enfield: Science Publishers.

Dobson, C., Giles, S., Johanson, Z., Liston, J., & Friedman, M. (2019). Cranial osteology of the Middle Jurassic (Callovian) *Martillichthys renwickae* (Neopterygii, Pachycormiformes) with comments on the evolution and ecology of edentulous pachycormiforms. *Papers in Palaeontology*, *7*(1), 1-26. doi: 10.1002/spp2.1276

Duffin, C. J. (1993). Teeth of *Hybodus* (Selachii) from the Early Jurassic of Lyme Regis, Dorset (southern England): preliminary note. In J. Herman & H. van Waes (Eds.), *Elasmobranches et Stratigraphie - Belgian Geological Survey, Professional Paper*, *264*, 45-52.

Duffin, C. J., & Thies, D. (1997). Hybodont shark teeth from the Kimmeridgian (Late Jurassic) of northwest Germany. *Geologica et Palaentologica*, *31*, 235-256.

Enault, S., Guinot, G., Koot, M. B., & Cuny, G. (2015). Chondrichthyan tooth enameloid: past, present, and future. *Zoological Journal of the Linnean Society*, *174*(3), 549-570. doi: 10.1111/zoj.12244

Fischer, J. (2012). *Palaeoecology, migration behavior, and reproductive pattern of Palaeozoic to Mesozoic freshwater sharks revealed by stable isotopes* (Ph.D. Thesis), 300 pp.

Fürsich, F. T. (1981). Salinity-controlled benthic associations from the Upper Jurassic of Portugal. *Lethaia*, *14*(3), 203-223. doi: 10.1111/j.1502-3931.1981.tb01690.x

Giles, S., Coates, M. I., Garwood, R. J., Brazeau, M. D., Atwood, R., Johanson, Z., & Friedman, M. (2015). Endoskeletal structure in *Cheirolepis* (Osteichthyes, Actinopterygii), An early ray-finned fish. *Palaeontology*, *58*(5), 849-870. doi: 10.1111/pala.12182

Giordano, P. G., Arratia, G., & Schultze, H. -P. (2016). Scale morphology and specialized dorsal scales of a new teleosteomorph fish from the Aptian of West Gondwana. *Fossil Record*, *19*(1), 61-81. doi: 10.5194/fr-19-61-2016

Grande, L. (2010). An empirical synthetic pattern study of gars (Lepisosteiformes) and closely related species, based mostly on skeletal anatomy. The resurrection of Holostei. *Copeia*, *6*, 1-871.

Guillaume, A. R. D. (2018). *Microvertebrates of the Lourinhã Formation (Late Jurassic, Portugal)* (Master's Thesis), 162 p.

Guinot, G., & Cappetta, H. (2011). Enameloid microstructure of some Cretaceous Hexanchiformes and Synechodontiformes (Chondrichthyes, Neoselachii): new structures and systematic implications. *Microscopy Research and Technique*, *74*(2), 196-205. doi: 10.1002/jemt.20892

Guinot, G., Adnet, S., Cavin, L., & Cappetta, H. (2013). Cretaceous stem chondrichthyans survived the end-Permian mass extinction. *Nature Communications*, *4*(1), 2669. doi: 10.1038/ncomms3669

Heckert, A. B. (2004). Late Triassic microvertebrates from the lower Chinle Group (Otischalkian-Adamanian: Carnian), southwestern USA. *New Mexico Museum of Natural History and Science Bulletin: 27*, 1-170.

Helfman, G. S., Collette, B. B., Facey, D. E., & Bowen, B. W. (Eds.). (2009). *The Diversity of Fishes: Biology, Evolution, and Ecology* (Second Edition). New Jersey: John Wiley & Sons.

Hill, G. (1989a). Distal alluvial fan sediments from the Upper Jurassic of Portugal: controls on their cyclicity and channel formation. *Journal of the Geological Society*, *146*(3), 539-555. doi: 10.1144/gsjgs.146.3.0539

Hill, G. (1989b). *The sedimentology and lithostratigraphy of the Upper Jurassic Lourinhã Formation, Lusitanian Basin, Portugal* (Ph.D. Thesis), 292 p.

Hodnett, J. P., Elliott, D. K., & Olson, T. J. (2013). A new basal hybodont (Chondrichthyes, Hybodontiformes) from the Middle Permian (Roadian) Kaibab Formation, of northern Arizona. *New Mexico Museum of Natural History and Science Bulletin: 60*, 103-108.

Hoffman, B. L., Hageman, S. A., & Claycomb, G. D. (2016). Scanning electron microscope examination of the dental enameloid of the Cretaceous durophagous shark *Ptychodus* supports neoselachian classification. *Journal of Paleontology*, *90*(4), 741-762. doi: 10.1017/jpa.2016.64

Hughes, L. C., Ortí, G., Huang, Y., Sun, Y., Baldwin, C. C., Thompson, A. W., Arcila, D., Betancur-R, R., Chenhong, L., Becker, L., Bellora, N., Zhao, X., Li, X., Wang, M., Fang, C., Xie, B., Zhou, Z., Huang, H., Chen, S., Venkatesh, B., & Shi, Q. (2018). Comprehensive phylogeny of ray-finned fishes (Actinopterygii) based on transcriptomic and genomic data. *Proceedings of the National Academy of Sciences*, *115*(24), 6249-6254.

Kardong, K. V. (Ed.). (2012). *Vertebrates: Comparative Anatomy, Function, Evolution* (Sixth Edition). New York: McGraw Hill Education.

Kardong, K. V. (Ed.). (2018). *Vertebrates: Comparative Anatomy, Function, Evolution* (Eighth Edition). New York: McGraw Hill Education.

Klug, S., Tütken, T., Wings, O., Pfretzschner, H. U., & Martin, T. (2010). A Late Jurassic freshwater shark assemblage (Chondrichthyes, Hybodontiformes) from the southern Junggar Basin, Xinjiang, Northwest China. *Palaeobiodiversity and Palaeoenvironments, 90*(3), 241-257. doi:1 0.1007/s12549-010-0032-2

Kovalchuk, O. M., & Anfimova, G. V. (2020). Lepisosteiform fish (Holostei) ganoid scales from the middle jurassic deposits of Ukraine. *Zoodiversity, 54*(1), 35-42. doi: 10.15407/zoo2020.01.035

Kriwet, J. (1998). Late Jurassic Elasmobranch and Actinopterygian fishes from Portugal and Spain. *Cuadernos de Geologia Ibérica, 24*, 241-260.

Kriwet, J. (2000). The fish fauna from the Guimarota mine. In M. Krebs (Eds.), *Guimarota: A Jurassic Ecosystem* (41-50). München: Verlag Dr. Friedrich Pfeil.

Kriwet, J. (2002). Pycnodont fish remains (Neopterygii: Pycnodontiformes) from the Kimmeridgian (Upper Jurassic) of the Lusitanian Basin (Central Portugal). *Neues Jahrbuch für Geologie und Paläontologie-Monatshefte, 2002*(10), 577-587. doi: 10.1127/njgpm/2002/2002/577

Kriwet, J. (2004). Late Jurassic selachians (Chondrichthyes: Hybodontiformes, Neoselachii) from Central-Portugal. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte, 2004*(4), 233-256. doi: 10.1127/njgpm/2004/2004/233

Kriwet, J. (2005a). An amioid fish (Neopterygii, Amiiformes) from the Late Jurassic of the Iberian Peninsula. *Geobios, 38*(1), 99-106. doi: 10.1016/j.geobios.2003.07.004

Kriwet, J. (2005b). A comprehensive study of the skull and dentition of pycnodont fishes. *Zitteliana, 45*, 135-188.

Kriwet, J., & Klug, S. (2008). Diversity and biogeography patterns of Late Jurassic neoselachians (Chondrichthyes: Elasmobranchii). *Geological Society, London, Special Publications, 295*(1), 55-70. doi: 10.1144/SP295.5

Kriwet, J., Kiessling, W., & Klug, S. (2009). Diversification trajectories and evolutionary life-history traits in early sharks and batoids. *Proceedings of the Royal Society B: Biological Sciences, 276*(1658), 945-951. doi: 10.1098/rspb.2008.1441

Kullberg, J. C. R. (2000). *Evolução Tectónica Mesozóica da Bacia Lusitaniana* (Ph.D. Thesis), 361 p.

Kullberg, J. C., Mouterde, R., & Rocha, R. B. (1997). Reinterpretation de l'Histoire Stratigraphique et Tectonique de la Structure de Serra de El-Rei (Portugal). *Cahiers Université Catholique de Lyon, 10*, 191-208.

Kullberg, J. C., Rocha, R. B., Soares, A. F., Rey, J., Terrinha, P., Callapez, P., & Martins, L. (2006). A Bacia Lusitaniana: Estratigrafia, Paleogeografia e Tectónica. In R. Dias, A. Araújo, P. Terrinha & J. C. Kullberg (Eds.), *Geologia de Portugal no contexto da Ibéria* (317-368). Évora: Universidade de Évora.

Leinfelder, R. R. (1986). Facies, Stratigraphy and Paleogeographic Analysis of Upper? Kimmeridgian to Upper Portlandian Sediments in the Environs of Arruda dos Vinhos, Estremadura, Portugal. *Münchner Geowissenschaftliche Abhandlungen, 7,* 1-216.

Leinfelder, R. R. (1987). Multifactorial control of sedimentation patterns in an ocean marginal basin: The Lusitanian Basin (Portugal) during the Kimmeridgian and Tithonian. *Geologische Rundschau*, *76*(2), 599-631. doi: 10.1007/BF01821094

Leinfelder, R. R. (1993). A sequence stratigraphic approach to the Upper Jurassic mixed carbonate-siliciclastic succession of the central Lusitanian Basin, Portugal. *Profil*, *5,* 119-140.

Leinfelder, R. R., & Wilson, R. C. L. (1989). Seismic and sedimentologic features of Oxfordian-Kimmeridgian syn-rift sediments on the eastern margin of the Lusitanian Basin. *Geologische Rundschau, 78*(1), 81-104. doi: 10.1007/BF01988355

Leuzinger, L., Cuny, G., Popov, E., & Billon-Bruyat, J. P. (2017). A new chondrichthyan fauna from the Late Jurassic of the Swiss Jura (Kimmeridgian) dominated by hybodonts, chimaeroids and guitarfishes. *Papers in Palaeontology*, *3*(4), 471-511. doi: 10.1002/spp2.1085

Long, J. A. (Ed.). (2011). *The Rise of Fishes: 500 Million Years of Evolution* (Second Edition). Maryland: John Hopkins University Press.

Lopez-Arbarello, A. (2012). Phylogenetic Interrelationships of Ginglymodian Fishes (Actinopterygii: Neopterygii). *PLoS One*, *7*(7), e39370. doi: 10.1371/journal.pone.0039370

López-Arbarello, A., & Sferco, E. (2018). Neopterygian phylogeny: the merger assay. *Royal Society Open Science*, *5*(3), 172337. doi: 10.1098/rsos.172337

Lund, R. (2000). The new actinopterygian order Guildayichthyiformes from the Lower Carboniferous of Montana (USA). *Geodiversitas*, *22*(2), 171-206.

Maisey, J. G. (1987). Cranial anatomy of the Lower Jurassic shark *Hybodus reticulatus* (Chondrichthyes: Elasmobranchii), with comments on hybodontid systematics. *American Museum Novitates, 2878,* 1-39.

Maisey, J. G. (2012). What is an 'elasmobranch'? The impact of palaeontology in understanding elasmobranch phologeny and evolution. *Journal of Fish Biology, 80,* 918-951. doi: 10.1111/j.1095-8649.2012.03245.x

Malafaia, E., Mocho, P., Escaso, F., Dantas, P., & Ortega, F. (2018). Carcharodontosaurian remains (Dinosauria, Theropoda) from the Upper Jurassic of Portugal. *Journal of Paleontology*, *93*(1), 157-172. doi: 10.1017/jpa.2018.47

Malafaia, E., Ortega, F., Escaso, F., Dantas, P., Pimentel, N., Gasulla, J. M., Ribeiro, B., Barriga, F., & Sanz, J. L. (2010). Vertebrate fauna at the *Allosaurus* fossil-site of Andrés (Upper Jurassic), Pombal, Portugal. *Journal of Iberian Geology, 36*(2), 193-204. doi: 10.5209/rev_JIGE.2010.v36.n2.7

Manuppella, G., Antunes, M. T., Pais, J., Ramalho, M. M., & Rey, J. (1999). Notícia

Explicativa da Folha 30-A, Lourinhã. *Instituto Geológico e Mineiro, Lisboa*, 83 p.

Martinius, A. W., & Gowland, S. (2010). Tide-influenced fluvial bedforms and tidal bore deposits (Late Jurassic Lourinhã Formation, Lusitanian Basin, Western Portugal). *Sedimentology*, *58*(1), 285-324. doi: 10.1111/j.1365-3091.2010.01185.x

Mateus, O., Dinis, J., & Cunha, P. P. (2013). Upper Jurassic to Lowermost Cretaceous of the Lusitanian Basin, Portugal – landscapes where dinosaurs walked. *Ciências da Terra*, *19*(1), 75-97. doi: 10.21695/cterra/esj.v19i1.355

Mocho, P., Royo-Torres, R., & Ortega, F. (2017). New data of the Portuguese brachiosaurid *Lusotitan atalaiensis* (Sobral Formation, Upper Jurassic). *Historical Biology*, *29*(6), 789-817. doi: 10.1080/08912963.2016.1247447

Moureau, M., & Brace, G. (Eds.). (2000). *Dictionnaire des Sciences de la Terre/Comprehensive Dictionary of Earth Science - English-French, French-English*. Paris: Éditions Technip.

Mouterde, R., Ramalho, M., Rocha, R. B., Ruget, C., & Tintant, H. (1972). Le Jurassique du Portugal - Esquisse Stratigraphique et Zonale. *Boletim da Sociedade Geológica de Portugal*, *18*(1), 73-104.

Parker, F. L. (1958). Contributions from the Cushman Foundation for Foraminiferal Research. *Volume IX, Part 1*, 24.

Rasmussen, E. S., Lomholt, S., Andersen, C., & Vejbæk, O. V. (1998). Aspects of the structural evolution of the Lusitanian Basin in Portugal and the shelf and slope area offshore Portugal. *Tectonophysics*, *300*(1-4), 199-225. doi: 10.1016/S0040-1951(98)00241-8

Rees, J. (2008). Interrelationships of Mesozoic hybodont sharks as indicated by dental morphology – preliminary results. *Acta Geologica Polonica*, *58*(2), 217-221.

Rees, J., & Underwood, C. J. (2005). Hybodont sharks from the Middle Jurassic of the Inner Hebrides, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, *96*, 351-363. doi: 10.1017/S0263593300001346

Rees, J., & Underwood, C. J. (2008). Hybodont sharks of the English Bathonian and Callovian (Middle Jurassic). *Palaeontology*, *51*(1), 117-147. doi: 10.1111/j.1475-4983.2007.00737.x

Reif, W. E. (1973). Morphologie und Ultrastruktur des Hai-“Schmelzes”. *Zoologica Scripta*, *2*(5-6), 231-250.

Romano, C., Koot, M. B., Kogan, I., Brayard, A., Minikh, A. V., Brinkmann, W., Bucher, H., & Kriwet, J. (2016). Permian–Triassic Osteichthyes (bony fishes): diversity dynamics and body size evolution. *Biological Reviews*, *91*(1), 106-147. doi: 10.1111/brv.12161

Sauvage, H. E. (1897-98). Vertébrés fossiles du Portugal - Contributions à l'étude des Poissons et des Reptiles du Jurassique et du Crétacique. *Direction des Travaux*

Géologiques du Portugal. Lisbonne: Imprimerie de l'Académie Royale des Sciences, 47 p., 10 pl.

Schneider, S., Fürsich, F. T., & Werner, W. (2009). Sr-isotope stratigraphy of the Upper Jurassic of central Portugal (Lusitanian Basin) based on oyster shells. *International Journal of Earth Sciences, 98*(8), 1949-1970. doi: 10.1007/s00531-008-0359-3

Schultze, H. -P. (1996). The scales of Mesozoic actinopterygians. In G. Arratia, & G. Viohl (Eds.), *Mesozoic Fishes - Systematics and Paleoecology* (83-93). München: Verlag Dr. Friedrich Pfeil.

Schultze, H. -P. (2018). Hard tissues in fish evolution: history and current issues. *Cybium: International Journal of Ichthyology*, *42*(1), 29-39.

Stumpf, S., & Kriwet, J. (2019). A new Pliensbachian elasmobranch (Vertebrata, Chondrichthyes) assemblage from Europe, and its contribution to the understanding of late Early Jurassic elasmobranch diversity and distributional patterns. *PalZ, 93*, 637-658. doi: 10.1007/s12542-019-00451-4

Stumpf, S., López-Romero, F. A., Kindlimann, R., Lacombat, F., Pohl, B., & Kriwet, J. (2021). A unique hybodontiform skeleton provides novel insights into Mesozoic chondrichthyan life. *Papers in Palaeontology*, *7*(3), 1479-1505. doi: 10.1002/spp2.1350

Taylor, A. M., Gowland, S., Leary, S., Keogh, K. J., & Martinius, A. W. (2013). Stratigraphical correlation of the Late Jurassic Lourinhã Formation in the Consolação Sub-basin (Lusitanian Basin), Portugal. *Geological Journal*, *49*(2), 143-162. doi: 10.1002/gj.2505

Wen, W., Zhang, Q. Y., Hu, S. X., Zhou, C. Y., Xie, T., Huang, J. Y., Chen, Z. Q., & Benton, M. J. (2012). A new basal actinopterygian fish from the Anisian (Middle Triassic) of Luoping, Yunnan Province, southwest China. *Acta Palaeontologica Polonica*, *57*(1), 149-160. doi: 10.4202/app.2010.0089

Wilson, R. (1979). A reconnaissance study of the Upper Jurassic sediments of the Lusitanian Basin. *Ciências da Terra (UNL), 5*, 53-84.

Zbyszewski, G., Almeida, F. M., & Assunção, C. T. (1955). Carta Geológica de Portugal à escala 1:50000. Notícia Explicativa da Folha 30-C Torres Vedras. *Serviços Geológicos de Portugal, Lisboa*, 33 p.

10.1 Websites consulted

Pollerspöck, J. & Straube, N. (2021). www.shark-references.com, World Wide Web electronic publication, Version 2021.