



HAL
open science

New marine vertebrates (elasmobranchs, actinopterygians, reptiles) from the Upper Cretaceous Arabic Platform of SE Turkey

Nathalie Bardet, Guillaume Guinot, İsmail Ömer Yılmaz, İzzet Hoşgör

► To cite this version:

Nathalie Bardet, Guillaume Guinot, İsmail Ömer Yılmaz, İzzet Hoşgör. New marine vertebrates (elasmobranchs, actinopterygians, reptiles) from the Upper Cretaceous Arabic Platform of SE Turkey. *Comptes Rendus. Palevol*, 2022, 21 (38), pp.837-845. 10.5852/cr-palevol2022v21a38. mnhn-03864253

HAL Id: mnhn-03864253

<https://mnhn.hal.science/mnhn-03864253>

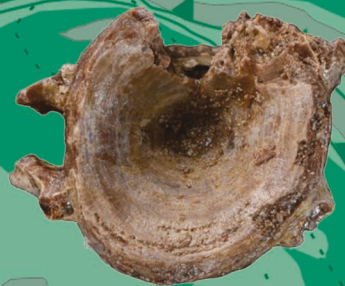
Submitted on 21 Nov 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

**New marine vertebrates (elasmobranchs,
actinopterygians, reptiles) from the Upper
Cretaceous Arabic Platform of SE Turkey**

Nathalie BARDET, Guillaume GUINOT,
İsmail Ömer YILMAZ & İzzet HOŞGÖR



DIRECTEURS DE LA PUBLICATION / PUBLICATION DIRECTORS :
Bruno David, Président du Muséum national d'Histoire naturelle
Étienne Ghys, Secrétaire perpétuel de l'Académie des sciences

RÉDACTEURS EN CHEF / EDITORS-IN-CHIEF: Michel Laurin (CNRS), Philippe Taquet (Académie des sciences)

ASSISTANTE DE RÉDACTION / ASSISTANT EDITOR: Adenise Lopes (Académie des sciences; cr-palevol@academie-sciences.fr)

MISE EN PAGE / PAGE LAYOUT: Audrina Neveu (Muséum national d'Histoire naturelle; audrina.neveu@mnhn.fr)

RÉVISIONS LINGUISTIQUES DES TEXTES ANGLAIS / ENGLISH LANGUAGE REVISIONS: Kevin Padian (University of California at Berkeley)

RÉDACTEURS ASSOCIÉS / ASSOCIATE EDITORS (*, *took charge of the editorial process of the article/a pris en charge le suivi éditorial de l'article*):

Micropaléontologie/*Micropalaeontology*

Maria Rose Petrizzo (Università di Milano, Milano)

Paléobotanique/*Palaeobotany*

Cyrille Prestianni (Royal Belgian Institute of Natural Sciences, Brussels)

Métazoaires/*Metazoa*

Annalisa Ferretti (Università di Modena e Reggio Emilia, Modena)

Paléochthyologie/*Palaeoichthyology*

Philippe Janvier (Muséum national d'Histoire naturelle, Académie des sciences, Paris)

Amniotes du Mésozoïque/*Mesozoic amniotes*

Hans-Dieter Sues (Smithsonian National Museum of Natural History, Washington)

Tortues/*Turtles*

Juliana Sterli* (CONICET, Museo Paleontológico Egidio Feruglio, Trelew)

Lépidosauromorphes/*Lepidosauromorphs*

Hussam Zaher (Universidade de São Paulo)

Oiseaux/*Birds*

Eric Buffetaut (CNRS, École Normale Supérieure, Paris)

Paléomammalogie (mammifères de moyenne et grande taille)/*Palaeomammalogy (large and mid-sized mammals)*

Lorenzo Rook (Università degli Studi di Firenze, Firenze)

Paléomammalogie (petits mammifères sauf Euarchontoglires)/*Palaeomammalogy (small mammals except for Euarchontoglires)*

Robert Asher (Cambridge University, Cambridge)

Paléomammalogie (Euarchontoglires)/*Palaeomammalogy (Euarchontoglires)*

K. Christopher Beard (University of Kansas, Lawrence)

Paléoanthropologie/*Palaeoanthropology*

Roberto Macchiarelli (Université de Poitiers, Poitiers)

Archéologie préhistorique/*Prehistoric archaeology*

Marcel Otte (Université de Liège, Liège)

RÉFÉRÉS / REVIEWERS: <https://sciencepress.mnhn.fr/periodiques/comptes-rendus-palevol/referes-du-journal>

COUVERTURE / COVER:

Teeth of the shark *Ptychodus* and the mosasaur *Platecarpus*, vertebra of the actinopterygian *Enchodus*. Credits: Philippe Loubry (CR2P, CNRS, MNHN).

Comptes Rendus Palevol est indexé dans / *Comptes Rendus Palevol is indexed by:*

- Cambridge Scientific Abstracts
- Current Contents® Physical
- Chemical, and Earth Sciences®
- ISI Alerting Services®
- Geoabstracts, Geobase, Georef, Inspec, Pascal
- Science Citation Index®, Science Citation Index Expanded®
- Scopus®.

Les articles ainsi que les nouveautés nomenclaturales publiés dans *Comptes Rendus Palevol* sont référencés par / *Articles and nomenclatural novelties published in Comptes Rendus Palevol are registered on:*

- ZooBank® (<http://zoobank.org>)

Comptes Rendus Palevol est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris et l'Académie des sciences, Paris
Comptes Rendus Palevol is a fast track journal published by the Museum Science Press, Paris and the Académie des sciences, Paris

Les Publications scientifiques du Muséum publient aussi / *The Museum Science Press also publish:*

Adansonia, Geodiversitas, Zoosystema, Anthropolozologica, European Journal of Taxonomy, Naturae, Cryptogamie sous-sections *Algologie, Bryologie, Mycologie*.

L'Académie des sciences publie aussi / *The Académie des sciences also publishes:*

Comptes Rendus Mathématique, Comptes Rendus Physique, Comptes Rendus Mécanique, Comptes Rendus Chimie, Comptes Rendus Géoscience, Comptes Rendus Biologies.

Diffusion – Publications scientifiques Muséum national d'Histoire naturelle

CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)

Tél.: 33 (0)1 40 79 48 05 / Fax: 33 (0)1 40 79 38 40

diff.pub@mnhn.fr / <https://sciencepress.mnhn.fr>

Académie des sciences, Institut de France, 23 quai de Conti, 75006 Paris.

© This article is licensed under the Creative Commons Attribution 4.0 International License (<https://creativecommons.org/licenses/by/4.0/>)
ISSN (imprimé / print): 1631-0683/ ISSN (électronique / electronic): 1777-571X

New marine vertebrates (elasmobranchs, actinopterygians, reptiles) from the Upper Cretaceous Arabic Platform of SE Turkey

Nathalie BARDET

Centre de Recherche en Paléontologie – Paris (CR2P),
UMR 7207 CNRS-MNHN-SU, Muséum National d'Histoire Naturelle,
CP 38, 57 rue Cuvier, 75005 Paris (France)
nathalie.bardet@mnhn.fr (corresponding author)

Guillaume GUINOT

Institut des Sciences de l'Evolution de Montpellier (ISEM),
Université de Montpellier, CNRS, IRD, CC 064, place Eugène Bataillon,
34095 Montpellier Cedex 5 (France)

İsmail Ömer YILMAZ

Department of Geological Engineering,
Middle East Technical University, 06800 Ankara (Turkey)

İzzet HOŞGÖR

Aladdin Middle East Ltd., 06680, Çankaya, Ankara (Turkey)

Submitted on 14 April 2021 | Accepted on 16 July 2021 | Published on 24 October 2022

urn:lsid:zoobank.org:pub:9380CB6F-4FA6-4D07-A58A-1976F141FA65

Bardet N., Guinot G., Yılmaz İ. Ö. & Hoşgör İ. 2022. — New marine vertebrates (elasmobranchs, actinopterygians, reptiles) from the Upper Cretaceous Arabic Platform of SE Turkey. *Comptes Rendus Palevol* 21 (38): 837-845. <https://doi.org/10.5852/cr-palevol2022v21a38>

ABSTRACT

Here we describe new marine vertebrate remains, mainly isolated teeth, from the Upper Cretaceous (Coniacian-Santonian) of near Mardin, SE Turkey. This is the first report in this area of ptychodontid sharks (elasmobranchs), enchodontid teleosts (actinopterygians) and mosasaurid squamates (reptiles). The respective taxa *Ptychodus* cf. *mortoni*, *Enchodus* sp., *Platecarpus* sp. and Mosasaurinae indet. are described. These new data improve our knowledge on early Late Cretaceous marine vertebrate faunas from the Arabic Platform, classically known previously mostly from the Maastrichtian outcrops of Middle-East and Northwestern Africa, and extend the palaeobiogeographical distribution of these taxa into the western part of the Mediterranean Tethys, confirming their cosmopolitan status.

KEY WORDS
Ptychodontidae,
Enchodontidae,
Mosasauridae,
Upper Cretaceous,
Turkey,
Arabic Platform,
palaeobiogeography.

RÉSUMÉ

Nouveaux restes de vertébrés marins (élasmobranches, actinoptérygiens, reptiles) du Crétacé supérieur de la Plateforme Arabique, SE de la Turquie.

Nous décrivons ici de nouveaux restes de vertébrés marins, principalement des dents isolées, provenant du Crétacé supérieur (Coniacien-Santonien) près de Mardin, au Sud-Est de la Turquie. C'est la première mention dans cette région de requins ptychodontidés (élasmobranches), de téléostéens enchodontidés (actinoptérygiens) et de squamates mosasauridés (reptiles). Les taxons respectifs, à savoir *Ptychodus cf. mortoni*, *Enchodus* sp., *Platecarpus* sp. et un Mosasaurinae indet., sont décrits. Ces nouvelles données améliorent notre connaissance des faunes de vertébrés marins du début du Crétacé supérieur de la Plateforme Arabique, auparavant classiquement connues principalement à partir des gisements du Maastrichtien du Proche-Orient et d'Afrique du Nord-Ouest, et étendent la distribution paléobiogéographique de ces taxons dans la partie occidentale de la Téthys méditerranéenne, confirmant leur caractère cosmopolite.

MOTS CLÉS

Ptychodontidae,
Enchodontidae,
Mosasauridae,
Crétacé supérieur,
Turquie,
Plateforme Arabique,
paléobiogéographie.

INTRODUCTION

Although Mesozoic vertebrate remains have been frequently mentioned in geological reports of Turkey in the last forty years, they remain mostly undescribed. Most remains have been found in the Triassic, namely fish and placodonts in the Middle Triassic of southwestern Turkey (Beltan *et al.* 1979), phytosaurs in the Late Triassic of southwestern Turkey (Buffetaut *et al.* 1988), ichthyosaurs in the Late Triassic of northwestern Turkey (Mouanga *et al.* 2011), and finally temnospondyls in the Early Triassic of southeastern Turkey (Fortuny *et al.* 2015). Fishes have also been described in the Late Jurassic of western Turkey (Forey *et al.* 1985).

As far as Cretaceous vertebrate remains are concerned, most have been found only recently. From the Pontids (northwestern Turkey), Bardet & Tunoğlu (2002) described from the Maastrichtian of near Kastamonu jaw fragments with teeth of the mosasaurid squamate *Mosasaurus hoffmanni* Mantell, 1829, whereas Jouve *et al.* (2017) described partial jaw and limb bones of the hylaeochampsid crocodylomorph *Turcosuchus okani* Jouve *et al.* 2017 in the Barremian of near Zonguldak (Fig. 1). In the Upper Cretaceous carbonate platform of the Mardin area (southeastern Turkey), Aslan (1975) was the first to mention the occurrence of the odontaspidid shark *Odontaspis cuspidata* (Agassiz, 1843) near Şanlı, in the Mazıdağı region (Figs 1; 2). This area preserves sediments that were deposited on the Mardin High. More recently, Yılmaz *et al.* (2018) described selachian teeth in the Coniacian-Santonian Karababa Formation of the close locality of Taşıt (Figs 1; 2), including the lamniform sharks *Squalicorax lindstromi* (Davis, 1890), *Pseudocorax cf. granti* Cappetta & Case, 1975 and *Scapanorhynchus cf. lewisii* (Davis, 1887), as well as the sclerorhynchiform ray *Ctenopristis jordanicus* Mustafa, Case & Zalmout, 2002. Finally, new marine vertebrate remains, including selacians, actinopterygiens and marine reptiles, were briefly mentioned in the Coniacian-Santonian Karababa Formation of Şanlı by Yılmaz *et al.* (2014) (Figs 1; 2), the aim of this paper being to describe them for the first time.

GEOLOGICAL AND STRATIGRAPHICAL SETTING

In Southeastern Turkey, the Mardin area (Figs 1; 2) offers a rare opportunity to study stratigraphical successions from Cambrian to Palaeogene (Yılmaz *et al.* 2018; Hoşgör & Yılmaz 2019). During most of the early Mesozoic, but more especially during Cretaceous to Eocene times, southeastern Turkey was situated at the southern margin of the Neo-Tethys Ocean (Barrier & Vrielynck 2008) (Fig. 3). During this period of global sea-level rise, this area was periodically covered by transgression, south and east, over the margins of the Arabian Platform (Ala & Moss 1979). As the transgression flooded the north-facing passive margin of the Arabian Platform during the Aptian to Campanian, the carbonates of the Mardin Group were deposited (Cater & Gillcrist 1994).

The best exposures of the Mardin Group (Areban, Sabunsuyu, Derdere and Karababa Formations) in this area are along the road from Derik to Mazıdağı, north of Mardin, and roadside quarries south of Mardin (Beer 1966; Yılmaz *et al.* 2018) (Fig. 2A). The base of the sequence (Areban clastics) is not exposed in the Mazıdağı area. The sequence above the Areban clastics is divided into the Sabunsuyu Formation (Albian), the Derdere Formation (Cenomanian-Turonian), and the Karababa Formation (late Coniacian-late Santonian) (Beer 1966; Yılmaz *et al.* 2018; Hoşgör & Yılmaz 2019) (Fig. 2B). In the Derik area, the Mardin Group is unconformably overlain by the middle Campanian Adiyaman Group (Karaboğaz Formation) and is itself conformably overlain by the Bozova (Campanian) and Maastrichtian Germav Formation (Cater & Gillcrist 1994; Hoşgör & Yılmaz 2019; Yılmaz *et al.* 2018, 2021).

In the Mazıdağı-Şanlı area, the age of the Karababa Formation that yielded the marine vertebrate remains here mentioned was determined by Köylüoğlu (1988) and Yılmaz *et al.* (2018), who found an association of common upper Coniacian-upper Santonian genera of benthic and planktonic foraminifers. A detailed description and analysis of the stratigraphic intervals of the Şanlı area (Fig. 2) can be found in Yılmaz *et al.* (2018).



Fig. 1. — Occurrences of Cretaceous vertebrate remains from Turkey. Data from Aslan (1975), Bardet & Tunçoğlu (2002), Jouve *et al.* (2017), Yılmaz *et al.* (2014, 2018) and this study. (Şanlı section, Mazıdağı area)

The Şanlı section (Fig. 2B) has a thickness of about 9 m and consists of light brown to beige bioclastic limestone, with intercalations of dark grey bioclastic phosphatic mudstone layers, representing a coastal marine environment where upwelling currents developed, which are associated with pelagic facies and phosphate deposits on the drowned carbonate platform.

The new vertebrate remains were collected from surface outcrops at the lower part of the Şanlı section (see Fig. 2B), which represents close stratigraphic levels to those of Taşit where the selachian remains of Yılmaz *et al.* (2018) were found.

PALAEONTOLOGY

The marine vertebrate fauna of the Coniacian-Santonian of Şanlı in SE Turkey includes remains of ptychodontid elasmobranchs (Chondrichthyes), enchodontid actinopterygians (Osteichthyes), mosasaurid squamates (Reptilia), as well as very fragmentary and undetermined fish vertebral centra. Though being scarce, these remains are interesting because they document a new Mesozoic vertebrate outcrop in Turkey, as well as an early Late Cretaceous marine vertebrate fauna of the Arabic Platform, in the Southern Margin of the Tethys Ocean. The specimens are kept in the collections of the Department of Geological Engineering, Middle East Technical University (Ankara, Turkey) under collection numbers P/S-C 0045 to P/S-C 0051.

ELASMOBRANCHS

Elasmobranchii includes all living sharks, rays and skates as well as their fossil relatives and several extinct clades. Although they probably originated in the late Paleozoic (Ivanov 2005), they remained inconspicuous before their first major radiation in the Jurassic (Guinot & Cavin 2016). This was followed by a series of diversification events until the Late Cretaceous, which

probably represents an all-time diversity peak for this clade (Guinot & Cavin 2016). The Late Cretaceous witnessed the diversification of many living elasmobranch clades, as well as several extinct groups. Among them, the family Ptychodontidae originated in the late Early Cretaceous and flourished in the Late Cretaceous with over 30 species. This family gathers durophagous taxa of whose higher-level systematic position has long remained uncertain, but are considered as belonging to elasmobranch sharks (Cappetta 2012; Hoffman *et al.* 2016; Cuny *et al.* 2017; Hamm 2019).

Ptychodontids are represented in our samplings by two latero-posterior teeth (P/S-C 0045 and P/S-C 0046, Fig. 4A-D) referred to the genus *Ptychodus* Agassiz, 1834. The teeth are low-crowned, asymmetrical and more developed mesio-distally than labio-lingually. The crown consists of a low conical cusp with numerous ridges radiating from its apex. The ridges successively bifurcate toward the marginal area where they gradually taper into a granular ornament made of short reticulated ridges. The marginal area is more developed mesially, where an articular depression is present although less developed in the lateral-most tooth (the smallest one, P/S-C 0046, Fig. 4C-D). Another articular depression is located on the lingual margin of the crown. The crown overhangs the anaulacorhizous root at all points in occlusal view. The root is asymmetrical with a convex basal face and several foramina just below the crown/root edge.

These teeth display a crown ornament made of ridges that radiate from the apex. Among nominal *Ptychodus* species, such radiating crown ornament is present in *P. mortoni* Mantell, 1836, *P. cyclodontis* Mutter, Iturralde-Vinent & Fernández Carmona, 2005 and *P. atcoensis* Hamm, 2009. The specimens reported here differ from *P. atcoensis* in having less coarse and non-chevron-like occlusal ridges and can be differentiated from laterals of *P. cyclodontis* by their broader marginal areas and lower cusp. These specimens more closely resemble latero-

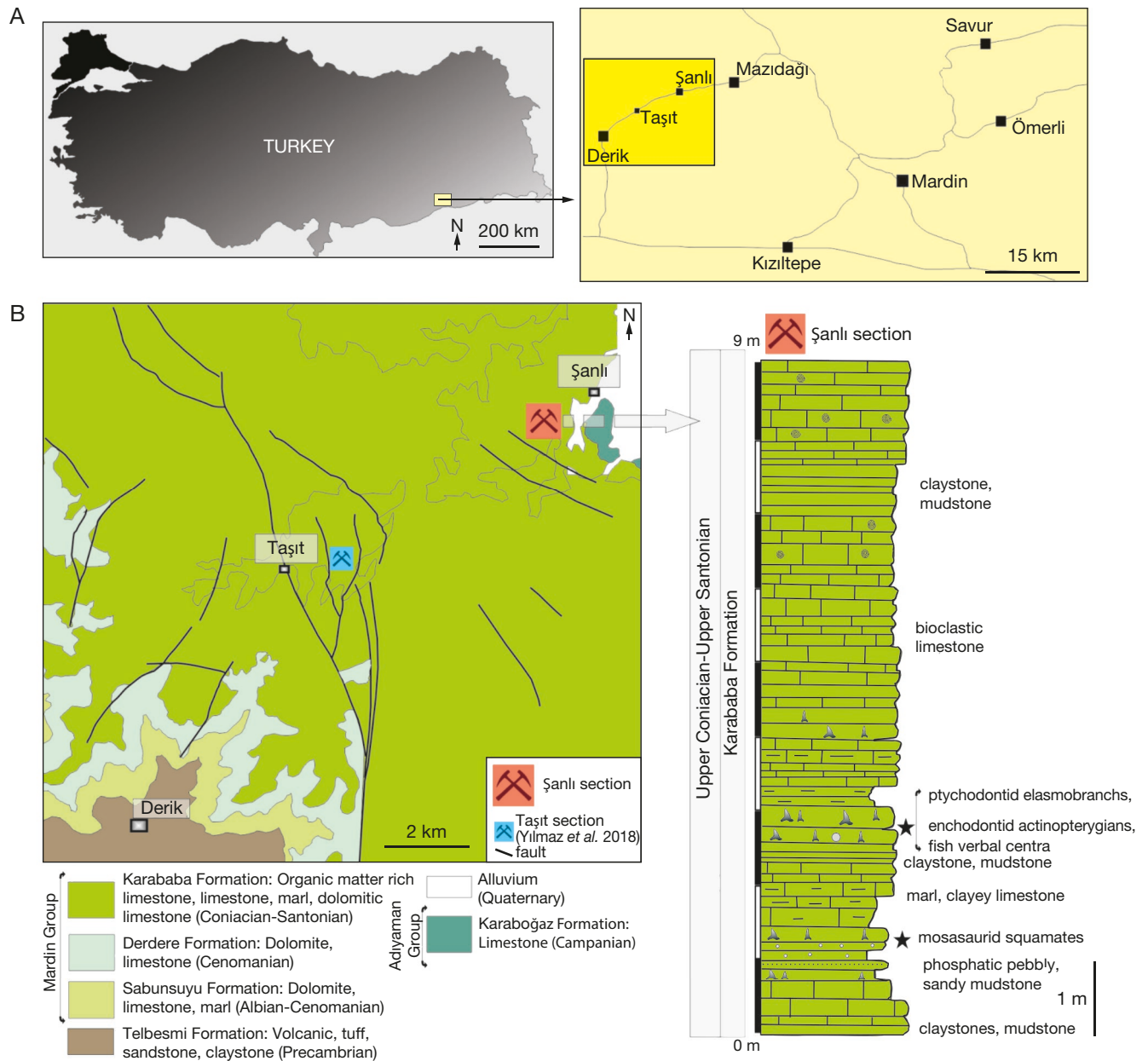


FIG. 2. — **A**, Geographic position, generalized geological and location map of the Mazıdağı-Şanlı area (after Beer 1966; MTA 2011; Yılmaz *et al.* 2018); **B**, Şanlı measured stratigraphic section.

posterior teeth of *P. mortoni* (see Hamm 2009; Shimada 2012) by their marginally bifurcating occlusal ridges and broad marginal areas. However, because of the limited number of specimens and lack of teeth from more anterior tooth files, it is preferred to refer these specimens to *Ptychodus cf. mortoni*.

ACTINOPTERYGIANS

Extant teleosts represent more than 99% of species of actinopterygians and nearly half of those of vertebrates. Represented by almost 27 000 species, teleosts are found in all marine and freshwater habitats, from abyssal to high mountain environments, and from hot springs to polar waters (Helfman *et al.* 1997). Known as early as the Early Triassic, they are well represented in the Jurassic period but one of their major diver-

sifications occurred during the Cretaceous (Guinot & Cavin 2016) where major clades still known nowadays appeared. During the Cenozoic, their tremendous diversification (Alfaro *et al.* 2009; Guinot & Cavin 2016) led to the settlement of current marine faunas.

P/S-C 0047 (Fig. 4E) is a very fragmentary but well recognizable palatine bone, bearing if complete a single terminal tooth, belonging to the genus *Enchodus* Agassiz, 1835. Though the tooth is basally broken, its cross-section is clearly asymmetrical, being anteriorly strongly convex and posteriorly almost flat with a median groove. It belongs to the “*petrosus*-type” as defined by Goody (1976) (see Carbot-Chanona & Than-Marchese 2013). Both the morphology and size of the specimen are reminiscent of *Enchodus elegans* Darteville &

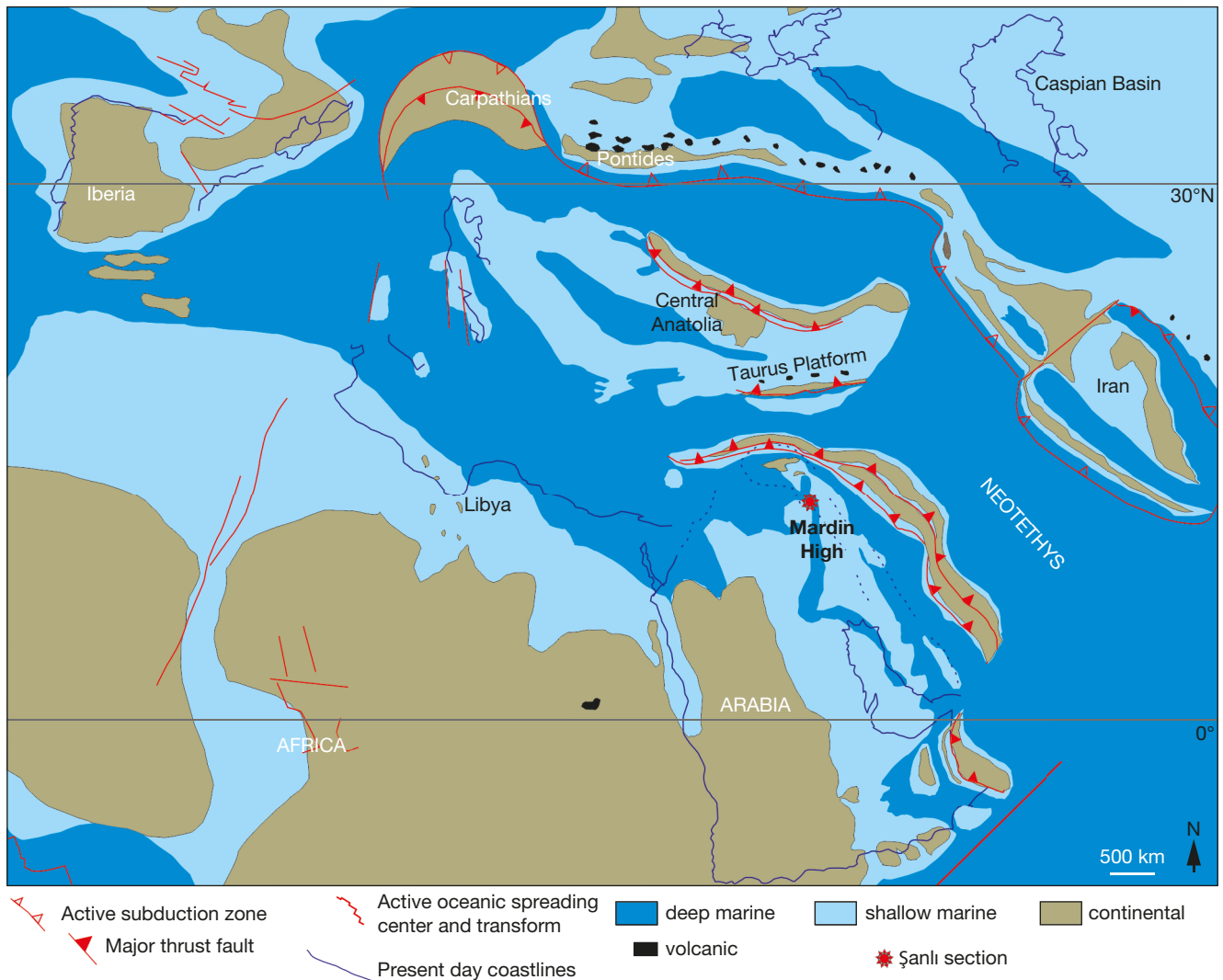


FIG. 3. — Palaeogeographical position of the studied area and facies belts during the Late Cretaceous (map after Barrier & Vrielynck 2008).

Casier, 1949 from the Maastrichtian of Middle East and North and West Africa (see bibliography in Bardet *et al.* 2000) but, due to the very fragmentary condition of the specimen, it is here referred to as *Enchodus* sp.

P/S-C 0048 (Fig. 4F) is a small vertebral centrum, around 11 mm of diameter and 8 mm long. The articular surfaces are strongly amphicoelous with acute margins. The lateral, ventral and dorsal surfaces are strongly excavated and divided by longitudinal ridges. This centrum could also belong to *Enchodus* to which it shows great similarities, especially to species known from the latest Cretaceous of Morocco and Syria (see Arambourg 1952 and Bardet *et al.* 2000).

REPTILES

Appeared as early as the Late Carboniferous and representing the first tetrapods fully adapted to life on land, reptiles underwent a spectacular secondary return to an aquatic life during the Mesozoic era, occupying a plethora of ecological niches comparable to those of current marine mammals (e.g. Bardet *et al.* 2014). Among these clades of marine reptiles

were the mosasaurids, extinct giant marine squamates 3 to 15 m long, that underwent an important radiation during the Late Turonian-Maastrichtian interval, before they disappear during the K/Pg extinction event (Bardet *et al.* 2014). They are mainly characterized by an elongated “varanoid” body, large and elongated kinetic skulls, large powerful flippers and often a hypocercal tail increasing their swimming capabilities (Lindgren *et al.* 2011). Being known by both high taxonomical diversity and ecological disparity, they were open-sea active top-predators able to cross large oceanic regions and displaying a cosmopolitan distribution favoured by marine routes largely opened during the Late Cretaceous (Bardet *et al.* 2014).

The specimens described here consist of three isolated teeth, representing two different taxa.

P/S-C 0049 (Fig. 4G-I) is an almost complete and well preserved tooth crown. It is small, being 16 mm tall, 8 mm long and 7 mm wide. In lateral view, it has the shape of a slender and narrow triangle strongly posteriorly recurved. The basal cross-section is almost rounded. The apex is sharp and bears

lingually a triangular wear facet. There is an anterior unserrated and sharp carina, extending along the height of the crown that bears in its upper half a wear facet. The posterior carina, also smooth, is less pronounced and extends on the upper half of the crown only. It is located postero-labially, indicating that the tooth belongs to the anterior to middle portion of the jaw. The labial surface is smaller than the lingual one. Both are convex. The labial surface bears smooth enamel and very poorly marked ridges located posteriorly and basally on the crown. The lingual surface is ornamented by minute ridges that are more numerous and marked on the lower half of the crown.

P/S-C 0050 (Fig. 4J-L) is an incomplete tooth crown very similar in both morphology and size to the previous one, so that it is not excluded that they could belong to the same individual. It is broken at mid-height. The basal cross-section, though slightly incomplete, appears almost circular. Anterior and posterior carinae, smooth and sharp, are preserved. They are almost antero-posteriorly aligned, indicating that this tooth was more posteriorly located on the tooth row than P/S-C 0049. As a result, the labial surface is slightly smaller than the lingual one and both are convex. The labial surface bears about ten small ridges, whereas the lingual one exhibits minute striae, more numerous and marked basally than apically.

These two teeth crown clearly belong to Russellosaurina *sensu* Bell (1997) because they bear very fine striae medially and slight ridges labially. Among russellosaurines, they clearly differ from those of Tylosaurinae which are large, robust and bear fluting and serrated carinae, and resemble those of Plioplatecarpinae that exhibit smaller teeth bearing a slender conical shape (Russell 1967; Bell 1997; Konishi & Caldwell 2011; Jiménez-Huidobro & Caldwell 2016). These teeth are clearly reminiscent to those of *Platecarpus* Cope, 1869 (see Russell 1967), and differs from those of the Campanian-Maastrichtian worldwide distributed *Plioplatecarpus* Dollo, 1882 that are more gracile, strongly posteriorly recurved and sharper (Lingham-Soliar 1994) and from all other plioplatecarpines (e.g. Russell 1967; Bell 1997; NB pers. obs). They are similar to those of *Platecarpus ictericus* (Cope, 1871) from the Coniacian-Santonian of the Western Interior Seaway of North America (Russell 1967), the Santonian of France (Bardet *et al.* 1991) and those of *P. cf. ictericus* from the Maastrichtian of Spain (see Bardet *et al.* 2013). However, this species (as well as *P. coryphaeus* (Cope, 1872)) have been synonymized with *P. tympaniticus* Cope, 1869 so that *Platecarpus* is considered now as a monotypic taxon (Konishi & Caldwell 2011). Due to the limited number of specimens however, these two teeth are here referred as *Platecarpus* sp.

P/S-C 0051 (Fig. 4M) is a large fragmentary tooth crown still embedded in a very hard mineralized matrix, preventing any safe extraction of the specimen. The crown, preserved with labial or lingual view visible, is about 34 mm high and 13 mm long basally. It has the shape of a narrow and long triangle slightly posteriorly recurved, with the anterior margin being convex and the posterior one being concave. No carinae are visible but they might be hidden by the matrix. The apex is gently rounded. The enamel, preserved on the apex only, is completely smooth and with a silky aspect. As a

whole, this tooth crown corresponds to a marginal one and occupied a median position on the tooth row. It is reminiscent of Mosasaurinae like *Mosasaurus* Conybeare, 1822, *Eremiasaurus* LeBlanc, Caldwell & Bardet, 2012 or some species of *Prognathodon* Dollo, 1889 with slender and sharp teeth like *P. kianda* Schulp, Polcyn, Mateus, Jacobs & Morais, 2008 or *P. mosasauroides* (Gaudry, 1892). Due to its very fragmentary status and the fact that these taxa are known for now only in the Maastrichtian, it is here referred with caution to an indetermined Mosasaurinae.

DISCUSSION AND CONCLUSION

The description of new marine vertebrate remains, including elasmobranchs, actinopterygians and marine reptiles, from the Coniacian-Santonian outcrop of Şanlı near Mardin in SE Turkey, permits to significantly improve our knowledge on the early evolution of Late Cretaceous marine vertebrate faunas from the Arabian Platform. Marine vertebrates from the southern Margin of the Mediterranean Tethys were so far better known by the classical faunas from the Maastrichtian phosphatic deposits of Northern Africa and Middle-East. Our work, along with the previously reported assemblage (Yılmaz *et al.* 2018), confirms the presence of a potentially diverse fauna in earlier (Coniacian-Santonian) geological formations of this region.

The elasmobranch remains reported here are referred to *Ptychodus cf. mortoni*. *Ptychodus mortoni* ranges from the Turonian to the early Campanian (see Hamm 2009) of North America (United States of America, Mexico), Europe (Italy, Belgium, United Kingdom) and Africa (Angola) and the Coniacian-Santonian specimens reported here, if proven to belong to this species, would extend its palaeobiogeographic range to the western part of the Mediterranean Tethys. To a greater extent, these two specimens are among the last records of the family Ptychodontidae, which is not found from rocks younger than early Campanian (Hamm & Shimada 2004; Cappetta 2012). This taxon adds to the elasmobranch assemblage previously reported from Taşıt (Yılmaz *et al.* 2018), which includes *Squalicorax cf. lindstromi*, *Pseudocorax cf. granti*, *Scapanorhynchus cf. lewisii*, and *Ctenopristis jordanicus*. The report of a *Ptychodus* species, which displays dental adaptations to durophagy, adds to the knowledge on the ecological structure of the elasmobranch assemblage, which contains mainly non-durophagous predators and a nectobenthic species. This assemblage is in agreement with a Coniacian-Santonian age of the sampled horizons. Furthermore, the presence of *C. jordanicus* tends to suggest a possible Santonian age for the Karababa Formation, since this species is else only known from the upper Santonian Wadi Umm Ghudran Formation of Jordan (Mustafa *et al.* 2002).

The enchodontid actinopterygian *Enchodus* is described for the first time in Turkey. *Enchodus* was a large Cretaceous open-sea predatory teleost known worldwide from about 30 species, particularly diverse during the Late Cretaceous, due to South Atlantic widening and Atlantic oceanic circu-

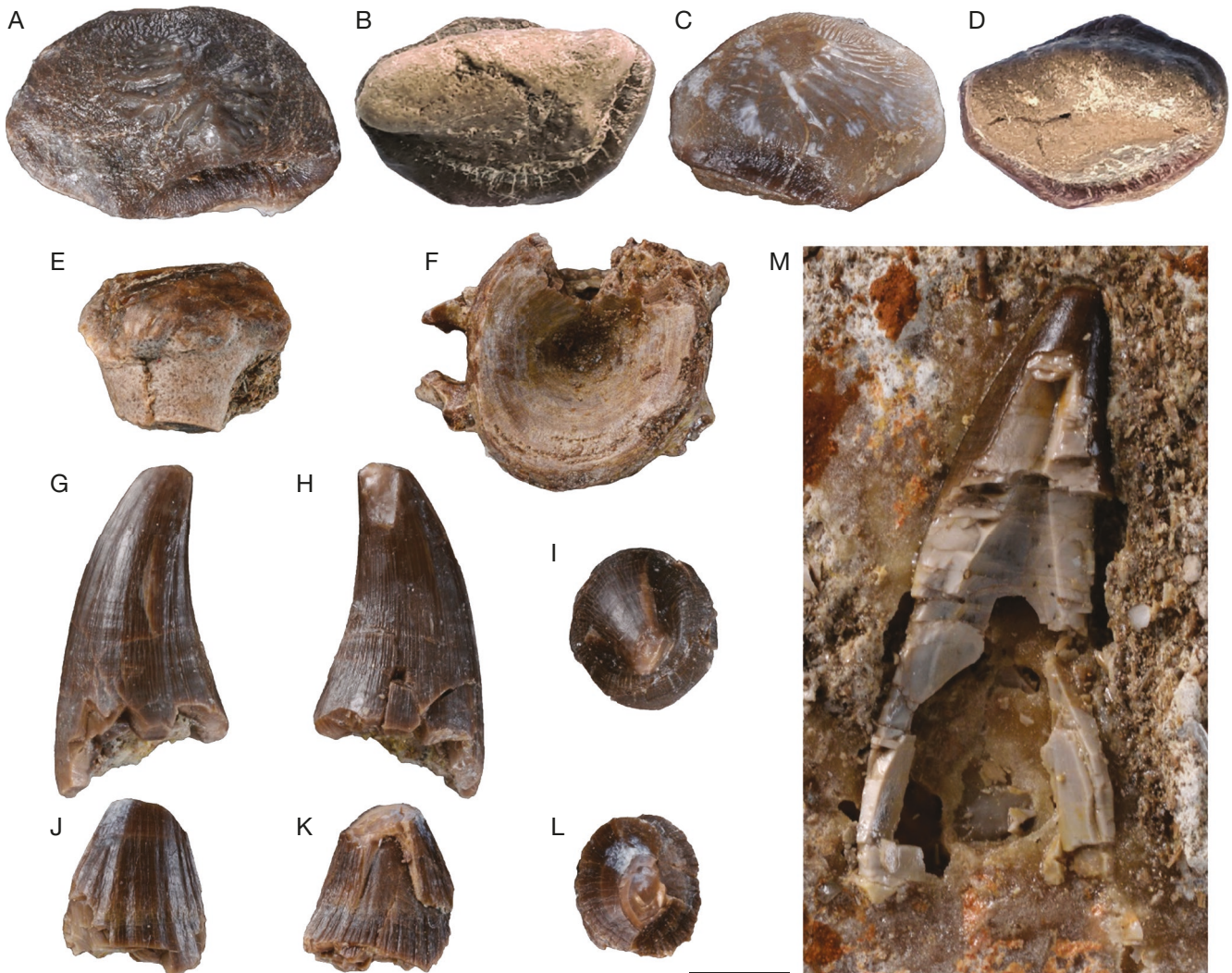


FIG. 4. — Marine vertebrate remains from the Coniacian-Santonian of Şanlı, Mardin area, southeastern Turkey: **A-D**, *Ptychodus* cf. *mortoni*: **A, B**, P/S-C 0045, latero-posterior tooth in occlusal and basal views; **C, D**, P/S-C 0046, latero-posterior tooth in occlusal and basal views; **E, F**, *Enchodus* sp.: **E**, P/S-C 0047, fragmentary palatine bone in lateral view; **F**, P/S-C 0048, vertebra in articular view; **G-L**, *Platecarpus* sp.: **G-I**, P/S-C 0049, antero-median marginal tooth in lateral, medial and occlusal views; **J-L**, P/S-C 0050, median marginal tooth in lateral, medial and occlusal views; **M**, Mosasaurinae indet., P/S-C 0051, median marginal tooth in lateral or medial view. Scale bar: 5 mm.

lation (Cavin *et al.* 2012; Andrade da Silva & Gallo 2016; Holloway *et al.* 2017). More than ten species of *Enchodus* have been described in the Late Cretaceous of North Africa and Middle-East (see bibliography in Holloway *et al.* 2017). The occurrence of *Enchodus* in Turkey represents thus both the oldest and the northernmost for the Arabic Platform.

Though both plioplatecarpine and mosasaurine mosasaurids are widespread during the Late Cretaceous, the referred specimens from the Coniacian-Santonian of Turkey represent the oldest occurrence of these two subfamilies –and also of the mosasaurid family– in this region. They also extend their palaeobiogeographical range to the western part of the Mediterranean Tethys and noteworthy attest of the early evolution of mosasaurid faunas on the Arabic Platform. *Platecarpus* is a widespread genus known mainly from the Coniacian-Campanian of North America (Western Interior Seaway; Russell 1967). Scarce remains have also been described from the Turonian-Coniacian of South America (Brazil; Bengston &

Lindgren 2005) and the Santonian and Maastrichtian of Southern Europe (France, Spain; Bardet *et al.* 1991, 2013). It is described here for the first time in Turkey, expanding considerably its palaeobiogeographical distribution to the western part of the Mediterranean Tethys and the Arabian Platform in particular.

Acknowledgements

This study is dedicated to the memory of both Zeki Yılmaz, the third author's father who passed away on October 2020, and Asiye Yılmaz, his mother who passed away on December 2020. It was supported partly by a national scientific project (TUBITAK-111Y138, The Scientific and Technological Research Council of Turkey). The authors warmly thank Philippe Loubry (CR2P, CNRS, MNHN, Paris) for the photographs of the specimens, Alexandre Lethiers (CR2P, IStEP, Paris) for the design and assembly of the plate, and Evariste Monvoisin (SEP,

MNHN, Paris) for the mechanical and chemical preparation of the specimens. Finally, we warmly thank the editor-in-chief, Michel Laurin, the associated editor, Juliana Sterli, the reviewer Anne Schulp (Leiden, The Netherlands) and an anonymous referee, which constructive comments improved our manuscript.

REFERENCES

- AGASSIZ L. 1834. — Verzeichniss der in der Peträrfakten-Sammlung des vaterländischen Museums befindlichen versteinerten Fische. *Verhandlungen der Gesellschaft des Vaterländischen Museums in Böhmen* 12: 66-71.
- AGASSIZ L. 1833-1844. — *Recherches sur les poissons fossiles*. Petit-pierre, Neuchâtel & Soleure, 442 p.
- ALA M. A. & MOSS B. J. 1979. — Comparative petroleum geology of southeast Turkey and northeast Syria. *Journal of Petroleum Geology* 1 (4): 3-27. <https://doi.org/10.1111/j.1747-5457.1979.tb00626.x>
- ALFARO M. E., SANTINI F., BROCK C., ALAMILLO H., DORNBURG A., RABOSKY D. L., CARNEVALE G. & HARMON L. J. 2009. — Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. *Proceedings of the National Academy of Sciences* 106 (32): 13410-13414. <https://doi.org/10.1073/pnas.0811087106>
- ANDRADE DA SILVA H. M. & GALLO V. 2016. — Distributional patterns of enchodontoid fishes in the Late Cretaceous. *Cretaceous Research* 65: 223-231. <https://doi.org/10.1016/j.cretres.2016.03.009>
- ARAMBOURG C. 1952. — Les vertébrés fossiles des gisements de phosphates (Maroc-Algérie-Tunisie). *Notes et Mémoires du Service Géologique du Maroc* 92: 1-372.
- ASLAN F. 1975. — Mardin-Mazıdağında bulunan bir balık dişi. *MTA Bulletin* 85: 176-177.
- BARDET N. & TUNOĞLU C. 2002. — The first mosasaur (Squamata) from the Late Cretaceous of Turkey. *Journal of Vertebrate Paleontology* 22 (3): 712-715. <https://doi.org/fnhw7m>
- BARDET N., BILOTTE M., CHRISTENSEN W. K., HANSOTTE M., MELCHIOR P. & RAYNAUD C. 1991. — Nouveaux restes et révisions de faunes exceptionnelles du Crétacé supérieur audois : les Belemnitellidae et Mosasauridae des Corbières. *Bulletin de la Société d'Études scientifiques de l'Aude* 91: 11-21.
- BARDET N., CAPPETTA H., PEREDA SUBERBIOLA X., MOUTY M., AL MALEH A. K., AHMAD A. M., KHRATA O. & GANNOUM N. 2000. — The marine vertebrate faunas from the Late Cretaceous phosphates of Syria. *Geological Magazine* 137 (3): 269-290. <https://doi.org/10.1017/S0016756800003988>
- BARDET N., MARTIN G., CORRAL J. C., PEREDA SUBERBIOLA X. & ASTIBIA H. 2013. — New mosasaurid teeth (Reptilia: Squamata) from the Maastrichtian of Albaina (Laño quarry, Condado de Treviño). *Spanish Journal of Palaeontology* 28 (1): 69-78. <https://doi.org/10.7203/sjp.28.1.17832>
- BARDET N., FALCONNET J., FISCHER V., HOUSSAYE A., JOUVE S., PEREDA-SUBERBIOLA X., PEREZ-GARCIA A., RAGE J.-C. & VINCENT P. 2014. — Mesozoic marine palaeobiogeography in response to drifting plate. *Gondwana Research* 26 (3-4): 869-887. <https://doi.org/10.1016/j.gr.2014.05.005>
- BARRIER E. & VRIELYNCK B. 2008. — *Paleotectonic maps of the Middle East*. Middle East Basins Evolution Programme, CCGM-CGMW, Paris.
- BEER H. 1966. — Mardin-Derik-Mazıdağı çevresindeki fosfatlı tabakaların jeolojisi. *Bulletin of Mineral Research and Exploration Institute* 66: 104-120.
- BELL G. B. 1997. — A phylogenetical revision of North American and Adriatic Mosasaurioidea, in CALLAWAY J. M. & NICHOLLS E. L. (eds), *Ancient Marine Reptiles*. Academic Press, San Diego: 293-332. <https://doi.org/10.1016/B978-012155210-7/50017-X>
- BELTAN L., JANVIER P., MONOD O. & WESTPHAL F. 1979. — A new marine fish and placodont reptile fauna of Ladinian age from Southwestern Turkey. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1979: 257-267.
- BENGSTON P. & LINDGREN J. 2005. — First record of the mosasaur *Platecarpus* Cope, 1869 from South America and its systematic implications. *Revista Brasileira de Paleontologia* 8 (1): 5-12. <https://doi.org/10.4072/rbp.2005.1.01>
- BUFFETAUT E., MARTIN M. & MONOD O. 1988. — Phytosaur remains from the Çenger Formation of the Lycian Taurus (Western Turkey): stratigraphical implications. *Geobios* 21 (2): 237-243. [https://doi.org/10.1016/S0016-6995\(88\)80020-2](https://doi.org/10.1016/S0016-6995(88)80020-2)
- CAPPETTA H. 2012. — *Chondrichthyes - Mesozoic and Cenozoic Elasmobranchii: Teeth, Handbook of Paleoichthyology*. Verlag F. Pfeil, Munich, 512 p.
- CAPPETTA H. & CASE G. R. 1975. — Sélaciens nouveaux du Crétacé du Texas. *Geobios* 8 (4): 303-307. [https://doi.org/10.1016/S0016-6995\(75\)80028-3](https://doi.org/10.1016/S0016-6995(75)80028-3)
- CATER J. M. L. & GILLCRIST J. R. 1994. — Karstic reservoirs of the Mid-Cretaceous Mardin Group, SE Turkey: Tectonic and eustatic controls on their genesis, distribution and preservation. *Journal of Petroleum Geology* 17 (3): 253-278. <https://doi.org/10.1111/j.1747-5457.1994.tb00134.x>
- CARBOT-CHANONA G. & THAN-MARCHESE B. 2013. — Presencia de *Enchodus* (Osteichthyes: Aulopiformes: Enchodontidae) en el Maastrichtiano (Cretácico tardío) de Chiapas, México. *Paleontología Mexicana* 63: 8-16.
- CAVIN L., ALEXOPOULOS A. & PIUZ A. 2012. — Late Cretaceous (Maastrichtian) ray-finned fishes from the island of Gavdos, southern Greece, with comments on the evolutionary history of the aulopiform teleost *Enchodus*. *Bulletin de la Société géologique de France* 183 (6): 561-572. <https://doi.org/10.2113/gssgfbull.183.6.561>
- CONYBEARE W. D. 1822. — *Mosasaurus*. The saurus of the Meuse, the Maestricht animal of Cuvier, in PARKINSON J. (ed.), *Outlines of oryctology; an introduction to the study of fossil organic remains; especially of those found in the British Strata: intended to aid the student in his enquiries respecting the nature of fossils, and their connection with the formation of the earth*. Sherwood, Neely and Jones and W. Phillips, London, 298 p.
- COPE E. D. 1869. — On the reptilian orders Pythonomorpha and Streptosauria. *Proceedings of the Boston Society of Natural History* 12: 250-266. <https://www.biodiversitylibrary.org/page/9493892>
- COPE E. D. 1871. — Verbal communication on pythonomorphs. *Proceedings of the American Philosophical Society* 11 (85): 571-572.
- COPE E. D. 1872. — Catalogue of the Pythonomorpha found in the Cretaceous strata of Kansas. *Proceedings of the American Philosophical Society* 12 (87), 264 and 12 (88): 265-287.
- CUNY G., GUINOT G. & ENAULT S. 2017. — *Evolution of Dental Tissues and Paleobiology in Selachians*. ISTE Press Limited, London, 138 p.
- DARTEVELLE E. & CASIER E. 1949. — Les poissons fossiles du Bas-Congo et des régions voisines (2^e partie). *Annales du Musée du Congo belge, A: Minéralogie, Géologie, Paléontologie* 3, 2 (2): 201-256.
- DAVIS J. W. 1887. — The fossil fishes of the chalk of Mount Lebanon, in Syria. *Scientific Transactions of the Royal Dublin Society* 2: 457-636.
- DAVIS J. W. 1890. — On the fossil fish of the Cretaceous formations of Scandinavia. *Scientific Transactions of the Royal Dublin Society* 4: 363-434.
- DOLLO L. 1882. — Note sur l'ostéologie des Mosasauridae. *Bulletin du Musée royal d'histoire naturelle de Belgique* 1: 55-80.
- DOLLO L. 1889. — Première note sur les mosasauriens de Mesvin. *Société Belge de Géologie et de Minéralogie* 3: 271-304.
- FOREY P. L., MONOD O. & PATTERSON C. 1985. — Fishes from the Akkuyu Formation (Tithonian), Western Taurus, Turkey. *Geobios* 18 (2): 195-201. [https://doi.org/10.1016/S0016-6995\(85\)80013-9](https://doi.org/10.1016/S0016-6995(85)80013-9)

- FORTUNY J., STEYER J. S. & HOŞGÖR İ. 2015. — First occurrence of temnospondyls from the Permian and Triassic of Turkey: Paleoenvironmental and paleobiogeographic implications. *Comptes Rendus Palevol* 14 (4): 281-289. <https://doi.org/10.1016/j.crpv.2015.03.001>
- GAUDRY A. 1892. — Les Pythonomorphes de France. *Mémoires de la Société géologique de France* 10: 13 + iv p.
- GOODY P. C. 1976. — *Enchodus* (Teleostei: Enchodontidae) from the Upper Cretaceous Pierre Shale of Wyoming and South Dakota with an evaluation of the North American enchodontid species. *Palaeontographica Abteilung A* 152 (4-6): 91-112.
- GUINOT G. & CAVIN L. 2016. — 'Fish' (Actinopterygii and Elasmobranchii) Diversification Patterns through Deep Time. *Biological Reviews* 91 (4): 950-981. <https://doi.org/10.1111/brv.12203>
- HAMM S. A. 2009. — New data on the occurrence and distribution of *Ptychodus* from the Upper Cretaceous (Coniacian-Santonian) of Texas. *Dallas Paleontological Society, Occasional Papers* 8: 1-31.
- HAMM S. A. 2019. — First associated tooth set of *Ptychodus anonymus* (Elasmobranchii: Ptychodontidae) in North America from the Jetmore Chalk in Kansas. *Transactions of the Kansas Academy of Science* 122 (1-2): 1-18. <https://doi.org/10.1660/062.122.0101>
- HAMM S. A. & SHIMADA K. 2004. — A Late Cretaceous durophagous shark, *Ptychodus martini* Williston, from Texas. *Texas Journal of Sciences* 56: 215-222.
- HELFMAN G. S., COLLETTE B. B. & FACEY D. E. 1997. — *The diversity of fishes*. Blackwell Science, Massachusetts: 1-736.
- 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. <https://doi.org/10.1017/jpa.2016.64>
- HOLLOWAY W. L., CLAESON K. M., SALLAM H. M., EL-SAYED S., KORA M., SERTICH J. J. W. & O'CONNOR P. M. 2017. — A new species of the neopterygian fish *Enchodus* from the Duwi Formation, Campanian, Late Cretaceous, Western Desert, Central Egypt. *Acta Palaeontologica Polonica* 62 (3): 603-611. <https://doi.org/10.4202/app.00331.2016>
- HOŞGÖR İ. & YILMAZ İ. Ö. 2019. — Paleogeographic northeastern limits of *Aphrodina dutruegi* (Cocquand, 1862) (Heterodonta, Bivalvia) from the Cenomanian of the Arabian Platform. *Rivista Italiana di Paleontologia e Stratigrafia* 125 (2): 421-431.
- IVANOV A. 2005. — Early Permian chondrichthyans of the Middle and South Urals. *Revista Brasileira de Paleontologia* 8 (2): 127-138. <https://doi.org/10.4072/rbp.2005.2.05>
- JIMÉNEZ-HUIDOBRO P. & CALDWELL M. W. 2016. — Reassessment and reassignment of the early Maastrichtian mosasaur *Hainosaurus bernardi* Dollo, 1885, to *Tylosaurus* Marsh, 1872. *Journal of Vertebrate Paleontology* 36 (3): 1-13. <https://doi.org/10.1080/02724634.2016.1096275>
- JOUBE S., SARIGÜL V., STEYER J. S. & SEN S. 2017. — The first crocodylomorph from the Mesozoic of Turkey (Barremian of Zonguldak) and the dispersal of the eusuchians during the Cretaceous. *Journal of Systematic Palaeontology* 17 (2): 111-128. <https://doi.org/10.1080/14772019.2017.1393469>
- KONISHI T. & CALDWELL M. W. 2011. — Two new plioplatecarpine (Squamata, Mosasauridae) genera from the Upper Cretaceous of North America, and a global phylogenetic analysis of plioplatecarpines. *Journal of Vertebrate Paleontology* 31 (4): 754-783. <https://doi.org/10.1080/02724634.2011.579023>
- KÖYLÜOĞLU M. 1988. — The paleontology and stratigraphy of the Beloka Formation in which Kasrik and Semikan phosphate deposits are found, Mardin-Mazıdagi, Southeast Turkey. *Bulletin of the Turkish Association of Petroleum Geologists* 1-2: 141-151.
- LEBLANC A. R. H., CALDWELL M. W. & BARDET N. 2012. — A new mosasaurine from the Maastrichtian (U. Cretaceous) phosphates of Morocco and the implications for the systematics of the Mosasaurinae. *Journal of Vertebrate Paleontology* 32 (1): 82-104. <https://doi.org/10.1080/02724634.2012.624145>
- LINDGREN J., POLCYN M. J. & YOUNG B. A. 2011. — Landlubbers to leviathans: evolution of swimming in mosasaurine mosasurs. *Paleobiology* 37 (3): 445-469. <https://doi.org/10.1666/09023.1>
- LINGHAM-SOLIAR T. 1994. — The Mosasaur *Plioplatecarpus* (Reptilia, Mosasauridae) from the Upper Cretaceous of Europe. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* 64: 177-211.
- MANTELL G. A. 1829. — A tabular arrangement of the organic remains of the county of Sussex. *Transactions of the Geological Society of London* S2-3 (1): 201-216. <https://doi.org/10.1144/transgslb.3.1.201>
- MANTELL G. A. 1836. — *A Descriptive Catalogue of the Objects of Geology, Natural History, and Antiquity (chiefly discovered in Sussex,) in the Museum attached to the Sussex Scientific and Literary Institution at Brighton*. Relfe and Fletcher, London, 41 p.
- MOUANGA G. H., SANDER M. P., KILIÇ A. M., HAGDORN H. & GÖNCÜOĞLU C. 2011. — Preliminary data on the finding of a new *Ichthyosaurus* (Family *Shastasauridae*) from the Lower Ladinian of *Kocaeli Triassic*. Proceedings of the 64th Geological Congress of Turkey, 2011: 261-262.
- MTA. 2011. — Diyarbakır-N 44 Paftası, no: 168., 1/100 000 ölçekli Türkiye Jeoloji Haritası: 42.
- MUSTAFA H. A., CASE G. R. & ZALMOUT I. S. 2002. — A new selachian fauna from the Wadi Umm Ghudran Formation (Late Cretaceous) - Central Jordan. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 226 (3): 419-444. <https://doi.org/10.1127/njgpa/226/2002/419>
- MUTTER R. J., ITURRALDE-VINENT M. & FERNÁNDEZ CARMONA J. 2005. — The first Mesozoic Caribbean shark is from the Turonian of Cuba: *Ptychodus cyclodontis* sp. nov. (?Neoselachii). *Journal of Vertebrate Paleontology* 25 (4): 976-978. [https://doi.org/10.1671/0272-4634\(2005\)025\[0976:TFMCSI\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2005)025[0976:TFMCSI]2.0.CO;2)
- RUSSELL D. A. 1967. — Systematics and morphology of American mosasurs. *Bulletin of the Peabody Museum of Natural History* 23: 1-240.
- SCHULP A. S., POLCYN M. J., MATEUS O., JACOBS L. L. & MORAIS M. L. 2008. — A new species of *Prognathodon* (Squamata, Mosasauridae) from the Maastrichtian of Angola, and the affinities of the mosasaur genus *Liodon*, in EVERHART M. J. (ed.), *Proceedings of the Second Mosasaur Meeting*. Fort Hays Studies Special Issue (Hays, Kansas) 3: 1-12.
- SHIMADA K. 2012. — Dentition of the Late Cretaceous shark, *Ptychodus mortoni* (Elasmobranchii, Ptychodontidae). *Journal of Vertebrate Paleontology* 32 (6): 1271-1284. <https://doi.org/10.1080/02724634.2012.707997>
- YILMAZ İ. Ö., HOŞGÖR İ., TUNOĞLU C., VINCENT P., HOUSSAYE A. & BARDET N. 2014. — *A new marine vertebrate outcrop from the Late Cretaceous (Campanian) of Southeastern Anatolia, Turkey*. Abstract Volume of the 74th Annual Meeting of the Society of Vertebrate Paleontology: 259.
- YILMAZ İ. Ö., COOK T. D., HOŞGÖR İ., WAGREICH M., REBMAN K. & MURRAY A. 2018. — The upper Coniacian to upper Santonian drowned Arabian carbonate platform, the Mardin-Mazıdag area, SE Turkey: sedimentological, stratigraphic, and ichthyofaunal records. *Cretaceous Research* 84: 153-167. <https://doi.org/10.1016/j.cretres.2017.09.012>
- YILMAZ İ. Ö., HOŞGÖR İ., OZKAN-ALTINER S., WAGREICH M. & KVAČEK J. 2021. — First record of late Campanian paleoceanographic and paleoclimatic changes, Arabian Platform, Mazıdag-Mardin area, SE Turkey. *Carnets Geol.* 21 (6): 137-162.

Submitted on 14 April 2021;
accepted on 16 July 2021;
published on 24 October 2022.