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New plesiosaur specimens from the Maastrichtian Phosphates of Morocco and their implications for the ecology of the latest Cretaceous marine apex predators

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ABSTRACT

Several clades of marine tetrapods, including the apex predators mosasaurs and plesiosaurs, disappeared during the mass extinction at the end of the Cretaceous, about 65 My ago. The extreme fossil richness of the Maastrichtian Phosphates of Morocco provides insights into the systematic diversity of the latest mosasaurs where about ten species are known. However, data of the coeval plesiosaurs are comparatively scarce. Up to now, only one species, the elasmosaurid *Zarafasaura oceanis*, is known. Here we describe new elasmosaurid plesiosaur post-cranial material from the Maastrichtian of the Oulad Abdoun Basin (Morocco) that provides new data about the taxonomical and morphological diversity of plesiosaurs in this area. Most of the new material consists of vertebrae that likely belong to a unique elasmosaurid taxon and differ from all other elasmosaurids documented so far. As *Zarafasaura* is known only from cranial material, it cannot be determined whether the new material may be assigned to this taxon. The new material shows that the latest Cretaceous plesiosaurs in this low latitude area (about 20°N) were rather gracile, most likely piscivorous taxa that occupied ecological niches similar to those of rather small mosasaurs (e.g., *Halisaurus* and "*Platecarpus*" *ptychodon*) but distinct from those of most coeval large mosasaur taxa. These plesiosaur fossils are also remarkable in that they consist of both juvenile and adult specimens, suggesting limited segregation between individuals of different ontogenetic stages, a feature that might be attributed to upwelling-related, high nutrient input and food availability in this area during the Maastrichtian. Moreover, the possible occurrence, with older specimens, of a neonate specimen – one among the very few known worldwide – suggests a possible social structure organization. The new data contribute to increase our understanding of Late Cretaceous plesiosaur biodiversity and provide new insights into the ecology of latest Cretaceous marine apex predators.

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1. Introduction

The transition between the Cretaceous and Palaeogene, about 65 My ago, witnessed the extinction of many groups of invertebrates and vertebrates, including several emblematic groups of both terrestrial and marine tetrapods (e.g., Bardet, 1994; Canudo et al., 2000). However, whereas the Late Cretaceous terrestrial vertebrate faunas is now rather well known (e.g., Carvalho et al., 2005), the diversity and disparity of marine vertebrates at this turnover remain poorly understood. This is particularly true for Plesiosauria, one of the most long-ranging groups of Mesozoic marine reptiles, with a known stratigraphic range spanning more than 140 My (Bardet, 1992; Storrs, 1994; Gasparini et al., 2003a; Benson et al., 2010; Sennikov and Arkhangelsky, 2010; Vincent et al., 2011).

During the Maastrichtian, plesiosaurians achieved a worldwide distribution, as shown by their remains found on all continents, including Antarctica (see Gasparini et al., 2003b), before becoming extinct relatively rapidly towards the end of this stage (Vincent et al., 2011). Although the fossil record of plesiosaurians is relatively well known in the Cretaceous strata of most continents (e.g., Carpenter, 1999; Gasparini et al., 2003a; Kear et al., 2008), it is poorly documented in Africa. Up to now only five valid taxa have been described: *Leptocleidus capensis* (Andrews, 1911) from the Lower Cretaceous (Valanginian) of South Africa (Andrews, 1911; Cruickshank, 1997), *Thililua longicollis* Bardet et al., 2003a, *Manemergus anguirostris* Buchy et al., 2005 and *Libonectes atlasense* Buchy, 2005, from the lower Upper Cretaceous (Turonian) of Morocco, and *Zarafasaura oceanis* Vincent et al., 2011 from the uppermost Cretaceous (Maastrichtian) of Morocco. Very fragmentary remains indeterminable at an infrafamilial

Abbreviations: AMNH, American Museum of Natural History, New York, USA; CM, Canterbury Museum, Christchurch, New Zealand; OCP, Office Chérifien des Phosphates Khouribga, Morocco.

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level were also described from the Maastrichtian of Egypt and Angola (see Vincent et al., 2011 for details).

From Morocco, Arambourg (1952) was the first to report plesiosaurian remains in the Meskala and Ganntour phosphatic basins, on which he erected a new species, *Plesiosaurus mauritanicus* Arambourg, 1952, now considered a *nomen dubium* (Vincent et al., 2011). Surprisingly, after Arambourg's pioneer works, vertebrate fossils from the Phosphates of Morocco – despite their known abundance – have been neglected for decades, except selachians that have been extensively studied since the 1980s (e.g., Cappetta, 1987; Noubhani and Cappetta, 1997 and references therein). Recently, abundant new vertebrate remains (including articulated skeletons) belonging to selachians (e.g., Noubhani and Cappetta, 1997), bony fishes (e.g., Cavin et al., 2000), as well as marine and continental sauropsids (e.g., Bardet et al., 2010) have been collected in the Phosphates of Morocco, under the framework of a French–Moroccan scientific program of collaboration (see acknowledgments). Among them, several plesiosaurian remains were discovered, including the subcomplete cranial remains of *Z. oceanis* (Vincent et al., 2011). This work describes newly collected postcranial plesiosaurian specimens from the Maastrichtian Phosphates of Morocco and discusses their ecological and palaeogeographical implications in the framework of the ecological relationships between large marine predators in latest Cretaceous oceans.

2. Geographical and stratigraphical occurrences

The phosphatic deposits of Morocco form part of the Mediterranean Tethyan phosphogenic province that extended from North Africa to the Middle East (Lucas and Prévôt-Lucas, 1996) and crops out in two main areas, the Oulad Abdoun and Ganntour basins. Stratigraphically, these strata range in age from the Late Cretaceous (Maastrichtian) to the Early Eocene (basal Lutetian), spanning the longest time interval of all Tethyan phosphates (Lucas and Prévôt-Lucas, 1996). The specimens described below come from the Maastrichtian phosphatic successions of the Oulad Abdoun Basin (see Bardet et al., 2010; Vincent et al., 2011 for details concerning geographical and stratigraphical data).

3. Systematic palaeontology

SAUROPTERYGIA Owen, 1860
PLESIOSAURIA de Blainville, 1835
PLESIOSAUROIDEA Welles, 1943
ELASMOSAURIDAE Cope, 1869
Elasmosauridae gen. et sp. indet.

Material — OCP-DEK/GE 49, six dorsal vertebrae; OCP-DEK/GE 69, sixteen cervical vertebrae; OCP-DEK/GE 115, forty cervical and fifteen dorsal vertebrae, ribs, pelvic girdle; OCP-DEK/GE 119, one cervical vertebra; OCP-DEK/GE 122, one dorsal vertebra, one rib; OCP-DEK/GE 130, ten cervical vertebrae; OCP-DEK/GE 136, ten dorsal vertebrae; OCP-DEK/GE 165, limb element; OCP-DEK/GE 204, limb element; OCP-DEK/GE 234, height dorsal vertebrae; OCP-DEK/GE 318, pectoral girdle; OCP-DEK/GE 358, gastralia; OCP-DEK/GE 647, pelvic girdle; OCP-DEK/GE 648, sixty-six cervical and pectoral vertebrae; OCP-DEK/GE 649, seventeen cervical vertebrae in articulation probably representing the mid-cervical region; OCP-DEK/GE 651, nine cervical vertebrae; and OCP-DEK/GE 652, four dorsal vertebrae.
Locality and horizon — Sidi Daoui area, near Oued Zem City, Grand Daoui Zone, northeastern part of the Oulad Abdoun Basin, Morocco; Upper CIII level, Upper Maastrichtian, Upper Cretaceous (Cappetta, 1987).

3.1. Description

3.1.1. Vertebral remains

Vertebrae are the most common remains of plesiosaurs found in the Oulad Abdoun Basin and are sometimes associated with ribs and girdle elements (e.g., OCP-DEK/GE 115, Fig. 1A). Most of them are isolated but some are preserved in articulation (e.g., OCP-DEK/GE 649, 69; Fig. 1H, I) or close association but with displacement before burial (e.g., OCP-DEK/GE 130; Fig. 1J). The most complete specimen (OCP-DEK/GE 648; Fig. 2A–D) is a series of 66 vertebrae. It consists of 62 cervicals, two pectorals sharing the rib facet between the neural arch and centrum, and two indeterminate vertebrae almost entirely hidden by rib fragments. There is no confidence about the completeness of the neck, to which the atlas-axis must be added. The vertebral series was found in articulation and is preserved in left lateral view. Based on Brown's (1981) criteria, all the newly discovered vertebrae (except OCP DEK/GE 652) can be considered as belonging to adult specimens because the neural arches and ribs are firmly sutured with the centra. The axial morphological diversity is most prevalent in cervical vertebrae and little taxonomic emphasis can be put on the specimens described below that only preserve a few dorsal vertebrae. The general morphology of the vertebrae found in the Oulad Abdoun Basin shows only little morphological variability and thus will be described by anatomical categories rather than by specimens.

3.1.1.1. Cervical and pectoral vertebrae. The general morphology of the cervicals is typical of Late Cretaceous elasmosaurids in having a wide centrum in anterior view, single-headed ribs (present in all plesiosauroids from the Middle Jurassic to the end of the Cretaceous) and a plate-like neural spine (OCP-DEK/GE 69, 115, 130, 648, 649, 651; Figs. 1, 2). The centra are ovoid in shape as in *Microcleidus* Watson, 1909, *Occitanosaurus* Bardet et al., 1999 and *Callawayasaurus* Welles, 1962. Most of the centra are broader than high and long, and taller than long (W>H>L) (OCP-DEK/GE 69, 115, 130, 649, 651), except in OCP-DEK/GE 648 for which variations are observable along the neck. The centra of OCP-DEK/GE 648 are as long as high in the first anterior vertebrae (the numbering starts with the first centrum preserved, nominally C1) but become longer than high from the cervicals C15–17 to the cervicals C33–35; they are then shorter than high until the end of the neck (Fig. 2). Changes in centrum proportions along the neck are usual among long-necked taxa (e.g., *Elasmosaurus* Cope, 1868 and *Hydralmosaurus* Welles, 1943; see Welles, 1952: tables 1, 3; Brown, 1981; O'Keefe and Hiller, 2006).

Cervical centra from the Oulad Abdoun Basin are usually platycoelous (e.g., OCP-DEK/GE 69, 115; Fig. 1A, D, I), as observed in *Callawayasaurus*, *Occitanosaurus*, and *Thalassomedon*; except in OCP-DEK/GE 130 where they are slightly amphicoelous (Fig. 1J). None of the cervical centra presents lateral longitudinal ridges, as observed in *Futabasaurus* Sato et al., 2006, except OCP-DEK/GE 115, which preserves a faint longitudinal ridge in some cervical centra (Fig. 1B), and OCP-DEK/GE 648 with its poorly developed lateral ridges on cervicals C16 and C17 (Fig. 2A).

The ventral surfaces of the centra are convex and bear rugosities (except in OCP-DEK/GE 130) at the level of the articular surfaces that correspond to ornamental longitudinal striations. None presents a ventral ridge (except OCP-DEK/GE 648; Figs. 2A, 3B) or a ventral notch comparable to that usually observed in Late Cretaceous elasmosaurids (Brown, 1993; Sato et al., 2006). The specimen OCP-DEK/GE 69 shows compression and distortion so that the slight ventral ridge observed ventrally between the two foramina subcentralia likely corresponds to a taphonomical artifact (Fig. 1I). The ventral view of the cervical vertebrae of OCP-DEK/GE 648 shows a strong ventral ridge between the foramina subcentralia in cervicals C1 and C2, which is also present but less developed in C3 (Fig. 3B). The cervical C4 does not preserve any ventral ridge and, the other cervical vertebrae being preserved in lateral view, it is not possible to determine whether a ventral ridge occurs.

Most of the cervical centra of the Oulad Abdoun Basin specimens bear two ventral foramina subcentralia but three cervical vertebrae of the specimen OCP-DEK/GE 130 only bear one nutritive foramen (Fig. 1L). When two occur, they are located very close to each other. It is usual to observe in Plesiosauria foramina subcentralia close to each other on the anteriormost vertebrae, whereas they usually progressively migrate laterally in posterior cervicals (Brown, 1981).

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