Marine reptiles from the Late Cretaceous Phosphates of Jordan: palaeobiogeographical implications

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ABSTRACT
Marine reptiles, including mosasaurs, plesiosaurs, turtles and crocodilians, from the Late Cretaceous (Maastrichtian) Phosphates of Ruseifa, Jordan, are reviewed on the basis of both historical collections and new discoveries. Mosasaurids are represented by mosasaurines (*Globidens* sp.), plioplatecarpines (*Platecarpus ptychodon* Arambourg, 1952, *Prognathodon giganteus* Dollo, 1904) and the basal *Halisaurus* Marsh, 1869. Indeterminate remains of elasmosaurid plesiosaurs, chelonioid turtles and crocodyliformes also occur. The marine reptile faunas from Jordan are reminiscent of those from the Late Cretaceous Phosphates of the Middle-East and of the southern margin of the Mediterranean Tethys in general.

KEY WORDS
Reptilia,
Mosasauridae,
Plesiosauria,
Chelonii,
Crocodyliformes,
Maastrichtian,
Phosphates,
Ruseifa,
Jordan,
palaeobiogeography.

RÉSUMÉ
Les reptiles marins des Phosphates du Crétacé supérieur de Jordanie : implications paléobiogéographiques.
Les faunes de reptiles marins, incluant mosasaures, plésiosaures, tortues et crocodiles, du Crétacé supérieur (Maastrichtien) des Phosphates de Roseifa en Jordanie sont revues à partir de collections historiques et de nouvelles découvertes. Les mosasauridés sont représentés par des mosasaurinés (*Globidens* sp.), des plioplatecarpinés (*Platecarpus ptychodon* Arambourg, 1952, *Prognathodon giganteus* Dollo, 1904) et par le taxon basal *Halisaurus* Marsh, 1869. Des restes indéterminés attribués à des plésiosaures élasmosauridés, des tortues chélonioïdes et des crocodyliformes sont aussi connus. Les faunes de reptiles marins de Jordanie sont comparables à celles des Phosphates du Crétacé supérieur du Proche-Orient et de la marge sud de la Téthys méditerranéenne en général.

MOTS CLÉS
Reptilia,
Mosasauridae,
Plesiosauria,
Chelonii,
Crocodyliformes,
Maastrichtien,
Phosphates,
Roseifa,
Jordanie,
paléobiogéographie.

INTRODUCTION

Marine vertebrates from the Late Cretaceous Phosphates of Jordan have been known for over 50 years (Avnimelech 1949). Avnimelech (1949) mentioned the occurrence of selachians, bony fishes and reptiles, including mosasaurids (*Globidens fraasi* Dollo, 1913), cheloniid turtles and crocodilians, from the Ruseifa Mine, near Amman. Later, Arambourg *et al*. (1959) described new vertebrate remains from the same mine, including teeth of selachians, actinopterygians and marine reptiles, as well as a pterosaur bone. Signeux (*in* Arambourg *et al*. 1959) identified three mosasaurids (*Mosasaurus* cf. *anceps* (Owen, 1840), *Platecarpus ptychodon* Arambourg, 1952, *Globidens aegyptiacus* Zdansky, 1935), one plesiosaur (*Plesiosaurus mauritanicus* Arambourg, 1952) and one crocodilian (*Crocodilus* sp.). More recently, a reappraisal of the pterosaur material has been proposed (Frey & Martill 1996), as well as the first description in Jordan of a dinosaur bone from the same deposits (Martill *et al*. 1996). With regard to marine vertebrates, only sharks and rays have received recent scientific attention (Mustafa & Zalmout 1999; Cappetta *et al*. 2000; Mustafa 2000). Here we review the marine reptile faunas (mosasaurs, plesiosaurs, turtles and crocodilians) from the Late Cretaceous Phosphates of Ruseifa on the basis of both historical collections and new discoveries.

ABBREVIATIONS
NHM The Natural History Museum, London;
JPMC Jordan Phosphate Mines Company, Amman;
MNHN Muséum national d'Histoire naturelle, Paris;
UD University of Damascus, Geology Department, Damascus.

GEOGRAPHICAL AND GEOLOGICAL SETTINGS

Phosphatic deposits are exposed over a large area of Jordan (Jallad *et al*. 1989). The principal phosphate-bearing regions are Ruseifa, Al Hasa and Eshidiya (Fig. 1). The phosphatic deposits are part of the Belqa Group (Quennell 1951) and have received several names according to various authors (see Shinaq & Bandel 1998: 166 for details); the most recently used ones are "Ruseifa Formation" (Shinaq & Bandel 1998) and "Al Hasa Phosphorite Formation" (Powell 1989).
All the marine reptile remains described here are from the Phosphates of the Ruseifa Quarry, which is located a few kilometers North-East of Amman (Fig. 1). In this mine (now closed), the Late Cretaceous phosphatic beds are well exposed and are approximately 20-25 m thick. Four phos-

phatic horizons (Fig. 1, I to IV) separated by marls, limestones and cherts are recognisable (Bender 1968; Bandel & Mikbel 1985; Jallad *et al*. 1989), with all these horizons yielding vertebrate remains.

As with many of the Late Cretaceous Middle-East Phosphates, the precise age of the phosphatic deposits (Campanian or Maastrichtian) of Jordan is subject of debate (see Bardet *et al*. 2000 for a discussion). In fact, the phosphatic series of Jordan is diachronous, becoming progressively younger towards the South-East (Bender 1968). As a result, phosphates were forming as early as the late Campanian in northwestern Jordan, during the Maastrichtian in central Jordan and the Maastrichtian-Palaeogene in southeastern Jordan (Bender 1968).

Bandel & Mikbel (1985) and Jallad *et al*. (1989) regarded the phosphatic series of Ruseifa as Maastrichtian, a view previously defended by Picard (1931) and Arambourg *et al*. (1959). A Maastrichtian age is also supported by selachian data (Cappetta *et al*. 2000).

The Ruseifa Phosphates were deposited in a shallow sea, when the underlying Wadi Sir Formation was eroded along an island chain that accompanied the Ruseifa fault and associated folds (Bandel & Mikbel 1985). A near-shore environment is suggested by the rare occurrence of dinosaur and pterosaur remains into the marine series.

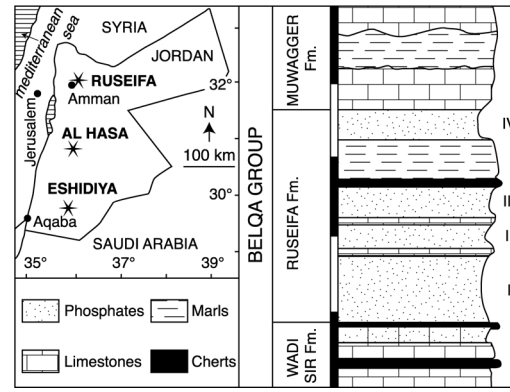

FIG. 1. — Geographical location and stratigraphical column, Ruseifa Quarry, near Amman, Jordan. **I** to **IV**: phosphatic horizons. Black/white bar: 5 m.

DESCRIPTION

The marine reptile specimens described here are kept in Paris (MNHN, collection number 1960-20), London (NHM, collection number R 5887), Damascus (UD, uncatalogued) and Amman (JPMC, uncatalogued). These remains have never been previously described, except those kept in Paris (Arambourg *et al*. 1959). They mainly comprise isolated teeth and vertebrae.

It has not been possible to locate material mentioned by Avnimelech (1949). Martill *et al*. (1996) noted that this material was kept in a small collection of rocks, fossils and minerals on display in the main office at the Ruseifa Mine. However, as the Avnimelech's material was uncatalogued and not figured, it is difficult to know if the remains kept in the Ruseifa collection correspond to those mentioned by Avnimelech (1949).

MOSASAURIDAE GERVAIS, 1853 (FIG. 2A-C, E-G)

Mosasaurid squamates are represented by isolated teeth of mosasaurines (*Globidens* sp.), plioplatecarpines (*Platecarpus ptychodon*, *Prognathodon giganteus* Dollo, 1904), and the basal *Halisaurus* Marsh, 1869.

The genus *Globidens* Gilmore, 1912 (MNHN 1960-20, UD uncatalogued) was previously described from Jordan by Avnimelech (1949) as *Globidens fraasi* and by Arambourg *et al*. (1959) as *Globidens aegyptiacus*. The crowns of the teeth are bulbous, subspherical and low with a constriction at the base of the crown; they bear an apical "nubbin" and two more or less prominent shallow vertical grooves (Fig. 2A, E, F). The supposed anterior teeth (Fig. 2A) are higher and slender than the posterior ones (Fig. 2E, F). All these teeth are similar to those described by Russell (1975) and Lingham-Soliar (2000) as *Globidens* "type 2", from the Late Cretaceous Phosphates of Negev (Raab 1963), Syria (Bardet *et al*. 2000), Egypt (Leonardi & Malaroda 1946),

Angola (Telles Antunes 1964) and Brazil (Price 1957). Compared to other mosasaurs with a crushing dentition, these teeth are different from those of *Globidens alabamaensis* Gilmore, 1912 and *G. dakotaensis* Russell, 1975 from the Campanian of North America, which exhibit regular subspherical crowns with small symetrical apical nubbin and very faint carinae and sulci (*Globidens* "type 1" of Russell 1975). They differ also from those of *Igdamanosaurus aegyptiacus* (Zdansky, 1935) from the Maastrichtian of Africa, which are characterised by high and rounded crowns with well developed carinae (*Globidens* "type 4" of Russell 1975). Finally, they differ from the teeth of *Carinodens belgicus* (Woodward, 1891) (= *Globidens fraasi*; see discussion in Kuypers *et al*. 1998) from the Maastrichtian of Europe, which shows bicarinate laterally compressed crowns with a subtriangular to subrectangular lateral profile (Russell 1975; Lingham-Soliar 2000). The Jordan teeth are here referred to *Globidens* sp.

Platecarpus ptychodon (MNHN 1960-20) has previously been reported in Jordan by Arambourg *et al.* (1959). This species is characterized by small teeth with bicarinate highly laterally compressed crowns, subequal lingual and labial surfaces bearing vertical striations that are more numerous on the lingual face and developed only on the two thirds of the crown height (Fig. 2B). The dental morphology of *P. ptychodon* is quite distinct from those of other mosasaurids, such that this taxon (which was erected on the basis of isolated teeth only) is provisionally regarded as valid. Similar teeth are also known from the Maastrichtian of Morocco (Arambourg 1952), Negev (Raab 1963), Syria (Bardet *et al.* 2000), and Angola ("Platecarpinae indet." of Telles Antunes 1964: pl. 26, fig. 11).

The teeth of *Prognathodon giganteus* are reported for the first time in Jordan. They were previously described as *Mosasaurus* cf. *anceps* by Arambourg *et al.* (1959). The teeth (NHM R 5887; MNHN 1960-20; UD uncatalogued) have large and robust crowns with subcircular basal cross-section, subequal convex labial and lingual faces, two carinae, and anastomosing enamel especially prevalent on the blunt apical region (Fig. 2G). These teeth differ from those of *Leiodon anceps* Owen, 1840 from the Campanian of England, which are laterally compressed, less robust and with a smooth enamel (Lingham-Soliar 1993). *P. giganteus* is known from the Maastrichtian of Belgium (Dollo 1904) and the Campanian of France (Bardet *et al.* 1997). This species also occurs in the Late Cretaceous Phosphates of Egypt ("mosasaur gen. et sp. indet." of Zdansky 1935: pl. 1), Negev (pers. obs.), Syria (Bardet *et al.* 2000) and tentatively Angola ("Mosasauridae indet." of Telles Antunes 1964: pl. 26, fig. 4). Moreover, isolated teeth from the Maastrichtian of Congo have been assigned to cf. *Prognathodon giganteus* (Lingham-Soliar 1994).

Finally, one isolated tooth (MNHN 1960-20) is here referred to *Halisaurus* sp. The tooth is small, slender, abruptly posteriorly recurved from near the midpoint of the crown, with a circular basal cross-section, two carinae, and subequal lingual and labial surfaces that are minutely striated (Fig. 2C). It resembles the teeth of *Plioplatecarpus* Dollo, 1882 but those of this genus are shorter and more slender. Until now, teeth were unknown in *Halisaurus* and the referral of the Jordan tooth to this genus is based on its great similarity with new unpublished material of *Halisaurus* from the Maastrichtian of Morocco (Bardet *et al.* in prep.). *Halisaurus* teeth are also known in the Late Cretaceous Phosphates of Syria ("Plioplatecarpini indet." of Bardet *et al.* 2000).

ELASMOSAURIDAE COPE, 1869 (FIG. 2D)

Elasmosaurid plesiosaurs are known from isolated teeth, vertebrae and propodial bones. The teeth (MNHN 1960-20) were refered to *Plesiosaurus mauritanicus* by Arambourg *et al.* (1959). They are long, slender, slightly recurved, and have finely ridged enamel crowns. Vertebrae (UD and JPMC uncatalogued) have platycoelous articular surfaces (diameter about 8 cm), which are dumbbell-shaped on the cervical ones, two characters considered as elasmosaurid features (Bardet *et al.* 1999). Two massive propodial bones (length about 30 cm) (UD uncatalogued) are probably

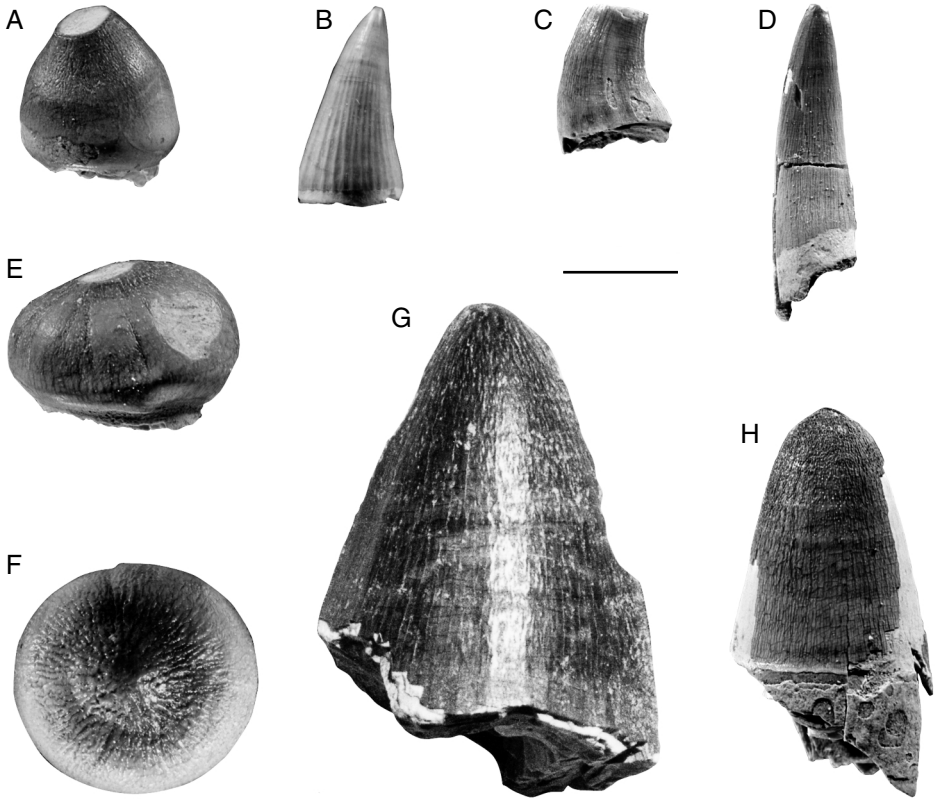

FIG. 2. — Marine reptiles from the Late Cretaceous (Maastrichtian) of the Ruseifa Quarry, near Amman, Jordan; **A**, **E**, **F**, *Globidens* sp. (MNHN 1960-20); **A**, anterior tooth in lateral view; **E**, **F**, median tooth in lateral and dorsal views; **B**, *Platecarpus ptychodon* Arambourg, 1952 (MNHN 1960-20), median tooth in lateral view; **C**, *Halisaurus* sp. (MNHN 1960-20), median tooth in lateral view; **D**, Elasmosauridae indet. (MNHN 1960-20), tooth in medial view; **G**, *Prognathodon giganteus* Dollo, 1904 (UD uncatalogued), median tooth in lateral view; **H**, Crocodyliformes indet. (MNHN 1960-20), median tooth in lateral view. Scale bar: 15 mm.

also elasmosaurid. Unfortunately, these remains do not exhibit diagnostic characters permitting a generic or specific identification, and are referred to Elasmosauridae indet.

CHELONIOIDEA OPPEL, 1811

Chelonioid marine turtles are represented by very large costal plates (preserved on about 10 cm wide and 20 cm long) and a cervical vertebra kept in Amman (JPMC uncatalogued). The cervical vertebra is low and wide, as in cheloniids, and distinct from those of dermochelyids and protostegids (Zangerl 1953; Hirayama & Chitoku 1996). The centrum is procoelous and bears reniform to elliptic articular surfaces. Using the articulation diagram of Williams (1950) for living cheloniids, this procoelous vertebra is interpreted as being possibly the fifth or the eighth of the cervical series. Similar cervical vertebrae are known from the Late Cretaceous Phosphates of Syria (Bardet *et al.* 2000). The costal plates do not bear any ornamentation and are only punctured by coarse nutrient foramina and sinuous grooves, like those of typical marine Chelonioidea.

CROCODYLIFORMES BENTON & CLARK, 1988 (FIG. 2H)

Crocodilian remains are only represented by a tooth referred to as *Crocodilus* sp. by Arambourg *et al.* (1959). The crown of this tooth is high, massive and rounded in basal cross-section. It bears two carinae and a finely anastomosing

enamel especially marked on the blunt apical region. Several Late Cretaceous crocodilian lineages have acquired a crushing dentition such that it is not possible to identify this tooth more precisely. It is therefore referred to Crocodyliformes indet. (*sensu* Benton & Clark 1988). The absence or extreme scarcity of crocodilian remains is noteworthy and is comparable to other Late Cretaceous phosphatic deposits worldwide where crocodilians are very rare.

DISCUSSION

The mosasaurid assemblage from Ruseifa, though being rather poor, includes a minimum of four genera, each represented by a single species: *Prognathodon giganteus*, *Platecarpus ptychodon*, *Globidens* sp. and *Halisaurus* sp. The same assemblage is known from the early Maastrichtian Phosphates of Syria and three of the four taxa are also known from Negev (see Bardet *et al*. 2000). *Platecarpus ptychodon* and *Globidens* sp. are characteristic of the southern margin of the Mediterranean Tethys (below palaeolatitude 20°N), as they have also been found in the latest Cretaceous of Egypt, Morocco, Angola and Brazil (see Bardet *et al*. 2000). The northern margin of the Mediterranean Tethys is mainly characterised by *Plioplatecarpus*, *Carinodens* Thurmond, 1969 and *Hainosaurus* Dollo, 1885 (see Bardet & Pereda Suberbiola 1996). *Mosasaurus* Conybeare, 1822, *Leiodon* Owen, 1840, *Prognathodon* Dollo, 1889 and *Halisaurus* are known from both realms but with different species, with the exception of *Prognathodon giganteus*.

With regard to actinopterygian fishes, the fauna of Ruseifa includes at least three enchodontid species (the commonest being *Enchodus elegans* Dartevelle & Casier, 1949), *Stratodus apicalis* Cope, 1872, *Stephanodus libycus* (Dames, 1883), *Pseudoegertonia* Dartevelle & Casier, 1949 and indeterminate pycnodonts (Signeux *in* Arambourg *et al*. 1959). As with the mosasaurids, this association is also typical of North-West Africa and the Middle-East (Arambourg 1952; Avnimelech 1949, 1957; Chalifa 1996; Chalifa & Lewy 1991; Dartevelle & Casier 1943, 1949, 1959; Raab 1963, 1967; Bardet *et al*. 2000). Moreover, *Enchodus elegans* and *Stephanodus lybicus* appear to be restricted to low palaeolatitudes (between 20°N and 20°S, see Camoin *et al*. 1993), while *Stratodus apicalis* has also been reported from higher palaeolatitudes (above 30-40°N) in North America (Cope 1872; Applegate 1970; Case 1979).

The selachian fauna of Ruseifa is mainly composed of *Scapanorhynchus* Woodward 1889, *Cretolamna biauriculata* Wanner, 1902, *Squalicorax bassanii* Gemmellaro, 1920, *Plicatoscyllium* Case & Cappetta, 1997 and *Rhombodus binkhorsti* Dames, 1881 (Cappetta *et al*. 2000). These taxa have also been found in the Maastrichtian of Syria (Bardet *et al*. 2000) and Morocco (Noubhani & Cappetta 1997).

Finally, the occurrence of the ammonoid *Lybicoceras ismaeli* (Zittel, 1895) (Sornay *in* Arambourg *et al*. 1959), which is rather abundant in the Ruseifa Quarry (pers. obs.), is also consistent with the association of marine vertebrates, as this species is exclusive to the low latitudes of the southern Tethyan margin (Zaborski & Morris 1999).

The marine vertebrate faunas from the Late Cretaceous Phosphates of Ruseifa are typical of the southern margin of the Mediterranean Tethys and show close affinities with those of the Late Cretaceous phosphatic deposits of North Africa and the Middle-East in general. Faunal differences between the southern and northern margins of the Mediterranean Tethys could be related to palaeolatitudinal temperature gradients (Bardet & Pereda Suberbiola 1996). Indeed, the marine vertebrate assemblages from the Middle-East and North Africa, as well as those from West Africa and eastern South America, are included within a palaeolatitudinal belt located between 20°N and 20°S.

CONCLUSION

A revision of historical collections (mainly isolated teeth) and newly discovered remains (teeth

and bones) of marine reptiles from the Late Cretaceous (Maastrichtian) phosphate-bearing beds of the Ruseifa Quarry of Jordan allow us to recognize the following taxa: *Platecarpus ptychodon*, *Prognathodon giganteus*, *Globidens* sp. and *Halisaurus* sp. (among mosasaurs); Elasmosauridae indet. (plesiosaurs); Chelonioidea indet. (marine turtles), and Crocodyliformes indet. (crocodilians). This fauna is similar to those of the early Maastrichtian of Syria (Bardet *et al*. 2000) and comparable to those of the southern margin of the Mediterranean Tethys in general.

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