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Reptilian assemblages from the latest Cretaceous – Palaeogene phosphates of Morocco: from Arambourg to present time

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Arambourg was the first to conduct methodical vertebrate palaeontological studies in the Oulad Abdoun and Ganntour phosphatic basins of Morocco between the 1930s and 1950s. As early as 1935, he identified the main stratigraphical levels of the phosphatic series, characterizing them by a specific association of vertebrates (mainly selachians), and proposed stratigraphical correlations between the phosphatic levels of these two basins. During the last decade, due to a French-Moroccan program of collaboration, vertebrate fossils have been collected in great abundance. Here we present an updated overview of the latest Cretaceous to Ypresian reptilian faunas from the Oulad Abdoun and Ganntour basins, on the basis of published data and new field records. In addition to advances in the study of the already known taxa (i.e., squamates, crocodyliforms, plesiosaurs), recent field works reveal new major reptilian taxa that were unknown (or undescribed) at Arambourg's time: very abundant and diversified marine chelonians (Maastrichtian to Ypresian), scarce dinosaurs and pterosaurs remains (Maastrichtian), and a well diversified marine avifauna (Thanetian and Ypresian). A significant increase in the number of described taxa (52 versus 13) and an improvement of the quality of the specimens found (articulated skeletons versus isolated remains) is worthy of consideration. The Maastrichtian reptilian assemblages are dominated by mosasaurid squamates whereas those of the Palaeogene are by the mirroring crocodyliforms (dyrosaurids and eusuchians).

Keyword: Lepidosauromorpha; Archosauromorpha; Chelonii; Maastrichtian-Ypresian; Phosphates; Morocco

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History of the discovery of phosphates in Morocco

The phosphates of Morocco are part of the 'Mediterranean Tethyan phosphogenic Province' (Lucas and Prévôt-Lucas 1996), a large belt of sedimentary deposits located around palaeolatitude 20°S. These phosphates currently crop out widely from Middle East up to the Pernambuco Province of Brazil, passing by North and West Africa, where they are exploited as a valuable economical resource.

In Morocco, these phosphatic deposits outcrop in several basins, which are from NE to SW: Oulad Abdoun, Ganntour, Meskala, Sous, and Oued Eddahab in the Western Sahara (Figure 1). Stratigraphically, they extend from the latest Cretaceous (Maastrichtian) to the middle Eocene (Lutetian), spanning the largest interval of time of all Tethyan phosphates (Lucas and Prévôt-Lucas 1996).

Brives (1905) was the first to recognize marine Eocene calcareous levels between Essaouira and Marrakech, in which a phosphatic layer was later identified in the Guergouri Plateau, SW of Marrakech (Brives 1908). If at that time the discovery of Eocene levels gave rise to strong stratigraphical controversies (see Roch 1930 for an overview), that of phosphates aroused little interest until 1917, when important phosphatic outcrops were discovered between Oued Zem and El Borouj cities (Oulad Abdoun Basin) (Figure 1).

After the foundation of the *Office Chérifien des Phosphates* (OCP) in 1920, large-scale economical exploitation of phosphates begun in 1921 in Khouribga (Oulad Abdoun Basin), followed by Youssoufia (formerly Louis Gentil, Ganntour Basin) in 1931 (see Salvan 1986) (Figure 1). As early as the 1930s, the exploitation of these phosphatic deposits represented a key-element in the economy of Morocco, and currently Morocco is the World's first phosphate exporter and one of the first phosphate-growing countries (Office Chérifien des Phosphates 1989). One of the main characteristics of these phosphates is their extreme richness in fossil vertebrate remains of latest Cretaceous-Palaeogene age.

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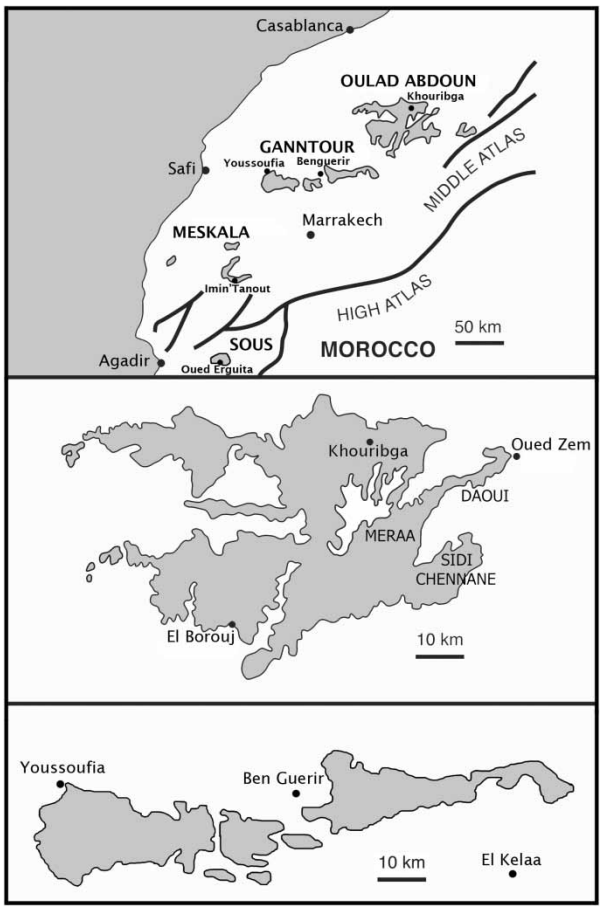

Figure 1. Map of the main phosphatic basins of Morocco from NE to SW: Oulad Abdoun, Ganntour, Meskala and Sous and details of the Oulad Abdoun and Ganntour basins.

Even though the recognition of the main phosphatic outcrops was already completed in the 1930s, their exact stratigraphical position remained imprecise. Indeed, stratigraphical problems of differentiation, datation and correlation of the different levels within and between basins (i.e. difficulties of correlations between Khouribga and Youssoufia levels) mainly occurred because: 1) phosphatic sediments, though globally very homogeneous, exhibit locally strong lateral facies changes; 2) most usual biostratigraphical markers such as invertebrates, microfossils and florae are scarce and/or poorly preserved in these deposits; 3) the first studies, mainly based on superficial surface collecting of often mixed vertebrate remains, were confusing and contradictory concerning the age of the phosphatic levels (see Arambourg 1952, p. 11-12; and Salvan 1986, p. 78-79 for details).

Terminology

We use here the term Reptilia *sensu* Modesto and Anderson (2004), an equivalent of the Sauropsida of Gauthier (1994), which include both 'classical' reptiles and birds.

Abreviations

MNHN, Muséum National d'Histoire Naturelle, Paris, France; OCP, Office Chérifien des Phosphates, Khouribga, Morocco.

The first vertebrate fossil discoveries

The first mention of vertebrate fossils in the phosphates of Morocco were made by Joleaud (1922) and Depéret and Russo (1924, 1925). Joleaud (1922), in a paper dedicated to the age of the Maghreb phosphates, briefly mentioned that the vertebrate faunas of the phosphates of Morocco included the Eocene crocodile *Dyrosaurus* and several Maastrichtian and Eocene selachian species. He thus corroborated the hypothesis of Gentil (1922) of a Late Cretaceous-Eocene age for the Moroccan phosphatic series, contrary to the opinion of Brives (1905, 1908) of an Eocene age only.

Isolated remains from Melgou (NE part of the Oulad Abdoun Basin) were later described (Depéret and Russo 1924, 1925) and referred to several selachians species and to marine reptiles, that are the mosasaurid squamate *Leiodon anceps* Owen, 1840 and the dyrosaurid crocodyliform *Dyrosaurus phosphaticus* (Thomas, 1893). These remains were mentioned to have been found together in the basement of the phosphatic series, that was considered at that time as Late Campanian – Early Maastrichtian in age. These first discoveries raised both systematical and stratigraphical

Figure 2. Portrait of Camille Arambourg (1885-1969).

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problems. First, the phosphatic series of Morocco are not older than Early Maastrichtian (i.e. Cappetta 1987; Office Chérifien des Phosphates 1989). Second, while the crocodyliform affinity of the dermal scute (Depéret and Russo 1925, pl. 19, fig. 2) is unequivocal, that of the large tooth (pl. 19, fig. 1) is questionable since it exhibits several mosasaurid characters, a conclusion already reached by Zdansky (1935, p. 89) and Arambourg (1952, p. 281). We agree with these authors and propose to refer this tooth to the large mosasaurine *Prognathodon*, a frequent taxon in the Maastrichtian phosphates of Morocco. As far as the dermal scute is concerned, its referral to *Dyrosaurus phosphaticus*, a taxon known from the Ypresian phosphates of Tunisia (Jouve et al. 2006b), is also doubtful; we propose here to refer it to Crocodyliformes indet. Moreover, if this scute really comes from the Maastrichtian, it corresponds to one of the very few crocodyliform reports from this age in the phosphates of Morocco (see Jouve et al., 2008b). But it cannot be discarded that this specimen comes from a Palaeogene level, as no details on the exact provenance of the material were given by Depéret and Russo (1924, 1925). Finally, we confirm the mosasaurid affinities of the toothed jaw fragment attributed to *Leiodon anceps* (Depéret and Russo 1925, pl. 19, fig. 3) but propose to refer it to *Prognathodon*, *Leiodon anceps* now being considered a *nomen dubium* (Schulp et al. 2008).

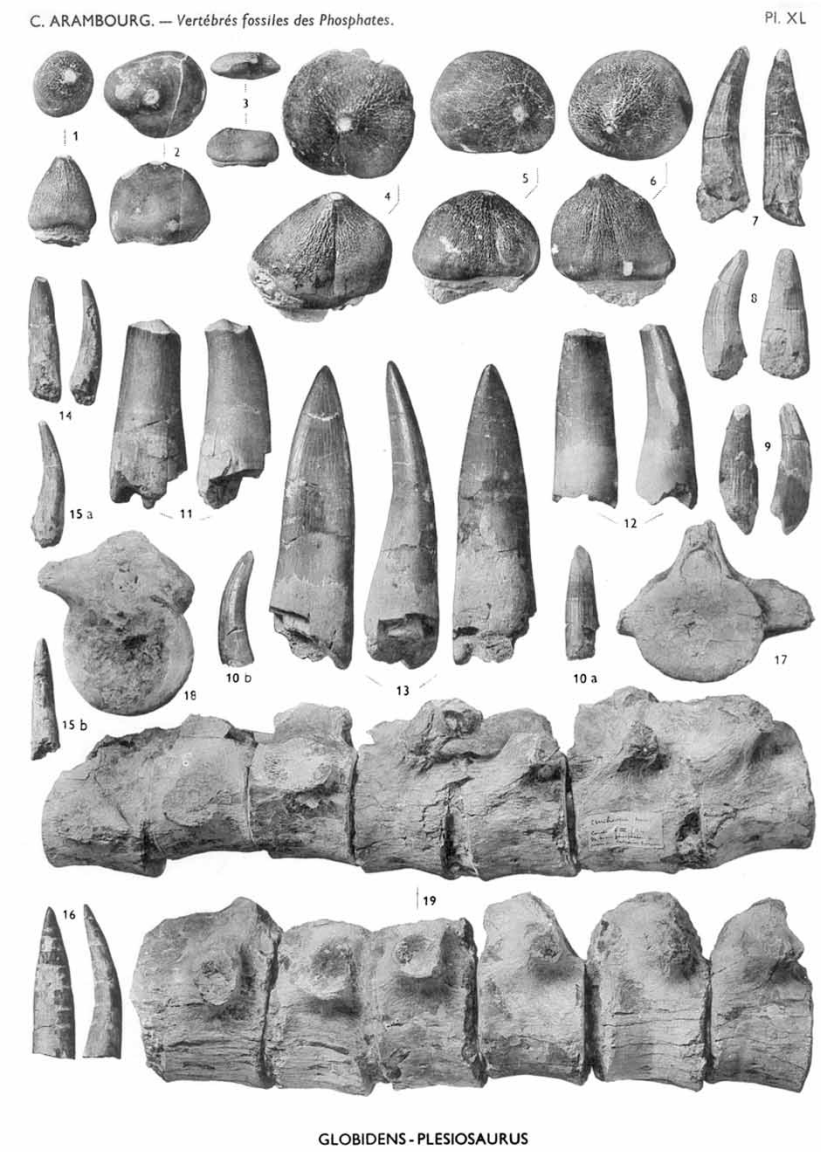

Figure 3. Reproduction of Plate XL of Arambourg (1952) as an example of the three major clades described by this author in the phosphates of Morocco and of the fragmentary status of the remains found at this time. 1-3: teeth of the mosasaurid *Globidens aegyptiacus* (figs. 4-6 are teeth from the phosphates of Koseir, Egypt); 7-10: crocodilian teeth; 11-19: teeth and vertebrae of the plesiosaur *Plesiosaurus mauritanicus* Arambourg, 1952.

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Arambourg's pioneer works

In 1934, in order to resolve the aforementioned stratigraphical problems of the phosphates of Morocco, the General Director of the OCP, Mr. Alfred Beaugé (to which the mosasaurid species *Mosasaurus beaugei* Arambourg, 1952 is dedicated), asked Prof. Camille Arambourg (*Muséum National d'Histoire Naturelle*, Paris) (Figure 2) to conduct a large-scale palaeontological work, on the basis of the most abundant and useful fossils available in the phosphatic series of Morocco: those of vertebrates, more precisely the selachian teeth.

These first methodical studies, which were systematical level-by-level *in situ* collecting and screening, were realized in the Khouribga-Oued Zem (Oulad Abdoun Basin) and Youssoufia (Ganntour Basin) regions as early as in 1934 (see Arambourg 1952, p. 10). Concerning screening, it probably represented one of the oldest ever realized. During over a decade of active works, Arambourg collected and studied an impressive amount of vertebrate fossils (Arambourg 1934, 1935, 1936, 1937, 1950, Ambroggi and Arambourg 1951). In total, about 100.000 specimens, mainly composed of isolated teeth, vertebrae and jaw remains were collected. They are now kept in the collections of the *Département Histoire de la Terre* of the MNHN (Paris). These specimens represent 150 marine species, mainly selachians, actinopterygian fishes and reptiles.

As early as in 1935, the main stratigraphical levels of the phosphatic series - each characterized by its specific association of fishes and reptiles - were defined in the Oulad Abdoun and Ganntour basins, and correlations were proposed between the phosphatic units of these two basins (Arambourg 1935). The complete results of this pioneer study were published in a large monograph (Arambourg 1952), in which were not only established the stratigraphical successions of the Moroccan phosphates, but also their extremely rich palaeontological assemblages of marine vertebrates, one of the richest from the K/T transition in the world. Later palaeontological studies based on invertebrates (Salvan 1954) and microfossils (Boujo and Rahhali 1971) corroborated and reinforced Arambourg's results.

With regards to stratigraphy, Arambourg defined three major phosphatic units (named beds or *Couches* in French) in the Oulad Abdoun and Ganntour basins (Table 1A). In the Oulad Abdoun Basin near Oued Zem city, the series is thin and includes Maastrichtian to Ypresian levels. In the Ganntour Basin near Youssoufia city, the succession is very thick and mainly considered as Late Cretaceous in age. Danian rocks were not clearly identified at this time. Important is the fact that Arambourg recognized a general increase of the phosphatic series from the NE to the SW of the Oulad Abdoun Basin, reaching maximum thickness in the Ganntour Basin. He also proposed correlations between the respective phosphatic levels of both basins (Table 1A). Currently, terms and ages proposed by Arambourg for the Oulad Abdoun Basin phosphatic levels remain almost unchanged, but those used for the Ganntour units substantially differ (Table 1B).

Table 1. Comparison of the stratigraphical names used for the different levels of the phosphatic series of Morocco in the Oulad Abdoun and Ganntour basins at Arambourg's time (**A**) and present time (**B**).

AGE		OULAD ABDOUN	GANNTOUR
A			
YPRESIAN		Couches I-0	–
THANETIAN		Couche II	Couche A
MAASTRICHTIAN or DANIAN?		Couche III	Couche B
MAASTRICHTIAN		–	Couche C
B			
YPRESIAN		(Sillons A-B) (Couches I-0)	Horizons B-F
THANETIAN		Couche IIa	Horizons A3-A1
DANIAN		Couche IIb	Couches 1-0
MAASTRICHTIAN	**U**	Couche III	(Sillon X) (Couches 4-2)
	L	–	Couches 6-5

Note that the Danian was not identified at Arambourg's time.

With regards to reptiles, Arambourg (1952) described taxa belonging to several major clades (squamates, crocodyliforms and plesiosaurs), ranging from the latest Cretaceous (Maastrichtian) to the Early Eocene (Ypresian) (Table 2). Curiously, Arambourg did not described any chelonian - though few specimens were mentioned in the Maastrichtian of Oued Erguita, Sous Basin (Ambroggi and Arambourg 1951) - nor any bird, both very abundant in the phosphatic beds of the Oulad Abdoun Basin. In total, 13 reptile species (of which 6 were new, see Table 2) were described by Arambourg, on the basis of isolated remains, mainly teeth, jaw fragments and vertebrae (Figures 3, 4). As a result of the non identification of the Danian stage at this time, no taxa of this age was identified by Arambourg, an artificial observation as Danian fossils have been unearthed since then. Below we give a synthesis of the taxa described by Arambourg (1952), with their original systematical assignments.

Squamata

Three different groups of squamates were described by Arambourg: Mosasauridae, Aigialosauridae and Palaeophidae. On the basis of the extremely numerous and highly diagnostic isolated mosasaurid teeth in the Maastrichtian phosphates of Morocco, he recognized 2 different species, *Mosasaurus* (*Leiodon*) cf. *anceps* Owen, 1840 (Arambourg, 1952, pl. 38) and *Globidens aegyptiacus* Zdansky, 1935 (opus cit., pl. 40; see Figure 3) and erected 2 others: *Mosasaurus beaugei* (opus cit., pl. 39) and *Platecarpus* (?) *ptychodon* (opus cit., pl. 39). In addition, he defined 2 new

Table 2. Comparison of the reptilian taxa known at Arambourg's and present times. New taxa are in boldface. Note the predominance, at both Arambourg's time and now, of squamates in the Maastrichtian and of crocodyliforms in the Palaeogene. Note also the occurrence at present time of clades completely undescribed at Arambourg's time: chelonians, avian and non-avian dinosaurs and pterosaurs.

TAXA		ARAMBOURG 1952	PRESENT TIME	AGE
SQUAMATA	**PAL**	***Palaeophis maghrebianus***	*Palaeophis maghrebianus*	**YPR**
		–	*Palaeophis* sp.	**PAL**
		–	*Palaeophis* sp.	**MAA**
	VAR	***Pachyvaranus crassispondylus***	*Pachyvaranus crassispondylus*	**MAA**
	MOS	***Mosasaurus beaugei***	*Mosasaurus beaugei*	**MAA**
		Platecarpus* (?) *ptychodon	*Platecarpus* (?) *ptychodon*	**MAA**
		Mosasaurus (*Leiodon*) cf. *anceps*	(***Prognathodon* n. sp.**)	**MAA**
			(**N. gen. et sp.**)	**MAA**
		–	*Prognathodon currii*	**MAA**
		–	*Prognathodon giganteus*	**MAA**
		Globidens aegyptiacus	(***Globidens phosphaticus***)	**MAA**
			(*Carinodens belgicus*)	**MAA**
			(***Carinodens minalmamar***)	**MAA**
		–	***Halisaurus arambourgi***	**MAA**
PLESIOSAURIA	**ELA**	***Plesiosaurus mauritanicus***	**Elasmosauridae n. gen. et sp.**	**MAA**
CROCODYLIFORMES	**CRO**	*Crocodylus* cf. *spenceri*	***Maroccosuchus zennaroi***	**YPR**
	GAV	–	*Thoracosaurus* sp.	**?**
		–	***Argochampsa krebsi***	**DAN**
		–	***Ocepesuchus eoafricanus***	**MAA**
	DYR	*Dyrosaurus phosphaticus*	***Dyrosaurus maghribensis***	**YPR**
		Dyrosaurus sp.	*Hyposaurus* sp.	**YPR**
		Dyrosaurus paucidens	*Hyposaurus paucidens*	**THA**
		Crocodilus sp.	Aff. *Phosphatosaurus gavialoides*	**THA**
		–	*Rhabdognathus* sp.	**THA**
		–	***Arambourgisuchus khouribgaensis***	**THA**
		–	***Chenanisuchus lateroculi***	**THA**
		–	***Atlantosuchus coupatezi***	**DAN**
	PHO	–	Pholidosauridae indet.	**DAN**
		Mesosuchia indet.	Crocodyliformes indet.	**MAA**
PTEROSAURIA	**AZH**	–	***Phosphatodraco mauritanicus***	**MAA**
NON-AVIAN DINOSAURIA	**TIT**	–	Titanosauriformes indet.	**MAA**
	ABE	–	Abelisauroidea indet.	**MAA**
AVES	**PRO**	–	***Lithoptila abdounensis***	**THA-YPR**
	PHA	–	***Phaethusavis pelagicus***	**YPR**
	ODO	–	*Dasornis toliapica*	**THA-YPR**
		–	*Dasornis emuinus*	**THA-YPR**
		–	***Dasornis* n. sp.**	**YPR**
CHELONII	**BOT**	–	***Rhothonemys brinkmani***	**?**
		–	***Phosphatochelys tedfordi***	**YPR**
		–	***Ummulisani rutgersensis***	**YPR**
		–	***Bothremys kellyi***	**YPR**
		–	*Taphrosphys* sp.	**THA**
		–	***Taphrosphys ippolitoi***	**DAN**
		–	***Bothremys maghrebiania***	**DAN**
		–	***Araiochelys hirayamai***	**DAN**
		–	***Labrostochelys galkini***	**DAN**
	CHE	–	***Argillochelys africana***	**YPR**
		–	***Tasbacka ouledabdounensis***	**THA**
		–	*Osteopygis emarginatus*	**DAN?**
		–	***Euclastes acutirostris***	**PAL**
		–	*Euclastes* sp.	**MAA**
	DER	–	Dermochelyidae indet.	**MAA**

Abbreviations: **Stratigraphy**: **DAN**, Danian; **MAA**, Maastrichtian; **PAL**, indeterminate Palaeocene; **THA**, Thanetian; **YPR**, Ypresian; **?**, indeterminate level; **Systematics**: **ABE**, Abelisauroidea; **AZH**, Azhdarchidae; **BOT**, Bothremydidae; **CHE**, Cheloniidae; **CRO**, Crocodyloidea; **DER**, Dermochelyidae; **DYR**, Dyrosauridae; **ELA**, Elasmosauridae; **GAV**, Gavialoidea; **MOS**, Mosasauridae; **ODO**, Odontopterygiformes; **PAL**, Palaeophiidae; **PHA**, Phaethontidae; **PHO**, Pholidosauridae; **PRO**, Prophaethontidae; **TIT**, Titanosauriformes; **VAR**, Varanoidea.

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squamates on the basis of isolated vertebrae: the Maastrichtian lacertilian *Pachyvaranus crassispondylus* (Aigialosauridae) (opus cit., pl. 41) and a new species of the Ypresian Palaeophidae (sic for Palaeophiidae) snake named *Palaeophis maghrebianus* (opus cit., pl. 41) (Figure 4).

Plesiosauria

Plesiosaurus mauritanicus was described and attributed to the family Plesiosauridae by Arambourg (1952, pl. 40-41; see Figure 3). This new species was based on Maastrichtian isolated teeth from the Ganntour Basin (pl. 40, figs. 11-16) and vertebrae from the Meskala Basin (pl. 40, figs. 17-19).

Crocodyliformes

Two major crocodyliform groups were recognized by Arambourg in the Thanetian and Ypresian levels on the basis of fragmentary jaws, isolated teeth and postcranial elements: 1) The Mesosuchian pholidosaurids, represented by *Dyrosaurus phosphaticus* (Thomas, 1893), *Dyrosaurus* sp. (Arambourg 1952, pl. 42) and the new species *Dyrosaurus paucidens* Arambourg, 1952 (pl. 44); 2) the Eusuchian crocodilids known by *Crocodilus* cf. *spenceri*

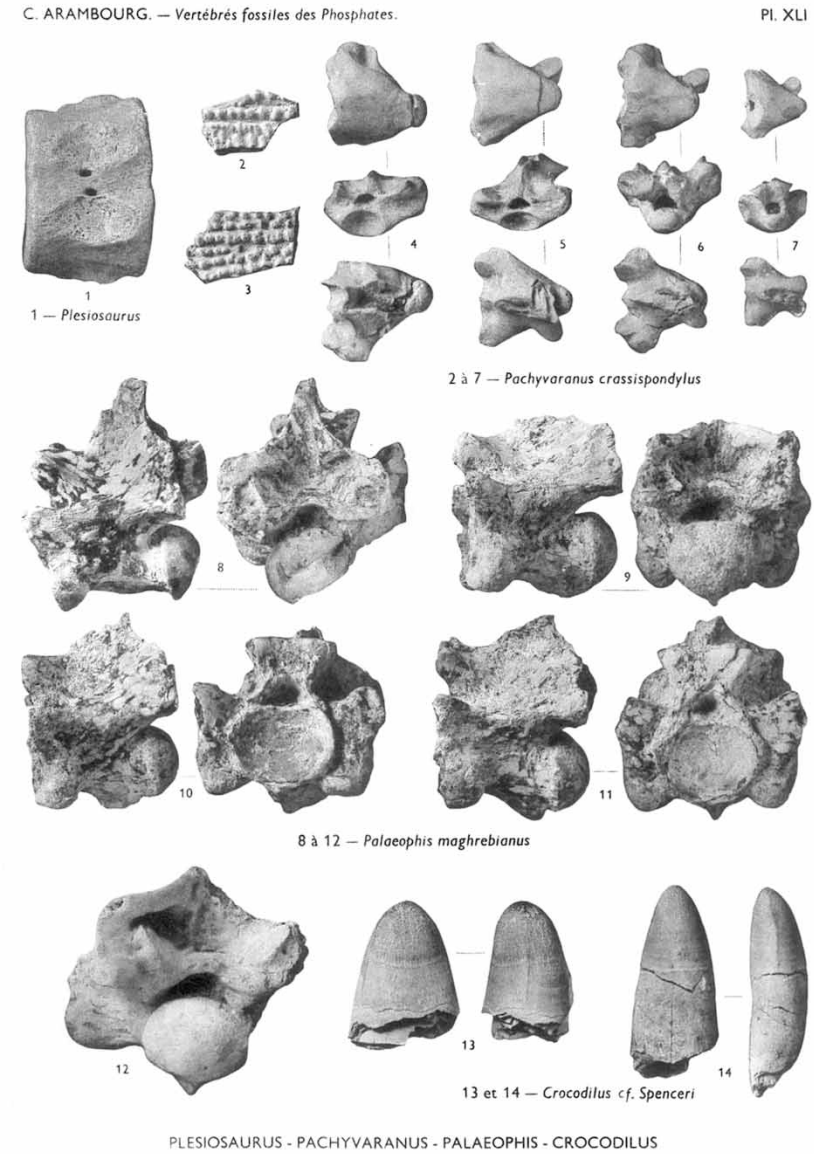

Figure 4. Reproduction of Plate XLI of Arambourg (1952) as an example of the three major clades described by this author in the phosphates of Morocco and the fragmentary status of the remains found at this time. 1: *Plesiosaurus* vertebra; 2-7: vertebrae and osteoderms of the varanoid *Pachyvaranus crassispondylus* Arambourg, 1952; 8-12: vertebrae of the snake *Palaeophis maghrebianus* Arambourg, 1952; 13-14: teeth of the eusuchian crocodile *Crocodilus* cf. *spenceri*.

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Buckland, 1836 (opus cit., pl. 41; see Figure 4) and *Crocodilus* sp (opus cit., pl. 42). Only scarce remains were described from the Maastrichtian: isolated teeth from Imi'n Tanout city (Meskala Basin) and Oued Erguita (Sous Basin) (opus cit., pl. 40; see Figure 3), as well as an isolated dermal scute from Youssoufia (opus cit., pl. 42), both referred to indeterminate 'mesosuchians'.

Chelonii

The first mention of turtle remains from the Moroccan phosphates is due to Ambroggi and Arambourg (1951) who reported on the presence of indeterminate chelonians from the Maastrichtian of Oued Erguita (Sous Basin). Curiously, no turtles were described by Arambourg in his monograph.

Recent and current works

Surprisingly, after Arambourg's pioneer works, vertebrate fossils from the phosphates of Morocco - despite their attested abundance - have been neglected for decades, except selachians that have been extensively studied since the 1980s (e.g. Cappetta 1987, Noubhani and Cappetta 1994, 1997 and references therein). Only punctual works have been published on crocodyliforms (Ennouchi 1957, Jonet and Wouters 1972, 1977, Buffetaut 1976, 1979, Hua 1995), turtles (Moody 1976, Gmira 1995) and snakes (Rage and Wouters 1979).

In 1996, the unexpected discovery of *Phosphatherium*, the oldest proboscidean known at this time, in the Palaeogene deposits of the Oulad Abdoun Basin (Gheerbrant et al. 1996) led to the resumption of large-scale palaeontological researches in the phosphates of Morocco. Interestingly, this was the first occurrence of a continental fossil vertebrate in these marine deposits. Nearly 60 years after Arambourg's first works, an official French-Moroccan program of collaboration (which aim was the study of the vertebrate faunas from the phosphates of Morocco) was signed between the *Office Chérifien des Phosphates* (Casablanca), The *Ministère de l'Energie, des Mines, de l'Eau et de l'Environnement* of Morocco (Rabat), the *Muséum National d'Histoire Naturelle/Centre National de la Recherche Scientifique* (Paris), and the Universities Cadi Ayyad (Marrakech) and Chouaîb Doukkali (El Jadida). This program, which was initiated in 1997, involves also vertebrate palaeontologists from the *Université des Sciences et Techniques du Languedoc* (Montpellier) and the *Universidad del País Vasco/E.H.U.* (Bilbao).

This active collaboration has led to the constitution of an important palaeontological collection and improves our knowledge of the vertebrate fossils from the phosphates of Morocco. A wealth of vertebrate remains has been collected, mainly including marine groups. Besides a better knowledge of the taxa already known (selachians, actinopterygian fishes, marine reptiles), these new fossis reveal the presence of taxa totally unknown at Arambourg's time: Maastrichtian non-avian dinosaurs and pterosaurs (see below), as well as Palaeogene continental mammals (see Gheerbrant et al. 2003, Solé et al. 2009 and references therein) and Palaeogene marine birds (see below). The material now includes nicely preserved skull and postcranial remains, and even complete articulated skeletons for mosasaurid squamates and crocodyliforms. Almost all this material is kept in the collections of the OCP (Khouribga, Morocco) and partly of the *Département Histoire de la Terre* of the MNHN (Paris, France). In parallel, many specimens are collected by local people for commercial purposes and several chelonian taxa have been erected, on the basis of specimens derived from the fossil trade and now kept in institutions in USA, France and Japan. The reptilian faunal list is summarized in Table 2 and briefly commented below.

Squamata

Mosasaurids constitute the bulk of the Maastrichtian marine reptiles, in the number of both specimens and taxa: Arambourg described 4 species but currently at least 10 are known. *Mosasaurus beaugei* Arambourg, 1952 has been revised and its knowledge significantly improved based on several recently found crania (Bardet et al. 2004). Arambourg (1952) described different morphologies of Maastrichtian globulous teeth under the same specific name, *Globidens aegyptiacus* Zdansky, 1935. A review of these teeth and the description of new material have shown that three different species of globidensine mosasaurids are in fact present: the new species *Globidens phosphaticus* Bardet and Pereda Suberbiola, 2005b, *Carinodens belgicus* (Woodward, 1891) and the new species *Carinodens minalmamar* Schulp, Bardet & Bouya, 2009 (Bardet et al. 2005b, 2008, Schulp et al. 2009). Both large and small teeth that are robust and smooth were described by Arambourg (1952) as *Mosasaurus* (*Leiodon*) cf. *anceps* Owen, 1840. Recently unearthed specimens, including cranial and postcranial skeletons, have shown that they belong respectively to a new species of the large mosasaurine *Prognathodon* (Bardet et al. in progress) and to a new plotosaurine genus (LeBlanc et al. in progress), whereas *Leiodon anceps* is considered a *nomen dubium* (Schulp et al. 2008). Two other species of *Prognathodon* have also been recognised: *Prognathodon currii* Christiansen & Bonde, 2002 (Bardet et al. 2005b) and *Prognathodon giganteus* Dollo, 1904 (NB pers. obs.). *Platecarpus* (?) *ptychodon* Arambourg, 1952 is now known by both cranial and postcranial specimens under preparation. Finally, a new species of halisaurimorph mosasaurid, *Halisaurus arambourgi* Bardet & Pereda Suberbiola, 2005a, has been described on the basis of numerous cranial and postcranial elements (Bardet et al. 2005a; Figure 5). This species, the smallest of the

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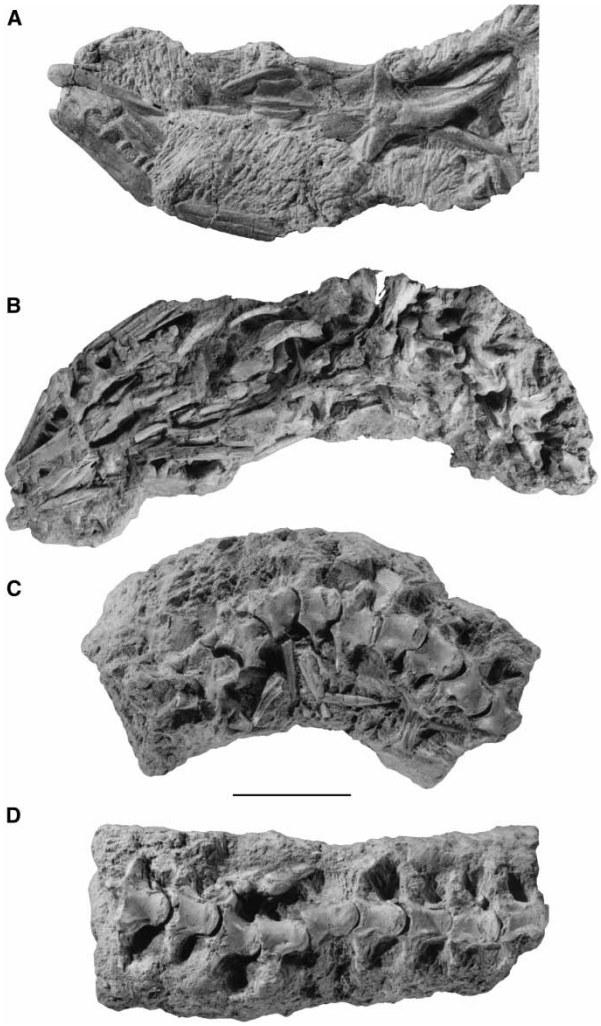

Figure 5. *Halisaurus arambourgi* Bardet & Pereda Suberbiola, 2005a, MNHN PMC 14 (holotype): incomplete skeleton, Grand Daoui, Oulad Abdoun Basin, level CIII, Maastrichtian (in Bardet et al. 2005a). **A**-**B**, skull in dorsal and ventral views; **C**, cervical and dorsal vertebrae in ventral view; **D**, dorsal and one isolated caudal vertebrae in ventral view. Scale = 10 cm.

mosasaurid fauna, is very frequent in the Maastrichtian of both the Oulad Abdoun and Ganntour basins, so that it is surprising that Arambourg did not describe or even mention it.

The varanoid lizard *Pachyvaranus crassispondylus* Arambourg, 1952 was erected on the basis of some isolated vertebrae (see Figure 4). Osteoderms were also referred to this species by Arambourg but their assignment to Squamata has been recently questioned (Houssaye et al. in press). The discovery of new specimens, including numerous isolated vertebrae as well as articulated vertebrae and ribs, enabled a new study of this taxon, from anatomical, systematical (Houssaye et al. in press) and histological (Buffrénil et al. 2008) points of view. *P. crassipondylus* belongs to a non pythonomorph new taxon of Varanoidea (Houssaye et al. in press). The intense pachyosteosclerosis of its vertebrae and ribs all along its axial skeleton, together with the sedimentary context, suggest an aquatic mode of life for this taxon (Buffrénil et al. 2008, Houssaye et al. in press).

Palaeophis maghrebianus Arambourg, 1952 is a large marine snake restricted to the Ypresian phosphatic beds of Morocco, where it is common (see Figure 4). Up to now, it has been only recovered from the Oulad Abdoun Basin. However, it cannot be discarded that its absence in the Ypresian of the Ganntour Basin might be linked to the lack of systematic prospections. As all palaeophiids, it is poorly known: only vertebrae, either isolated or making up comparatively short articulated portions of vertebral columns, and fragmentary ribs, are available. Snakes of this family had several hundred vertebrae (one presumed palaeophiid had more than 560 vertebrae) (Rage 1984) and the material referred to *Palaeophis* represents a part of the vertebral column insufficient for thorough studies. However, it may be stated that among palaeophiids, *P. maghrebianus* is one of the less adapted to aquatic life since its vertebrae are not clearly compressed laterally. Material attributed to *Palaeophis* sp. has also been described in the Oulad Abdoun Basin: 1) a single vertebra from the Maastrichtian near Khourigba represents the earliest and only confirmed palaeophiid from the Mesozoic (Rage and Wouters 1979); 2) some vertebrae from the Thanetian rank among the extremely scarce palaeophiids reported from the Palaeocene (JCR pers. obs.). These Maastrichtian and Thanetian discoveries, though isolated, significantly improve the stratigraphical distribution of palaeophiids, previously known with confidence only from the Eocene.

Plesiosauria

Compared to mosasaurids, plesiosaur remains are relatively scarce in the Maastrichtian phosphates of Morocco. They mainly consist of isolated teeth and vertebrae. Recently, new diagnostic cranial elements have been discovered, and represent a new genus and species (Vincent et al. submitted). This study also shows that the status of *Plesiosaurus mauritanicus* Arambourg, 1952 should be reconsidered and that up to now, apparently only one elasmosaurid taxon seems to be present (Vincent et al. submitted).

Crocodyliformes

If mosasaurid squamates were the most important marine reptiles in the Maastrichtian, crocodyliforms are undoubtedly the major Palaeogene group. Arambourg described 6 taxa in the Oulad Abdoun Basin, but recent studies based on the revision of already described material and the discovery of new specimens allowed to identify 14 species (Jouve 2004, 2007, Jouve et al. 2005a, 2005b, 2006a, 2006b, 2008a, 2008b). The Crocodyliformes of the Oulad

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Abdoun Basin belong to two major clades: the Crocodylia (sensu Benton and Clark 1988, see Brochu et al. 2009), represented by 3 gavialoids and a tomistomine crocodyloid, and the highly diversified marine Dyrosauridae, known by 8 species. Recently, postcranial material belonging to a third group, the Pholidosauridae, has been discovered in the Danian of the Oulad Abdoun Basin and is currently under study (Jouve et al. in prep.).

Dyrosaurids are known in all the Palaeogene levels of the phosphatic series. From the Danian, new cranial material of *Atlantosuchus coupatezi* Buffetaut, 1979 has permitted to significantly improve our knowledge of this taxon (Jouve et al. 2008a). This species, with a snout of more than 79% of its total skull length, is the most longirostrin dyrosaurid. The highest diversity of dyrosaurids is found in the Thanetian, with 5 known taxa. Two new genera and species have been recently described: the basalmost short-snouted *Chenanisuchus lateroculi* Jouve et al., 2005b and the longirostrine *Arambourgisuchus khouribgaensis* Jouve et al., 2005a. Several cranial specimens have been attributed to *Rhabdognathus* (Jouve 2007). New cranial material of *Hyposaurus paucidens*, initially described as *Dyrosaurus paucidens* by Arambourg (1952) and referred to *Hyposaurus* by Buffetaut (1976), is now available (Jouve 2004). Arambourg (1952) described a mandible as *Crocodylus* sp. and, belonging to the same taxon, only several teeth have been recovered recently. The whole of this material (mandible and teeth) exhibits clear dyrosaurid characteristics, and is comparable to *Phosphatosaurus gavialoides* from the Ypresian (Buffetaut 1978, 1980, Moody and Buffetaut 1981). So that it could belong to the genus *Phosphatosaurus* (Jouve 2004). The durophageous tooth described by Karl (2004) as *Phosphatosaurus gavialoides* is probably from the same species. However, the Maastrichtian stratigraphic identification given by Karl, based on the yellow colour of the matrix, could be erroneous as yellow phosphates also occur in the Palaeocene. Two dyrosaurid taxa are known from the Ypresian. The remains described by Arambourg (1952) as *Dyrosaurus* sp. have been reattributed to *Hyposaurus* sp. (Jouve 2004). A new species of *Dyrosaurus*, *D. maghribensis* Jouve et al., 2006b, has been erected on the basis of several subcomplete specimens allowing a nearly complete reconstruction of its skeleton (Jouve et al. 2006b; Figure 6), but also musculature and bracing system (Schwarz 2003, Schwarz et al. 2006, Schwarz-Wings et al. 2009). It should be noted that several Moroccan specimens (Arambourg 1934, 1935, 1952, Hua 1995) previously described as belonging to *D. phosphaticus* (Thomas, 1893) in fact belong to *D. maghribensis* (Jouve et al. 2006b).

The Crocodylia are known by 3 gavialoids and a tomistomine crocodyloid. The gavialoids are represented by the Maastrichtian *Ocepesuchus eoafricanus* Jouve et al., 2008b, which is the oldest known African Crocodylia,

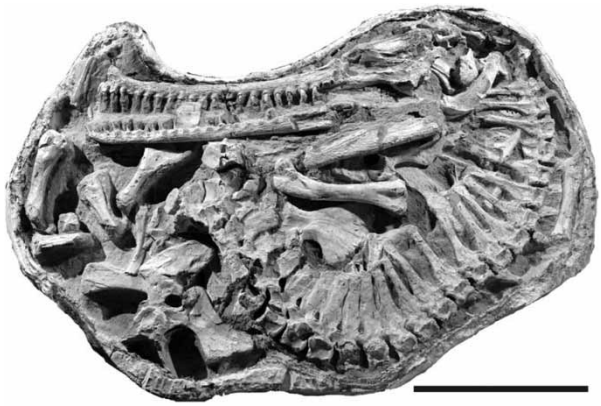

Figure 6. *Dyrosaurus maghribiensis* Jouve et al., 2006b, OCP DEK/GE 255 (holotype): subcomplete skeleton, Meraa el Arech, Oulad Abdoun Basin, level CI, Ypresian (in Jouve et al. 2006b). Scale = 50 cm.

the Danian *Argochampsa krebsi* Hua & Jouve 2004, which is a basal gavialoid with a particular snout shape (Jouve et al., 2006a), and finally a third form, whose stratigraphical origin remains unknown, that was briefly described and referred to as *Thoracosaurus* sp. (Jouve 2004). The presence of a crocodyloid in the Ypresian of Morocco was first mentioned by Arambourg (1934, 1935) on the basis of jaw fragments, and assigned to as '*Crocodilus*' cf. *spenceri* (Arambourg, 1952). Later, additional cranial and postcranial specimens from the Ypresian phosphates of Morocco were described by Jonet and Wouters (1972, 1977), but the authors ignored Arambourg's specimens and erected the new taxon *Maroccosuchus zennaroi* Jonet and Wouters, 1977. A revision of these previously described specimens, under the light of new well preserved remains, demonstrated that all can be referred to as *Maroccosuchus zennaroi*, which is considered as the basalmost Tomistominae (Jouve 2004).

Chelonii

Up to recently, only fragmentary specimens from Benguerir (Ganntour Basin) were briefly mentioned in first the Maastrichtian: a humerus referred to an indeterminate chelonian (Moody 1976, Gmira 1995) and a skull attributed to the cheloniid *Rhetechelys* sp. (= *Euclastes* sp.) (Gmira 1995), and second the Thanetian: a shell, firstly attributed to a pelomedusoid close to *Podocnemis* (Moody 1976), later referred to the bothremydid *Taphrosphys* sp. (Antunes and Broin 1988, Gmira 1995).

Our recent field works as well as wild excavations by local people for commercial purposes have shown that chelonian remains are very frequent in the phosphates of Morocco and highly diversified both in the latest Cretaceous and Palaeogene levels. Most Palaeogene taxa, including chelonioid cryptodirans and bothremydid

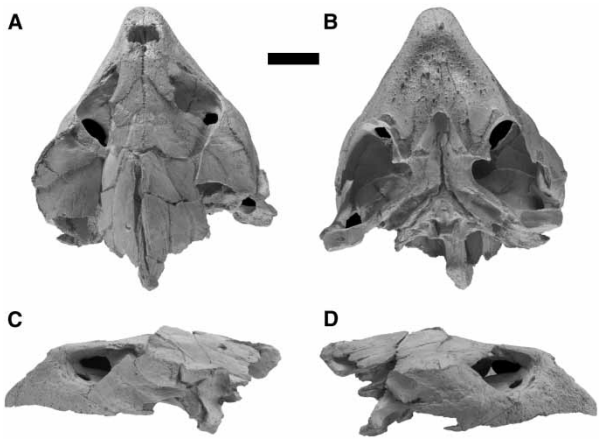

Figure 7. *Euclastes acutirostris* Jalil et al., 2009, OCP DEK/GE 408 (holotype): skull, Sidi Chennane, Oulad Abdoun Basin, level CII, Danian-Thanetian (in Jalil et al. 2009). **A**, dorsal view; **B**, ventral view; **C**, left lateral view; **D**, right lateral view. Scale = 3 cm.

pleurodirans, have been described on the basis of specimens (essentially skulls) derived from the fossil trade, and supposedly coming from the Oulad Abdoun Basin.

The Chelonioidea include a Maastrichtian isolated hypoplastron referred to an indeterminate Dermochelyidae close to *Corsochelys* (Tong and Hirayama 2004), as well as several Palaeogene skulls referred to Cheloniidae: *Euclastes acutirostris* Jalil et al., 2009 from the Danian-Thanetian (Figure 7), *Tasbacka ouledabdounensis* Tong and Hirayama, 2002 from the Thanetian, *Argillochelys africana* Tong and Hirayama, 2008 from the Ypresian, and finally *Osteopygis emarginatus* Cope, 1868 (= *Osteopygoides priscus* Karl et al. 1998). This species has been considered as Danian in age because the specimens recovered from the fossil trade were indicated as possibly coming from the 'dalle couche 2' of the Oulad Abdoun Basin (Hirayama and Tong 2003). However, 'dalle couche 2' does not exist in the local mining terminology and, though it can be suspected - especially on selachian evidences as given by the authors - that it refer to the Danian 'Couche II' (Note: Arabic numbers are used for the beds of the Ganntour Basin, *versus* Roman ones for the beds of the Oulad Abdoun Basin, see Table 1), the Danian age of this species cannot be confirmed confidently.

The Bothremydidae are the most abundant and diversified turtles from the Palaeogene phosphates of Morocco, being represented by 8 new taxa, also erected on the basis of skulls recovered from the fossil trade. Four species are known from the Danian (*Araiochelys hirayamai* Gaffney et al., 2006, *Bothremys maghrebiania* Gaffney et al., 2006, *Labrostochelys galkini* Gaffney et al., 2006 and *Taphrosphys ippolitoi* Gaffney et al., 2006) and 3 from the Ypresian (*Phosphatochelys tedfordi* Gaffney and Tong, 2003, *Ummulisani rutgersensis* Gaffney et al., 2006 and *Bothremys kellyi* Gaffney et al., 2006) (Gaffney et al. 2006, Gaffney and Tong 2008). Finally, *Rhothonemys brinkmani* Gaffney et al., 2006 was described from an indeterminate Palaeogene level (Gaffney et al. 2006).

Pterosauria

The pterosaurs are represented by the azhdarchid *Phosphatodraco mauritanicus* Pereda Suberbiola et al., 2003, which is based on a series of disarticulated but closely associated five mid to posterior cervical vertebrae from the Maastrichtian phosphates of the Oulad Abdoun Basin (Pereda Suberbiola et al., 2003; Figure 8). This large animal (wingspan close to 5 m) is one of the latest known pterosaurs and represents the first record of azhdarchids in the latest Cretaceous of northern Africa (Pereda Suberbiola et al. 2003). New material has been recently discovered and is currently under study (Pereda Suberbiola et al. in prep.).

Non avian Dinosauria

Non-avian dinosaurs are scarce in the Maastrichtian phosphates of the Oulad Abdoun Basin and represented by sauropod and theropod saurischians. Hindlimb bones (femur, tibia and fibula) from a medium-sized sauropod have been attributed to a non-titanosaur titanosauriform as Titanosauriformes indet. (Pereda Suberbiola et al. 2004; Figure 9). A large isolated tooth has been referred to an abelisaurid theropod (Buffetaut et al. 2005); however this

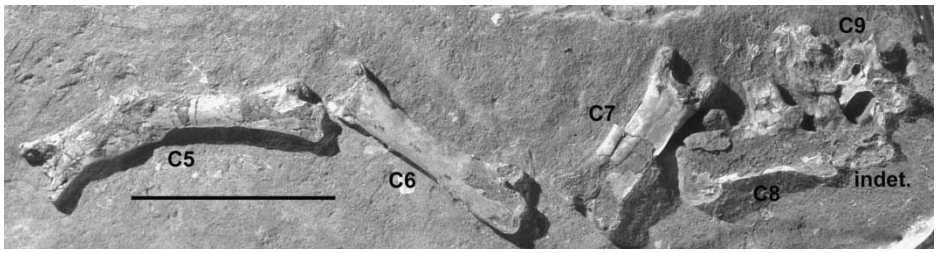

Figure 8. *Phosphatodraco mauritanicus* Pereda Suberbiola et al., 2003, OCP DEK/GE 111 (holotype): cervical series composed of five vertebrae (C5 to C9), Grand Daoui, Oulad Abdoun Basin, level CIII, Maastrichtian (in Pereda Suberbiola et al. 2003). **C5**, ventral to left-lateral view; **C6**, ventrolateral to left lateral view; **C7**, ventral view. **C8**, left lateral view; **C9**, posterior view. Scale = 20 cm.

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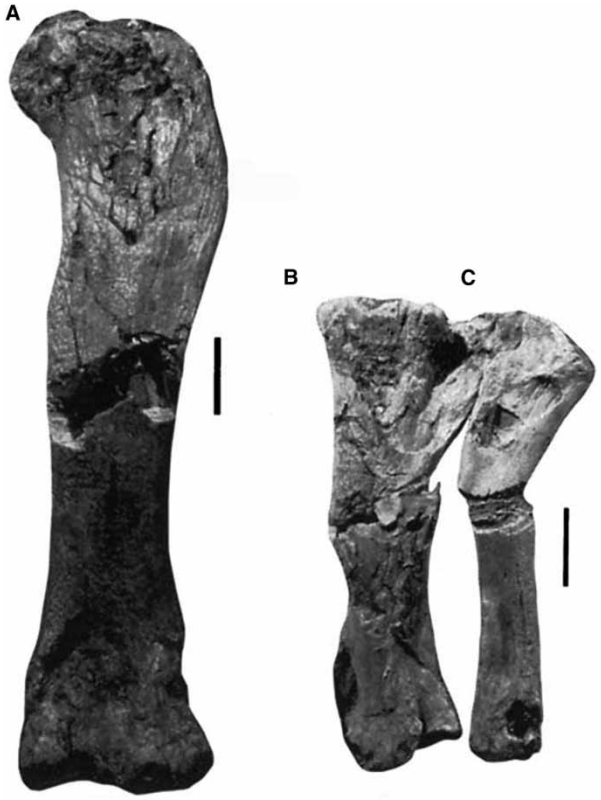

Figure 9. Titanosauriformes indet., OCP DEK/GE 31: femur, tibia and fibula, Grand Daoui, Oulad Abdoun Basin, level CIII, Maastrichtian (in Pereda Suberbiola et al. 2004). **A**, femur in posterior view; **B**, tibia in posterior view; **C**, fibula in medial view. Scale = 10 cm.

assignment has been regarded as tentative by Smith and Lamanna (2006). Two additional theropod teeth have been recently found and will be described elsewhere (Pereda Suberbiola et al. in prep.). All these dinosaur remains may be remnants of floating carcasses that drifted over a distance from a land area.

Aves

No fossil birds have been found so far in the Maastrichtian phosphates, but an abundant material, mainly disarticulated skulls and postcranial elements, have been discovered in the Palaeogene of the Oulad Abdoun Basin. They are found in Upper Palaeocene (Thanetian) and Lower Eocene (Ypresian) levels, and most of them are dated as basal Ypresian (Intercalary bed II/bed I of the mining terminology). This avifauna represents the oldest known modern birds (Neornithes) from Africa and is almost exclusively composed of seabirds (Bourdon 2006).

So far, described taxa comprise 2 species of tropicbird-like seabirds, namely the prophaethontid *Lithoptila abdounensis* Bourdon, 2005 (Bourdon et al. 2005, 2008a; Figure 10) and the possibly phaethontid *Phaethusavis pelagicus* Bourdon, 2008 (Bourdon et al. 2008b). Both taxa are related to extant tropicbirds (*Phaethon*) and reached a wingspan of approximately 1 m.

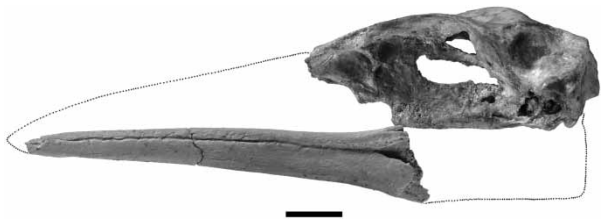

Figure 10. *Lithoptila abdounensis* Bourdon, 2005, reconstruction of the skull in left lateral view. Left, OCP.DEK/GE 1089, fragment of left mandible, Grand Daoui, Oulad Abdoun Basin, intercalary level CII/CI, basal Ypresian (in Bourdon et al. 2008a); right, OCP.DEK/GE 1087 (holotype), braincase, Grand Daoui, Oulad Abdoun Basin, level CIIa, Thanetian (in Bourdon et al. 2005). Scale = 1 cm.

The Odontopterygiformes (pseudo-toothed birds) constitute the dominating group of the Oulad Abdoun avifauna (Bourdon 2005, 2006; Bourdon et al. submitted). The Moroccan fossils are among the oldest representatives of this extinct group (Bourdon 2005, 2006, Bourdon et al. submitted) and are known by 3 species of the genus *Dasornis*: *D. toliapica* (Owen, 1873) (2-3 m wingspan), *D. emuinus* (Bowerbank, 1854) (3.5-4.5 m wingspan), and a third new species representing the smallest known pseudo-toothed bird (1.6 m wingspan).

Conclusion

This paper is an update on the reptilian faunas of the phosphates (Maastrichtian to Ypresian) of Morocco. The pioneer work of Arambourg (1952), which was mainly focused on the Oulad Abdoun Basin (and to a lesser extent on the Ganntour Basin), has permitted to recognize 13 taxa of squamates, crocodyliforms and plesiosaurs. Arambourg erected one new genus, *Pachyvaranus*, which is still considered valid nowadays (Houssaye et al. in press), as well as 6 new species, all but one considered valid today, even if their generic attribution has changed for half of them (see Table 2).

Since a decade, the renewal of palaeontological works in the phosphates of Morocco after a gap of 50 years, has permitted a significant improvement in our knowledge of reptilian assemblages, with the description of 17 new genera and 29 new species; currently, at least 52 species are recognised (Table 2). These taxa represent major clades, including squamates (palaeophiid snakes, varanoid and mosasaurid lizards), plesiosaurs (elasmosaurids), crocodyliforms (gavialoid and crocodyloid eusuchians, dyrosaurids, pholidosaurids), pterosaurs (azhdarchids), non-avian dinosaurs (titanosauriform sauropods, abelisauroid theropods), aves (prophaethontids, phaethontids, odontopterygiforms) and chelonians (bothremydid pleur-

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odirans, cheloniid and dermochelyid chelonioid cryptodirans). Importantly, four major groups (chelonians, pterosaurs, avian and non-avian dinosaurs) were unknown (or undescribed) at Arambourg's time.

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