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## A strange new chelonioid turtle from the Latest Cretaceous Phosphates of Morocco

*Une étrange nouvelle tortue chélonioïde du Crétacé terminal des Phosphates du Maroc*France de Lapparent de Broin<sup>a,\*</sup>, Nathalie Bardet<sup>a</sup>, Mbarek Amaghazaz<sup>b</sup>, Saïd Meslouh<sup>c</sup><sup>a</sup> CR2P, UMR 7207 CNRS-MNHN-UPMC, département Histoire de la Terre, MNHN, CP38, 57, rue Cuvier, 75231 Paris cedex 05, France<sup>b</sup> OCP, centre minier de Khouribga, Khouribga, Morocco<sup>c</sup> MEMEE, Rabat, Morocco

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## ABSTRACT

A new genus and species of huge marine turtle (superfamily Chelonoidea, epifamily Dermochelyoidea) is described from the Maastrichtian Phosphates of the Oulad Abdoun Basin of Morocco. A new type of feeding apparatus, adapted for a powerful crushing pattern, illustrates the noteworthy diversity of fossil vertebrates of the Maastrichtian-Ypresian Phosphates of Morocco. No other crushing cryptodire or bothremydid pleurodire has this morphology. During the Maastrichtian, the known crushing pattern of chelonioids was different, close to that of modern cheloniids, as illustrated in Morocco in the Maastrichtian Ganntour Basin and the Palaeogene Oulad Abdoun Basin. This new taxon exhibits unusual cranial characters (fusion of premaxillae associated with a backward and dorsal retraction of the naris, horizontal stretching of the dorsal *meatus quadrati*), that are shared only with another new turtle, known also from the same Maastrichtian Phosphates of Morocco.

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## R É S U M É

Un nouveau genre et une nouvelle espèce de grande tortue marine (superfamille Chelonoidea, épifamille Dermochelyoidea), des Phosphates maastrichtiens du Bassin des Oulad Abdoun, Maroc, sont décrits. Un nouveau type d'appareil alimentaire, conçu pour un régime broyeur puissant, est représenté, illustrant la remarquable diversité en vertébrés fossiles des Phosphates maastrichtiens-ypresiens du Maroc. Aucun autre cryptodire ou pleurodire bothrémydidé broyeur n'a cette morphologie. Au Maastrichtien, le seul mode broyeur de chélonioïde connu était différent, proche de celui des Cheloniidae modernes, tel qu'illustré au Maroc à la fois dans le Bassin des Ganntour au Maastrichtien et dans le Bassin des Oulad Abdoun au Paléogène. Ce nouveau taxon présente des caractères crâniens inhabituels (fusion des prémaxillaires, associée au recul dorsal de la narine, étirement à l'horizontale de la partie dorsale du *meatus quadrati*) qu'il ne partage qu'avec une autre nouvelle tortue, elle aussi connue dans les mêmes Phosphates maastrichtiens du Maroc.

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## 1. Introduction

The great diversity of fossil vertebrates in the Phosphates of Morocco has been known since [Arambourg \(1952\)](#) and has been enhanced these last fifteen years by new palaeontological studies undertaken by French-Moroccan collaborations.

In these Maastrichtian-Ypresian phosphatic deposits that crop out mainly in the Oulad Abdoun and Ganntour basins, intensively exploited for economic resources (see [Bardet et al., 2010](#) for details), turtles are particularly well represented by both cryptodirans and pleurodirans ([Bardet et al., 2010, 2013, in press; Gaffney et al., 2006; Gmira, 1995; Hirayama and Tong, 2003; Jalil et al., 2009; Lapparent de Broin, 2000; Tong and Hirayama, 2002, 2004, 2008; Tong and Meylan, 2013](#)).

Most turtle specimens have been unearthed from Palaeogene phosphatic deposits; Maastrichtian discoveries remain rare up to now. The new turtle here described is the fourth taxon from the Maastrichtian levels, along with *Euclastes* sp. from Ben Guérir (Ganntour Basin) ([Gmira, 1995; Jalil et al., 2009](#)), an indeterminate chelonoid from the Oulad Abdoun Basin ([Tong and Hirayama, 2004](#)) based only on a palstral fragment that could correspond to the present new taxon (only known by a skull up to now), and a new astonishing giant longirostrine taxon from the Maastrichtian of Sidi Chennane (Oulad Abdoun Basin) ([Bardet et al., 2013](#)).

## 2. Geological and stratigraphical settings

The phosphatic deposits of Morocco are part of the Mediterranean Tethyan phosphogenic province, which extends from North Africa to the Middle-East ([Lucas and Prévôt-Lucas, 1996](#)). They crop out in four basins, the most important and only economically exploited ones being the Oulad Abdoun and Ganntour ones (see [Bardet et al., 2010](#) for details) ([Fig. 1A](#)). Stratigraphically, they extend from the Late Cretaceous (Maastrichtian) to the base of the Middle Eocene (Lutetian), spanning the largest interval of time of all Tethyan Phosphates ([Lucas and Prévôt-Lucas, 1996](#)).

The Maastrichtian phosphatic series of the Oulad Abdoun Basin (“Couche III” of the miners, or Level III) is very condensed in the Grand Daoui zone, northeastern part of the basin (near Oued Zem city), being only about 2–5 m thick. It is composed from the bottom to the top of a basal grey bone-bed, soft yellow (Lower Level III) and soft grey (Upper Level III) exploited Phosphates, separated by a yellow marly level ([Fig. 1B](#)).

The type specimen of the new taxon, a complete skull with its associated mandible, was discovered in 2006 by local people in the Upper Level III (Upper Maastrichtian) of the Sidi Daoui area of Grand Daoui zone, northeastern part of the Oulad Abdoun Basin.

**Institutional Abbreviations:** CNRS, Centre National de la Recherche Scientifique (France); MEMEE, Ministère de l'Énergie, des Mines, de l'Eau et de l'Environnement (Rabat, Morocco), MNHN, Muséum National d'Histoire Naturelle (Paris, France), RA–AC, Reptiles and

Amphibians – Comparative anatomy; OCP, Office Chérifien des Phosphates, Service géologique (Khouribga, Morocco).

## 3. Systematic palaeontology

Order: CHELONII Latreille, 1800

Suborder: CRYPTODIRA Cope, 1868

Superfamily: CHELONIOIDEA Opperl, 1811

Epifamily: DERMOCHELYOIDEA Fitzinger, 1843

Genus *Alienochelys* nov.

*Alienochelys selloumi* nov. sp.

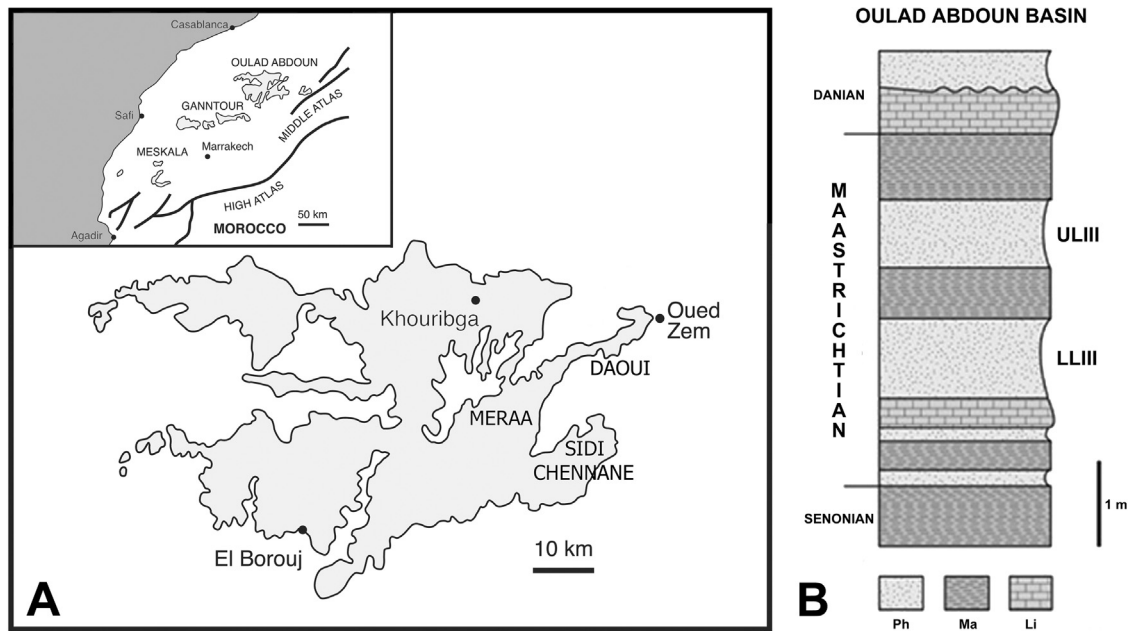
**Holotype:** OCP DEK/GE 393, a complete large skull with its associated lower jaw and the axis lying in the orbit; the left neural arch of atlas. OCP collections, Khouribga (Morocco) ([Figs. 2 and 3](#)). No referred material known up to now.

**Derivatio nominis:** Genus name from *aliena*: stranger in latin, and *chelys*: turtle in latin (issued from greek χελύζ); species name in honor to Mr. Omar Selloumi, OCP technician geologist (now retired) at the Geological Survey in Khouribga, in acknowledgement of his constant help and friendship since fifteen years during our fieldwork and stays in Khouribga.

**Type locality and horizon:** Trench TS, Sidi Daoui area, Grand Daoui zone, Northeastern part of the Oulad Abdoun Basin near the city of Oued Zem, Khouribga Province, Morocco, ([Fig. 1A](#)). Phosphatic deposits, near the base of the Upper Level III (ULIII) ([Fig. 1B](#)), Upper Maastrichtian (Uppermost Cretaceous) ([Cappetta, 1987](#)).

**Diagnosis:** For genus and species, by monotypy. *Alienochelys selloumi* nov. gen. nov. sp. is a gigantic chelonoid turtle (holotype maximal skull length without lower jaw: 41,5 cm) belonging to the epifamily Dermochelyoidea notably by full reduction of the medial ventral process of the jugal beneath the orbit, not contacting the pterygoid and the maxilla, as well as by palatines meeting medially ventroposteriorly to the vomer. It differs from all other turtles by its lower and upper jaw triturating surfaces, considerably developed and constituting a powerful crushing apparatus that forms a half circle arch with rounded extremities, developed as follows:

- lower jaw: wide and dorsoventrally flattened fused dentaries, with surface barely wider at the coronoid-dentary suture level than at the symphysis area one, dorsally barely undulated with a small tomial rolled border;
- upper jaw: anteroposteriorly gently inclined, very widely protruding snout, with a low triturating surface poorly concave, also nearly as wide medially as laterally and with a narrowly rounded tomial border; wide and long triturating surfaces, anterolaterally constituted by both long and wide maxillae and fused premaxillae and medially by the vomer and palatines that are linked anteriorly to the choanae; but, unlike other crushing chelonoids, no secondary palate, the external naris being pushed backward so that it is superimposed to the choanae and the air conduct being vertical between the naris and the choanae;



**Fig. 1.** A. Geographical location of the main phosphatic basins of Morocco. OCP DEK/GE 393 comes from the Sidi Daoui area, in Grand Daoui zone, north-eastern part of the Oulad Abdoun Basin. B. Grand Daoui quarrying area, synthetic stratigraphical column. ULIII, Upper Level III (where *Alienochelys* has been found); LLIII, Lower Level III.

**Fig. 1.** A. Localisation géographique des principaux bassins à Phosphates du Maroc. OCP DEK/GE 393 provient de Sidi Daoui, dans la zone de Grand Daoui, Nord-Est du Bassin des Oulad Abdoun. B. Zone d'exploitation de Grand Daoui, colonne stratigraphique synthétique. ULIII, Couche III supérieure (où *Alienochelys* a été trouvée); LLIII, Couche III inférieure.

- upper and lower jaw triturating surfaces all along particularly rough with short crests and protuberances unlike other crushing chelonioids.

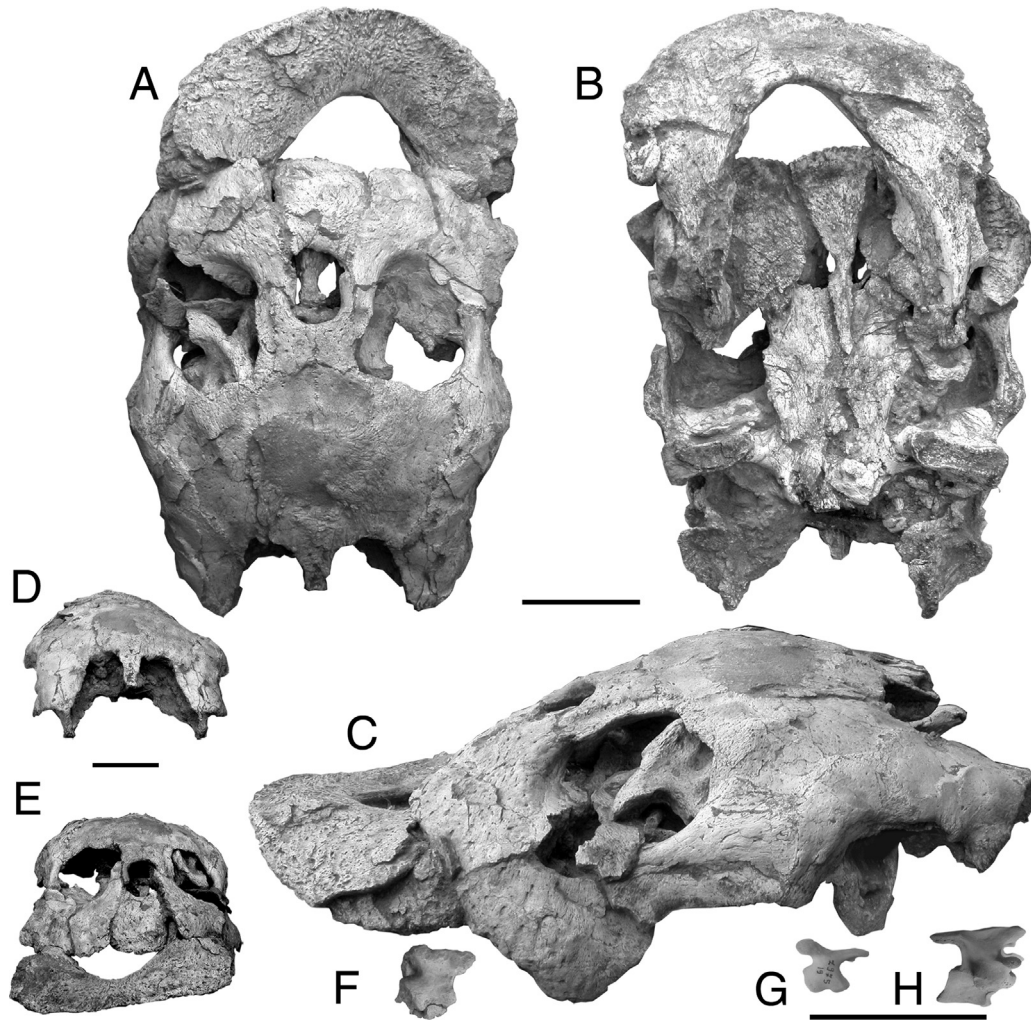
Below orbit and jugal, considerably elongated posterolateral maxillary process, extending posteriorly up to the anterolateral border of the quadrate, excluding jugal and quadratojugal from the moderate cheek emargination. *Foramen posterius canalis carotici interni* forming a ventrally open groove, at the basioccipital-basisphenoid and pterygoid contact, and carotid running into a closed *canalis carotici interni* between pterygoid and basiphenoid. No scute sulci.

*Alienochelys selloumi* nov. gen. nov. sp. shares some unusual characters with only another new chelonioid from the coeval Maastrichtian Phosphates of Morocco (in this work called the “other new Maastrichtian Moroccan form”) that are: anteroposteriorly inclined snout with orbits facing anterolaterodorsally, fusion of the premaxillae, dorsal and nearly horizontal external naris pushed back between the orbits and superimposed on the choanae, which are latero-anteriorly framed by the maxillae processes (which are horizontal instead of vertical), small lateral prefrontals located lateral to nasals, and with processes extending horizontally below the maxillae (before descending anteriorly). It also shares with this other new taxon a horizontally stretched *meatus quadrati* area, facing ventrally in a half circle shape, with the *incisura columellae auris* ventrally open. The new turtle differs from the other one by the presence of anterior horizontal processes of the nasals framing

lateroposteriorly the external naris, frontals not reaching the orbits and parietals not contacting the squamosals, and finally, an unique crushing apparatus, totally different from the suction feeding one of the other new Maastrichtian Moroccan form (distinguished by a bony-pipette longirostrine snout).

**Description:** The holotype skull, preserved with its associated attached lower jaw and not completely prepared interiorly, exhibits two fractures on its anterior left part (Fig. 2C) and is slightly damaged ventroposteriorly in some places (Fig. 2B).

The skull is rather low, roughly rectangular (median skull length: 37.5 cm; maximal width: 35.5 cm; full skull length with lower jaw: 55.5 cm; maximal dentary width: 33 cm, symphysis length: 7.8 cm) with a long and wide snout (wider than the skull at the orbital level) anteriorly inclined, and large orbits (12.1 × 10.6 cm). Snout and orbit portions constitute half the skull length. The skull table is irregularly bulged dorsally. There are no scute sulci but marked nutritive foramina and short canals on the whole external skull surface. Some radiating rounded ridges issue from a center that is situated rather anteriorly on the midline suture between the parietals (Fig. 2A). Much more pronounced foramina located on the snout indicate the emplacement of the upper rhamphotheca (Fig. 2C) while the ventral surface of the dentary is covered with small protruding polygons, completing the dorsal rough surface and marking the emplacement of the lower rhamphotheca part (Fig. 2B). Skull structures decrease in size as follows:



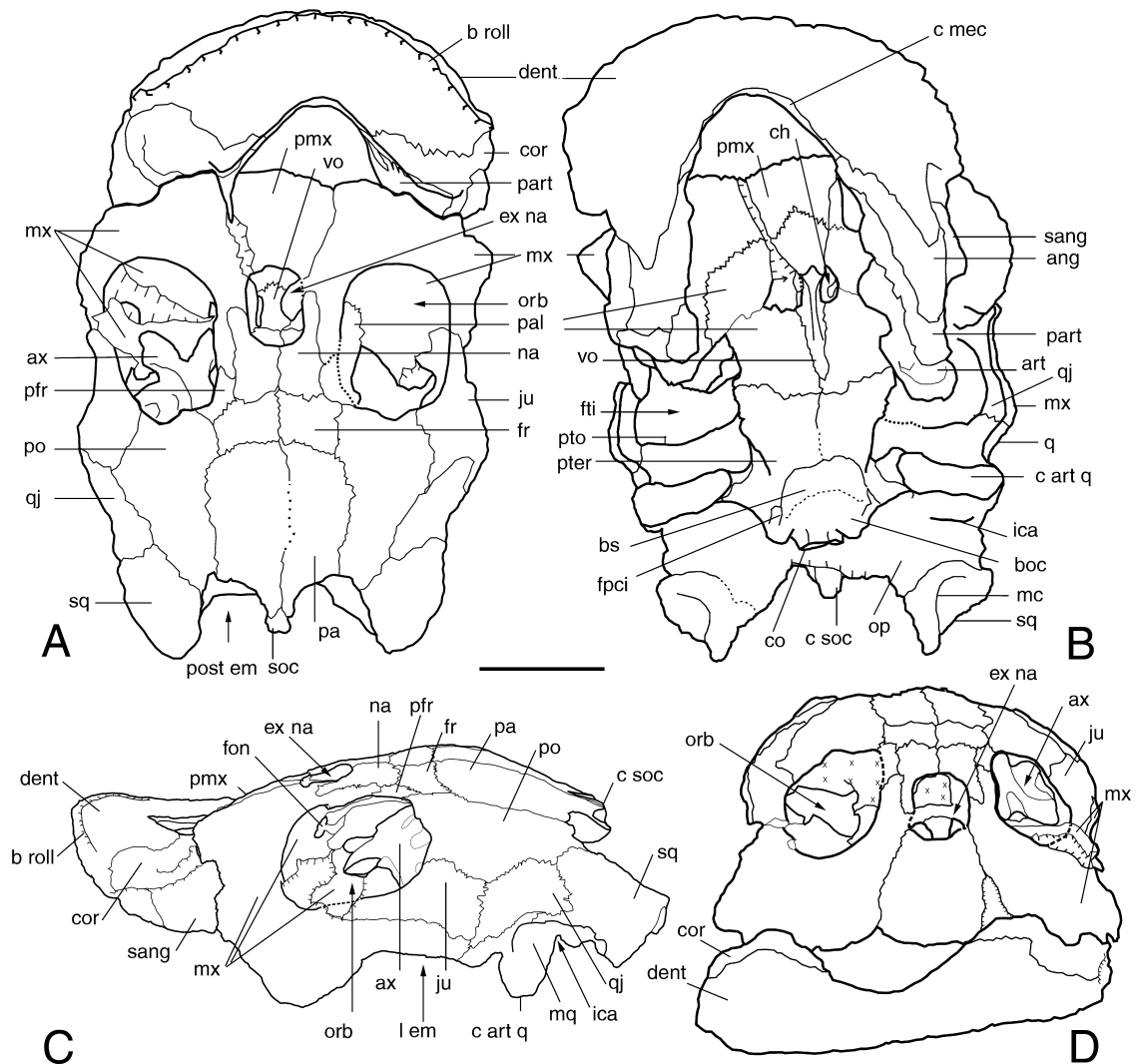
**Fig. 2.** *Alienochelys selloumi* nov. gen. nov. sp. Oulad Abdoun Basin, Morocco, Late Maastrichtian. Holotype OCP DEK/GE 393; photographs of the skull with lower jaw in A, dorsal; B, ventral; C, left lateral slightly dorsal with the axis lying in the left orbit, in right lateral view; D, dorso-posterior views. Atlas, F, left neural arch with a fragment of the intercentrum, left lateral view. *Chelonia mydas*, MNHN RA, AC 1975-19, G, atlas, left neural arch, H, axis, left lateral views. Scale bars, 10 cm.

**Fig. 2.** *Alienochelys selloumi* nov. gen. nov. sp. Bassin des Oulad Abdoun, Maroc, Maastrichtien supérieur. Holotype OCP DEK/GE 393; photographies du crâne avec mandibule en vues : A, dorsale ; B, ventrale ; C, latérale gauche légèrement dorsale, avec l'axis situé dans l'orbite gauche en vue latérale droite ; D, dorso-postérieure ; et E, fronto-dorsale. Atlas : F, arc neural gauche avec fragment d'intercentre, vue latérale gauche. *Chelonia mydas*, MNHN RA, AC 1975-19, G, atlas, arc neural gauche, H, axis, vues latérales gauches. Échelles, 10 cm.

- the rectangular-ovoid orbits;
- the suborbital arch, constituted by both the jugal and maxillary posterior process situated one above the other all along the jugal length, from the mid orbit length up to their posterior extremity;
- the interorbital space;
- the rectangular external naris.

Through the external naris opening the vomer is visible, contacting the palatines and maxillae. Laterally, the contact of the descending process of the prefrontal with the maxilla and the dorsal border of the *foramen orbitonasale* is visible, but its contact with the vomer remains unclear. Ventrally, posterior to the triturating surface, the vomer forms a vertical short pillar that is not hidden by the triturating part of the linked vomer and palatines, the triangular

choanae remaining well visible on each side. The posterior process of the vomer is long between palatines, but does not reach the pterygoid (shortly sutured palatines). The external pterygoid processes (slightly eroded on the right side) are reduced, without any vertical flange posteriorly to the slight palatine narrowing. This is due to the reduction of the *foramen palatinum posterius* and the fully reduced medioventral process of the jugal. The pterygoids are wide, not narrowed and medially flat; they extend lateroposteriorly up to the basisphenoid-basioccipital boundary and inferiorly extend partly on the articular quadrate processes. The moderately large and flat basisphenoid has an anteriorly rounded shape. The carotid canal is not completely embedded in bone. It begins posteriorly, not covered ventrally at the basioccipital – pterygoid boundary, and then it runs anteriorly, covered ventrally between the pterygoid



**Fig. 3.** *Alienochoelys selloumi* nov. gen. nov. sp., Oulad Abdoun Basin, Morocco, Late Maastrichtian. Holotype OCP DEK/GE 393; interpretative drawings of the skull with lower jaw in: A, dorsal, B, ventral, C, left lateral slightly dorsal, and D, frontal views with the axis lying in the left orbit, in dorsal view. cm. Areas with crosses: not visible sutures. Scale bars, 10 cm. ang, angular; art, articular; ax, axis; b roll, tomial border roll; boc, basioccipital; bs, basisphenoid; c art q, *condylus articularis quadrati*; ch, choana; c mec, *canalis meckelii*; co, *condylus occipitalis*; cor, coronoid; c soc, *crista supraoccipitalis*; dent, dentary; ex na, external naris; fon, *foramen orbitonasale*; fpci, *foramen posterius canalis carotici interni*; fr, frontal; fti, *fossa temporalis inferior*; ica, *incisura columellae auris*; ju, jugal; l em, lateral emargination; mc, muscular crest; mq, *meatus quadrati*; mx, maxilla; na, nasal; op, opisthotic; orb, orbit; pa, parietal; pal, palatine; part, prearticular; pfr, prefrontal; pmx, premaxilla; po, postorbital; post em, posterior emargination; pter, pterygoid; pto, *processus trochlearis oticus*; q, quadrate; qj, quadratojugal; sang, surangular; soc, supraoccipital; sq, squamosal; vo, vomer.

**Fig. 3.** *Alienochoelys selloumi* nov. gen. nov. sp., Bassin des Oulad Abdoun, Maroc, Maastrichtien supérieur. Holotype OCP DEK/GE 393, dessins interprétatifs du crâne avec mandibule en vues : A, dorsale, B, ventrale, C, latérale gauche légèrement dorsale et D, frontale, avec l'axis situé dans l'orbite gauche en vue dorsale. Zones avec croix : sutures non visibles. Échelles, 10 cm.

and the basisphenoid; as a result, the posterior foramen of the carotid is not embedded into the pterygoid extremity. In the inferior temporal fossa, the cryptodiran *processus trochlearis oticus* is barely visible ventrally (Figs. 1B and 2B), largely constituted by the quadrate: no prootic participation is visible at least ventrally (incomplete preparation). It constitutes a wide facet, anteriorly oriented and slightly laterally protruding, with a concave anterior border. The *condylus articularis quadrati* is wide, rectangular, with rounded angles and is slightly biconcave. The occipital

condyle is tripartite, formed by the two exoccipitals and the basioccipital, and is located behind and above the rounded *tuberculum basioccipitale* (better preserved on the right). The *columella auris* groove is ventrally visible on the left side, at the base of the quadrate articular process. The posteroventral part of the squamosals has a medial longitudinal muscular crest. The supraoccipital crest shortly appears posterior to the condyle. Laterally, the maxillae are strikingly so much posteriorly expanded up to the quadrate that they exclude both the jugal and quadratojugal from the

cheek emargination. The quadratojugal and dorsal part of the quadrate are horizontally stretched, so that the *meatus quadrati* forms a half circular structure ventrally facing with the *incisura columellae auris*. However, the articular process of the quadrate is ventrally not stretched and well protruding. The *antrum postoticum* is moderately developed.

The lower jaw of *Alienochelys* presents numerous adaptations for a strong crushing diet above described, such as a semi-circular broadly enlarged shape, global robustness, particularly medially flattening with anterior thinning, and roughness surfaces. On the other hand, it possesses the general structure of a moderately advanced chelonioid in the evolutionary schema presented in the various phylogenetic analyses such as those of Hirayama (1995), Kear and Lee (2006) and Parham and Pyenson (2010), with a dentary not expanded posteriorly toward the articular surface and a moderately anteriorly developed surangular. The coronoid is wide, low and rounded, and integrated into the triturating surface (Fig. 2A, B). The area posterior to the triturating surface is as long as it, and robust to support its weight.

The axis is preserved into the left orbit (posteriorly facing) (Figs. 2C and 3C) and a part of the atlas (neural arch with a fragment of the intercentrum) was preserved in the matrix just lateral to the skull (Figs. 2F and 3D). They are similar to those of *Chelonia*, being just slightly relatively deeper. The atlas postzygapophyses are slightly more robust. The axis postzygapophyses are more curved and the axis anterior process is more dorsally protruding.

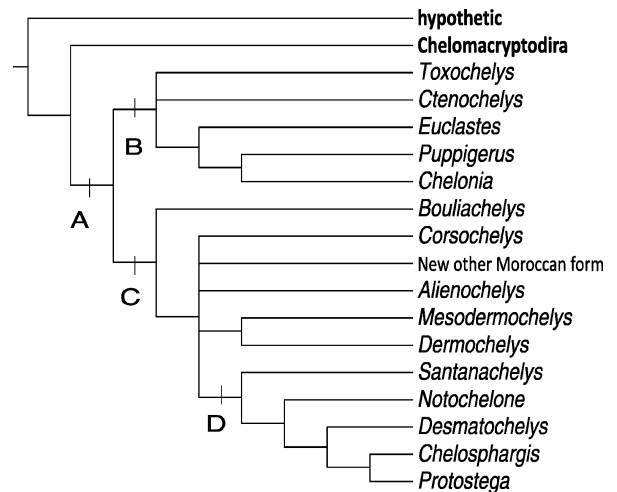
## 4. Phylogenetic Relationships

### 4.1. Material and Methods

*Alienochelys selloumi* nov. gen. nov. sp. has been included into a matrix (103 characters, 22 taxa) slightly modified from that of Bardet et al. (2013), performed for the other new Maastrichtian Moroccan form, itself slightly modified from that of Kear and Lee (2006) based on Hirayama (1998). See the Electronic appendix (complementary details, characters, results and various obtained cladograms).

### 4.2. Comparative results

The absence of postcranial material and the impossibility of observing the inner skull characters do not permit us to detect all the chelonioid apomorphies corresponding to the character analysis (such as those of the paddles, *dorsum sellae*, *rostrum basisphenoidale*, position of inner carotid foramina in the *sella turcica*, relative size of the inner arterial canals and of the *processus inferior parietalis*). However, the results (Fig. 4; Appendix Figs. 1 to 3) clearly show that, among Chelonioida, *Alienochelys* nov. gen. belongs to the epifamily Dermochelyoidea (sensu Bour and Dubois, 1986, emend. Gaffney and Meylan, 1988), sharing several synapomorphies of the superfamily (homoplastic here or there in few Chelomacryptodira and Plesiochelyidae) including: the complete ventral reduction of the jugal below the orbit, not contacting the pterygoid (10/1 and 11/1), and the palatines posteriorly meeting (vomer not contacting the pterygoids (20/1)) as in other taxa of the epifamily (except *Dermochelys*, but by reversion as shown



**Fig. 4.** Strict consensus tree obtained from the matrix, slightly modified, provided in Bardet et al. (2013), for another new chelonioid from the Maastrichtian Phosphates of Moroccan. Modified from Kear and Lee (2006) with, as outgroups, an hypothetical taxon and Chelomacryptodira, and including *Alienochelys selloumi* nov. gen. nov. sp. A. Chelonioida. B. Cheloniidae. C. Dermochelyoidea. D. Protostegidae. L = 222, Ci = 51, Ri = 59.

**Fig. 4.** Arbre de Consensus Strict obtenu à partir de la matrice légèrement modifiée produite par Bardet et al. (2013) pour un autre chélonioïde nouveau des Phosphates maastrichtiens du Maroc. Modifiée de Kear et Lee (2006), avec, comme groupes externes, un taxon hypothétique et les Chelomacryptodira et avec addition d'*Alienochelys selloumi* nov. gen. nov. sp. A. Chelonioida. B. Cheloniidae. C. Dermochelyoidea. D. Protostegidae. L = 222, Ci = 51, Ri = 59.

by the visible anterior extraordinary pterygoid expansion). The absence of *foramen palatinum posterius* (21/1) is also shared with Dermochelyoidea in which the character reduction presents two states:

- the most basal state (here shown), with the foramen laterally widely open, making a weak lateral notch anterior to the pterygoid process, that is still slightly protruded as in *Bouliachelys* Kear and Lee, 2006, the primitive protostegids *Santanachelys* Hirayama, 1998, *Rhinochelys pulchriceps* (Owen, 1851) (Collins, 1970), and *Desmatochelys lowi* Williston, 1894 (Zangerl and Sloan, 1960) (Hirayama, 1995) (particularly morphologically close in that point to *Alienochelys* nov. gen. due to an elongation of the maxillary-palatine gulf);
- the pterygoid process and lateral notch fully disappear together with a strong pterygoid narrowing in the advanced Protostegidae *Protostega gigas* Cope, 1872 (Hirayama, 1995), *Archelon* Wieland, 1896 (Hay, 1908), and *Calcarichelys gemma* Zangerl, 1953a (Hooks, 1998).

The jugal-ptyergoid contact is also lost in the Maastrichtian cheloniid *Allopleuron hofmanni* (Gray, 1831), the jugal being ventrally partly reduced, but the *foramen palatinum posterius* is present, small and often laterally fissured, and the pterygoid process is not reduced. The foramen fully disappears in all other Cheloniidae with a secondary palate, and derived compared to *Toxochelys* and *Ctenochelys* (Zangerl, 1953b), but in which the jugal-ptyergoid contact is preserved (Hirayama, 1995). The absence of *foramina*

*praepalatina* (14/1) is shared by the Dermochelyoidea and all Cheloniidae more derived than *Toxochelys*.

However, *Alienochelys* nov. gen. is not a cheloniid because of its pterygoid (not contacting the jugal which is reduced here (10, 11)), the lack of any sagittal crest unlike most cheloniids (23/0), its basisphenoid without a V-shaped crest and posterolateral projections (31/0), and finally because of the preservation of other primitive characters, beside the advanced Dermochelyoidea characters given above. The posterior carotid foramen (29/1), located posteriorly but not fully embedded into the pterygoids, is primitive in relation to Cheloniidae, slightly less derived than in the other new Maastrichtian Moroccan form (29/2), but derived in relation to Protostegidae (29/0). The absence of a parietal-squamosal contact (7/1) is variable in Dermochelyoidea, so it does not appear to be decisive.

In chelonioids, the deep modification of the limbs into rigid paddles reflects adaptation to an open marine life – the fore paddles being much longer than the hind ones – by a series of changes that may vary according to the groups and is very important in the resulting relationships of the taxa. So, if *Alienochelys* nov. gen. is clearly a Dermochelyoidea, its current lack of postcranial material means that its ingroup relationships remain unresolved with respect to *Dermochelys* and Protostegidae. For comparable reasons, the affinities of *Bouliachelys* and of the other new Maastrichtian Moroccan form (Bardet et al., 2013) also remain unresolved.

*Alienochelys* nov. gen. approaches the protostegid condition by an expansion of the pterygoid on the quadrate articular process (24/1) that however remains less extensive, as in the other new Maastrichtian Moroccan form (24/0), although slightly more extended in *Alienochelys* nov. gen. than in the latter because it reaches the condyle (Bardet et al., 2013. See [Electronic appendix](#)). Its relative basal position and derivation is explained by the presence of a combination of primitive characters, some of them being shared with the other new Maastrichtian Moroccan form (long nasals and lateral position of the prefrontals, short *crista supraoccipitalis*, relatively short posterior emargination), as with the most primitive protostegids (those presenting various relative shape and position of the bones surrounding the external naris and orbits) (Hirayama, 1995). Both Moroccan forms are derived in relation to cheloniids and primitive protostegids by the absence of scute sulci (1/1) (like *Dermochelys* and advanced protostegids) and a more posterior position of the carotid foramen (29/1) than in protostegids. This character is however less derived in *Alienochelys* than in the other new Maastrichtian Moroccan form in which the carotid foramen is located as posteriorly as in *Dermochelys* and like that of Cheloniidae (29/2). Moreover, they are the only two taxa to share the following derived characters, not yet included in the performed analyses, and that probably indicate close relationships: fused premaxillae, posterodorsal migration of the external naris and consecutive modification of the surrounding bones and structures, quadrate meatus area becoming horizontally stretched, and ventral orientation of the *incisura columellae auris* notch. Among these, the random distribution in Dermochelyoidea of some derived features approaching those of these two taxa

is noteworthy. For example, *Dermochelys* has a maxilla slightly prolonged posteriorly to the orbit (but not excluding the jugal from the cheek emargination) (unlike the other new Maastrichtian Moroccan form) and an incisura facing rather ventrally (like both Moroccan forms, but without meatus stretching). In Protosteginae (Hooks, 1998; Wieland, 1909; Zangerl, 1953a), the skull remains poorly described: *Archelon ischyros* Wieland, 1896 and *Protostega gigas* Cope, 1872 seem to have an external naris opening dorsally and partly moved above the choanae, and the anterior part of the palate of *Protostega gigas* could be elongated without hiding the choanae (Hirayama, 1995, Figs. 2i and 3i) whereas *Microstega copei* (Wieland, 1909) has an *incisura columellae auris* ventrally facing (but without meatus stretching).

This new chelonioid, *Alienochelys* nov. gen., exhibiting a new type of feeding apparatus among the turtles from the Maastrichtian Phosphates of the Oulad Abdoun Basin, is adapted for a powerful crushing diet of hard preys. As in the other new Maastrichtian Moroccan form, (a suction feeder provided by a unique bony elongated tubular snout), whereas the choanae remain posterior, the elongation of the triturating surfaces is accompanied by the step backward of the external naris up to be superimposed on the choanae. In cheloniids, when the triturating surfaces are elongated, the skull is provided with a secondary palate, permitting the conduction of air to be prolonged inside the skull between the external naris and the choanae. When these cheloniids are adapted to a crushing feeding, the upper jaw fits with the skull by an expanded lower jaw symphysis (exception in “*Syllomus aegyptiacus*” in Hasegawa et al., 2005, with a short but very denticulated dentary) and the triturating surfaces are more or less crested, directly on the bony structure and/or on the rhamphothecae, differently according to the preys and the taxa, but not as in *Alienochelys* nov. gen. Among such cheloniids, are represented all the members of the “*Euclastes* group” (sensu Jalil et al., 2009, i.e. the “Durophagous Stem Cheloniids” of Parham and Pyenson, 2010, including *Erquelinnesia*, *Pacificchelys* and *Mexichelys*), as well as “*Argillochelys*” *africana* Tong and Hirayama, 2008 and *Tasbacka* (Tong and Hirayama, 2002). It should be noted that these last two taxa and *Euclastes* are present in the Phosphates of Morocco. They have smooth bony triturating surfaces like some living and Tertiary forms. Other extant taxa and the Maastrichtian cheloniid *Allopleuron* have much more crested jaws. In conclusion, *Alienochelys* nov. gen. is unique among chelonioids by the lack of a secondary palate (also absent in other Dermochelyoidea and primitive cheloniids) despite of a crushing diet. Among Dermochelyoidea, *Dermochelys* is a ram feeder of soft preys that has very thin and smooth “triturating” surfaces, contrasting with the strong ridged and tuberculated triturating surfaces of *Alienochelys* nov. gen. However, like *Dermochelys* and unlike the other new Maastrichtian Moroccan form, *Alienochelys* bears a palatine extension up to the choanae and a vertical short vomer pillar that is, like the choanae, not hidden ventrally.

Among sea turtles, the *Alienochelys* nov. gen. jaw surfaces, though exhibiting a different morphology, evoke the crushing diet also present in various bothremydid

pleurodires, a family worldwide spread during the Maastrichtian–Palaeogene. In bothremydids, the enlargement of the surfaces is realized around the palatal medial sulcus, without secondary palate, and the choanae are not moved backward. Among them, the Bothremydini in particular (only known during the Palaeogene in Phosphates of Morocco but present otherwise in the Late Cretaceous, for example in Europe; Gaffney et al., 2006), have wide and smooth dorsal triturating surfaces, laterally expanded in width with posterior characteristic pits. Although the Nigereomydinae (sensu “Nigeremys group” Broin, 1988, Lapparent de Broin and Werner, 1998, Nigereomydina Gaffney et al., 2006, 2007) have strong ridged dorsal triturating surfaces on a widened triangular snout, with crests that are parallel to the labial border (see original figures in Lapparent de Broin and Werner, 1998), they more evoke the *Alienochelys* pattern by their strength and mode of action. The Nigereomydinae are known during the Maastrichtian–Palaeocene in the northern part of Africa (Egypt, Mali, Niger), but not in the Moroccan Phosphates together with *Alienochelys*. In these phosphatic deposits, *Alienochelys* gen. nov. is, up to now, the only Maastrichtian turtle adapted to a crushing diet, i.e. occupying such an ecological niche. It shows that marine turtles were much more diversified than previously thought in the Maastrichtian Phosphates of Morocco. Together with the other new Maastrichtian Moroccan form which also exhibits a unique suction feeding apparatus among tetrapods (Bardet et al., 2013), they illustrate the important taxonomic and ecological diversity of the fossil vertebrates of the Maastrichtian–Ypresian Phosphates of Morocco.

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## Appendix A. Supplementary data

Supplementary data (*Alienochelys* gen. nov. – Phylogenetical Analysis elements) associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.crpv.2013.07.008>.

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