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Systematic Palaeontology (Vertebrate Palaeontology)

A new mosasauroid (Squamata) from the Late Cretaceous (Turonian) of Morocco

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Abstract

Tethysaurus nopcsai gen. et sp. nov. is described on the basis of both cranial and postcranial material from the Late Cretaceous (Early Turonian) of the Goulmima region, southern Morocco. This new mosasauroid is mainly characterized by a parietal table ending posteriorly in two pointed pegs; jugal with a large ascending ramus; splenial with a large and notched dorsomedial process; surangular exposed medially ventral to the coronoid; large paracotylar and parazygosphenal foramina on vertebrae. A phylogenetic analysis shows that *Tethysaurus* is the sister-group of Mosasauridae. It fills the gap between the aigialosaurids (mainly Cenomanian) and the mosasaurids (known from the Middle-Late Turonian to the Latest Maastrichtian). ***To cite this article: N. Bardet et al., C. R. Palevol 2 (2003).***

Résumé

Un nouveau mosasauroïde (Squamata) du Crétacé supérieur (Turonien) du Maroc. *Tethysaurus nopcsai* gen. et sp. nov. repose sur du matériel crânien et postcrânien provenant du Crétacé supérieur (Turonien inférieur) de la région de Goulmima, Sud du Maroc. Ce nouveau mosasauroïde est notamment caractérisé par une table pariétale se terminant postérieurement par deux pointes ; jugal à branche montante développée ; splénial portant un grand processus dorsomédial entaillé ; surangulaire exposé médialement ventralement au coronoïde ; vertèbres à grands foramens paracotylaires et parazygosphéniens. Une analyse phylogénétique montre que *Tethysaurus* est le groupe-frère des Mosasauridae. Il comble une lacune entre les aigialosauridés (essentiellement cénomaniens) et les mosasauridés (connus du Turonien moyen-supérieur à la fin du Maastrichtien). ***Pour citer cet article : N. Bardet et al., C. R. Palevol 2 (2003).***

Keywords: Squamata; Mosasauroidea; Late Cretaceous; Turonian; Morocco; new taxon

Mots clés : Squamata ; Mosasauroidea ; Crétacé supérieur ; Turonien ; Maroc ; nouveau taxon

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Introduction

L'intervalle Cénomanien-Turonien (gisements d'Europe et du Proche-Orient) représente une période clef dans la radiation précoce des squamates varanoïdes aquatiques le long des marges de la Tethys [8,18]. Ces squamates, à savoir mosasauroïdes, coniasaures, dolichosaures, adriosaures et pachyophiidés, sont au centre du débat concernant l'origine des serpents et leurs relations de parenté [15,16,19,22]. Au sein des Mosasauroidea (= Aigialosauridae + Mosasauridae, *sensu* [5,15]), les relations phylogénétiques demeurent non résolues parmi les aigialosauridés, contrairement aux mosasauridés [2,9]. Nous décrivons ici un nouveau genre de mosasauroïde basal du Turonien inférieur du Maroc (conservé au Muséum national d'histoire naturelle de Paris - MNHN), qui améliore notre connaissance sur la radiation de ces squamates aquatiques.

Contexte géologique

Les spécimens (MNHN GOU 1-3) proviennent de la région de Goulmima, Province d'Er-Rachidia, Sud du Maroc, bien que leur origine géographique exacte reste inconnue. Les gisements localisés lors de travaux de terrain près des villages de Tadirhourst et Asfla (Nord de Goulmima) ont livré une riche faune de vertébrés marins, ainsi que des ammonites [1,11]. Les fossiles sont préservés dans des nodules ovoïdes concentrés dans l'Unité 4 de la Barre calcaire du Cénomanien-Turonien [14], une référence lithostratigraphique dans toute l'Afrique du Nord. L'Unité 4 est d'âge Turonien inférieur et correspond à un environnement de plate-forme ouverte, lié au maximum de la transgression cénomano-turonienne [14].

Systématique

Squamata Oppel, 1811
Mosasauroidea Camp, 1923
Tethysaurus gen. nov.

Etymologie – De *Tethys*, déesse de la mer dans la mythologie grecque et *sauros*, lézard en Grec.

Espèce type – *Tethysaurus nopcsai* sp. nov.

Diagnose – Comme pour l'espèce type et unique espèce.

Tethysaurus nopcsai sp. nov.

Etymologie – En l'honneur du Baron Ferenc Nopcsa, paléontologue hongrois.

Holotype - MNHN GOU1, crâne et mandibule subcomplets articulés (Fig. 1).

Localité et Horizon type – Près de Goulmima, Province d'Er-Rachidia, Sud du Maroc ; Unité 4 de la Barre calcaire du Cénomanien-Turonien, Crétacé supérieur, Turonien inférieur [14].

Spécimens rapportés de même provenance géographique et stratigraphique - MNHN GOU2, crâne et mandibule incomplets désarticulés (Fig. 2B-D, F) ; MNHN GOU3, squelette partiel désarticulé incluant des os crâniens, des vertèbres et des os des ceintures et des membres (Fig. 2A, E, G-Q).

Diagnose – Mosasauroïde de moins de 3 m de long ; préfrontal fortement voûté en vue antérieure ; pariétal à table triangulaire se terminant postérieurement par deux pointes surplombant le supraoccipital ; jugal à branche montante grande et évasée ; plancher du foramen magnum percé par trois foramens ; splénial à grand processus dorsomédial entaillé ; surangulaire exposé médialement ventralement au coronoïde ; formule dentaire : 19-20 dents sur le maxillaire, 15-19 sur le ptérygoïde, au moins 19 sur le dentaire ; vertèbres à grands foramens paracotylaires et parazygosphéniens.

Discussion et conclusion

Tethysaurus nopcsai partage la plupart des synapomorphies des pythonomorphes (*sensu* [15]) telles que la présence de quatre dents ou moins sur le prémaxillaire, un ptérygoïde portant de grandes dents recourbées, une symphyse mandibulaire très mobile, une articulation intramandibulaire (splénial-angulaire), un complexe zygosphène-zygantrum et des os pelviens non fusionnés [5,15].

Parmi les Pythonomorpha, *Tethysaurus* montre la majorité des synapomorphies des Mosasauroidea, parmi lesquelles un contact prémaxillaire-frontal, un nasal vestigial ou absent, des narines longues et reculées, des frontaux fusionnés participant aux narines, un postfrontal et un postorbitaire fusionnés, un jugal s'étendant en avant de l'orbite, un carré à cavité tympanique importante et processus suprastapédial grand et incurvé, des dents marginales en nombre supérieur à treize et pas de zygapophyses ou de processus transverses sur les vertèbres caudales distales [5,15].

Les Aigialosauridae (*sensu* [15]), qui forment une polytomie non résolue contrairement aux Mosasauridae [2,4,6,7,9], incluent *Aigialosaurus dalmaticus* et *Opetiosaurus bucchichi* (passage Cénomanien-Turonien [13], Slovénie) [10,12] ; *Carsosaurus marchesetti* et l'« aigialosaure de Trieste » (Cénomanien supérieur [13], Croatie) [9,10,12] ; et probablement *Haasiasaurus gittelmani* (Cénomanian inférieur du Proche-Orient) [18] et l' « aigialosaure » de Dallas (Turonien moyen du Texas, non publié) [2].

Afin de déterminer les relations de parenté de *Tethysaurus nopcsai* au sein des Mosasauroidea, une analyse cladistique a été effectuée (options « Branch and Bound » et « Heuristic » de PAUP 3.1.1 [20], caractères non ordonnés et non pondérés), utilisant la matrice de Caldwell [7] (66 caractères, 12 taxons intragroupe + *Tethysaurus* ; cf. Appendice). L'analyse a généré dix-huit arbres plus parcimonieux (131 pas, C.I. = 0.611, H.I. = 0.397, R.I. = 0.643).

L'arbre de consensus majoritaire (50%, Fig. 3) montre que *Tethysaurus* est le groupe-frère des Mosasauridae (*Halisaurus* (autres mosasauridés)), résultat obtenu dans tous les arbres. Le clade *Tethysaurus* + Mosasauridae repose sur plusieurs synapomorphies telles que des processus basiptérygoïdes du basisphénoïde en forme d'éventail, des branches suspensoriales du pariétal horizontales, un jugal à processus postéroventral, le bord médial du dentaire atteignant la moitié de la hauteur du bord latéral et une scapula plus petite que le coracoïde [6,7]. *Tethysaurus* ne possède aucun des caractères dérivés des Mosasauridae, tels qu'une suture prémaxillaire-maxillaire se terminant postérieurement à la quatrième dent du maxillaire, moins de dix-neuf dents sur le dentaire, des arcs hémaux fusionnés aux vertèbres caudales, une scapula en forme d'éventail et non fusionnée au coracoïde [6,7]. *Tethysaurus* se différencie de tous les autres mosasauroïdes par la combinaison des caractères autapomorphiques mentionnés dans la diagnose.

La distribution spatio-temporelle de *Tethysaurus* et sa position phylogénétique comblent une lacune entre les aigialosauridés (essentiellement du Cénomanien du Proche-Orient et de la région adriatique) [10,12,13,18] et les mosasauridés (plus ancienne mention dans le Turonien moyen d'Amérique du Nord et le Turonien supérieur de Colombie et d'Angola) [3,17,21]. De surcroît, sa distribution dans le Turonien inférieur d'Afrique du Nord s'inscrit dans la paléobiogéographie des organismes marins du Cénomanien-Turonien, qui peut être corrélée aux modèles de reconstruction des paléocourants parcourant la Téthys d'est en ouest à travers (voir [8]).

1. Introduction

The Cenomanian-Turonian interval is a key period in lepidosauromorph evolution, corresponding to the early radiation of aquatic varanoid squamates within the Tethys margin habitats of Europe and Middle-East [8,18]. These squamates, namely mosasauroids, coniasaurs, dolichosaurs, adriosaurs and pachyophiids, are involved in the controversy concerning snake origins and their phylogenetical relationships [15,16,19,22]. Among Mosasauroidea (= Aigialosauridae + Mosasauridae, *sensu* [5,15]), the affinities of aigialosaurids remain currently unresolved with regard to mosasaurids [2,9]. Here we report on the discovery of a new basal mosasauroid from the Early Turonian of Morocco that adds to our knowledge of this aquatic squamate radiation.

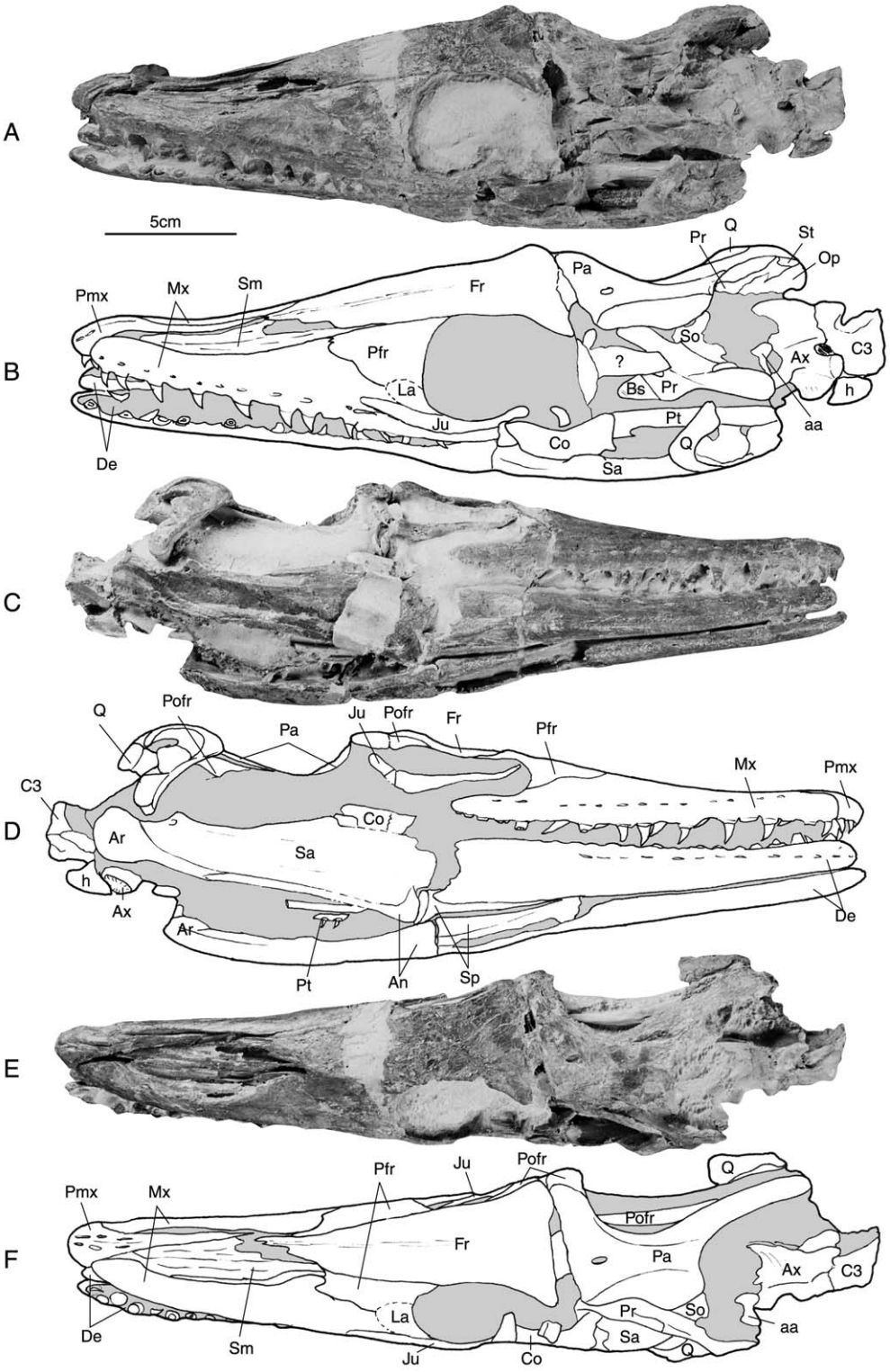
Abbreviation: MNHN, 'Muséum national d'histoire naturelle', Paris (France).

2. Geological context

The specimens come from the Goulmima region in the southern slope of the High-Atlas of Morocco. Though their exact provenance remains unknown, fieldwork has allowed to locate several fossiliferous localities near the villages of Tadirhourst and Asfla, north of Goulmima, Er-Rachidia Province. These sites have yielded a rich fauna of marine vertebrates, including actinopterygians, mosasauroids, turtles and plesiosaurs, as well as ammonites [1,11]. The fossils are preserved in ovoid calcareous nodules that are concentrated in the Unit 4 of the Cenomanian-Turonian limestone bar [14], a reference level in North Africa. The Unit 4 is Early Turonian in age and corresponds to an open platform environment related to the maximum of the Cenomanian-Turonian transgressive phase [14].

3. Systematic Palaeontology

Squamata Oppel, 1811
Mosasauroidea Camp, 1923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Tethysaurus gen. nov.

Etymology – From *Tethys*, goddess of the Sea in Greek mythology and *sauros*, lizard in Greek.

Type species – *Tethysaurus nopcsai* sp. nov.

Diagnosis – As for type and only species.

Tethysaurus nopcsai sp. nov.

Etymology – In honour of the Hungarian palaeontologist Baron Ferenc Nopcsa, for his pioneer studies on Adriatic aquatic squamates.

Holotype - MNHN GOU1, nearly complete articulated skull and mandible (Fig. 1).

Type locality and horizon – Near Goulmima, Er-Rachidia Province, southern Morocco; Unit 4 of the Cenomanian-Turonian limestone bar, Late Cretaceous, Early Turonian [14].

Referred specimens from the same area and horizon – MNHN GOU2, incomplete disarticulated skull and mandible (Fig. 2B-D, F); MNHN GOU3, partial skeleton including mostly disarticulated cranial, vertebral and appendicular bones (Fig. 2A, E, G-Q).

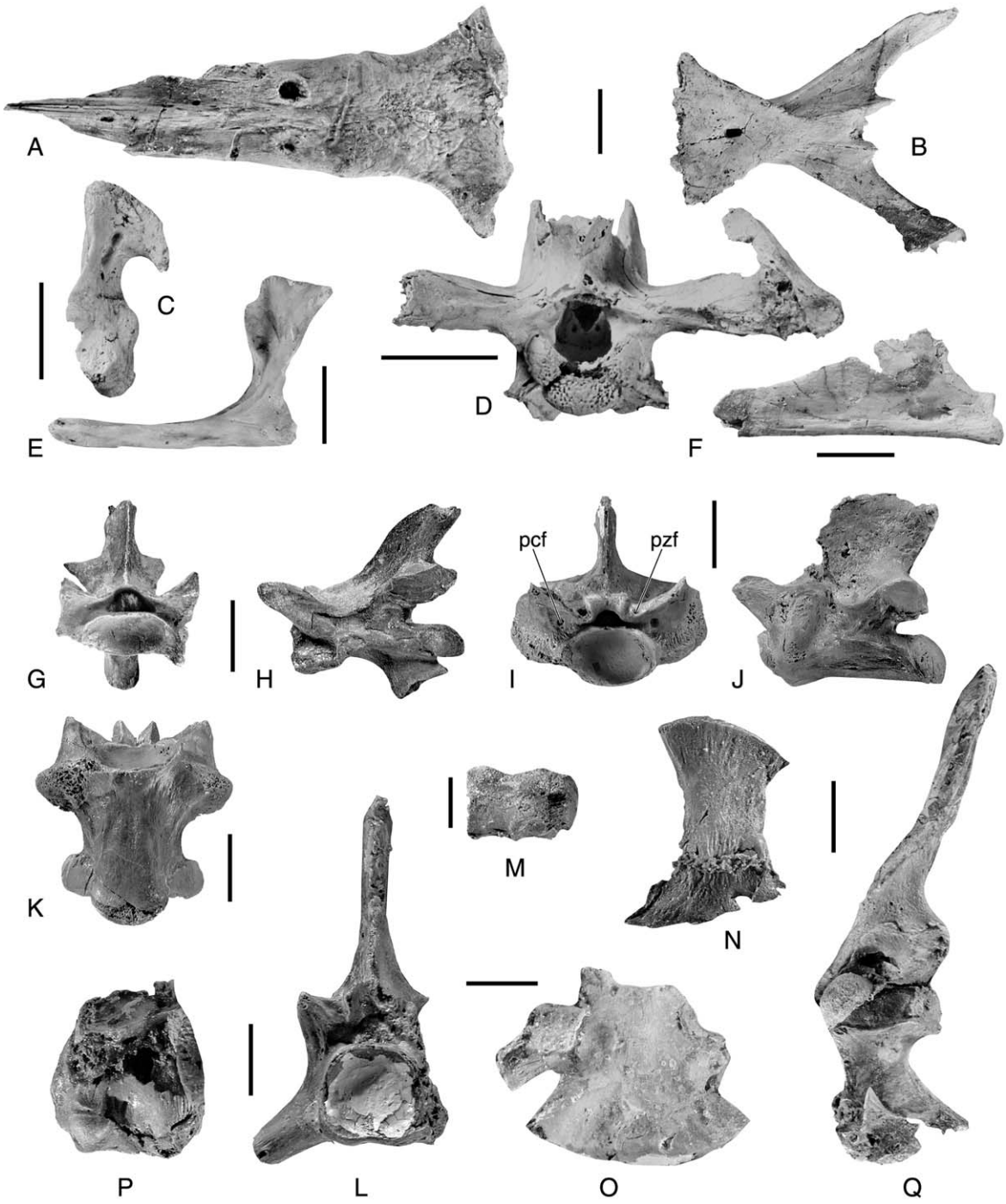
Diagnosis – Medium-sized mosasauroid less than 3 meters in length; prefrontal strongly vaulted in anterior view; parietal exhibits a triangular table ending posteriorly in two pointed pegs overlying the supraoccipital; jugal with a large and wide ascending ramus; medullar floor of the basioccipital pierced by three foramina; splenial with a large notched dorsomedial process; surangular exposed medially ventral to the coronoid; dental formula: 19-20 maxillary, 15-19 pterygoid and at least 19 dentary teeth; large paracotylar and parazygosphenal foramina on vertebrae.

Description

Skull (Figs. 1, 2A-E). The premaxilla is broad and rounded anteriorly, without rostrum. It bears two pairs of teeth. The maxilla has 19-20 teeth and a medial parapet half the height of the lateral one. The long and slender external nares extend from the second to the 12-13th maxillary teeth, representing about a fifth of the skull total length. The septomaxillae form the floor of the nares. There is no evidence of a nasal bone. The prefrontal is strongly vaulted in anterior view. It takes part into the margins of the external nares and lacks a supraorbital ridge. Isolated elements of the sclerotic ring are represented by thin quadrangular plates, each one about 1 cm^2. The frontal is a long and narrow triangular bone (Fig. 2A). It shows pointed posterolateral corners, slightly sinusoidal lateral margins and a median dorsal ridge on about two thirds of its length. Ventrally, the articulation surfaces for the prefrontal and postorbitofrontal are large and separated; there is no olfactory canal embrasure. The frontal-parietal suture is nearly straight. The parietal has a smooth triangular table ending posteriorly in two pointed pegs overlying the supraoccipital (Fig. 2B). The small, oval parietal foramen is located a distance twice its length from the frontal suture. The suspensorial rami are horizontal. The suture of the postorbitofrontal with the frontal is longer than that with the parietal. The posterior ramus of the postorbitofrontal does not reach the rear margin of the temporal fenestra. The jugal is L-shaped and bears a strong posteroventral process and a large ascending ramus (Fig. 2E). The quadrate is a narrow conch with a short and slender suprastapedial process that does not contact the small infrastapedial process (Fig. 2C). The stapedial pit is long and narrow (length to width ratio approximately 4:1). The distal condyle is saddle-shaped. The basioccipital has large basal tubera and the medullar floor is pierced by 3 small foramina. The basioccipital-basiphenoid suture is straight. The basipterygoid processes of the

Fig. 1. *Tethysaurus nopcsai* gen. et sp. nov., holotype MNHN GOU 1, Goulmima region, Turonian, Morocco. Skull, mandible and associated first cervical vertebrae in left dorsolateral (A), right ventrolateral (C), and dorsal (E) views; B, D and F, interpretative drawings. Abbreviations: aa, atlas arch; An, angular; Ar, articular; Ax, axis; C3, third cervical; Bs, basisphenoid; Co, coronoid; De, dentary; Fr, frontal; h, hypapophysis; Ju, jugal; La, lacrymal; Mx, maxilla; Op, opisthotic; Pa, parietal; Pfr, prefrontal; Pmx, premaxilla; Pofr, postorbitofrontal; Pr, prootic; Pt, pterygoid; Q, quadrate; Sa, surangular; So, supraoccipital; Sp, splenial; Sm, septomaxilla; St, supratemporal.

Fig. 1. *Tethysaurus nopcsai* gen. et sp. nov., holotype MNHN GOU 1, région de Goulmima, Turonien, Maroc. Crâne, mandibule et premières vertèbres cervicales associées en vues dorsolatérale gauche (A), ventrolatérale droite (C) et dorsale (E) ; B, D et F, dessins interprétatifs. Abréviations : aa, arc de l'atlas ; An, angulaire ; Ar, articulaire ; Ax, axis ; C3, troisième cervicale ; Bs, basisphénoïde ; Co, coronoïde ; De, dentaire ; Fr, frontal ; h, hypapophyse ; Ju, jugal ; La, lacrymal ; Mx, maxillaire ; Op, opisthotique ; Pa, pariétal ; Pfr, préfrontal ; Pmx, prémaxillaire ; Pofr, postorbitofrontal ; Pr, prootique ; Pt, ptérygoïde ; Q, carré ; Sa, surangulaire ; So, supraoccipital ; Sp, splénial ; Sm, septomaxillaire ; St, supratemporal.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basisphenoid are thick and fan-shaped. The supraoccipital is not attached to the parietal (Fig. 2D). The prootic exhibits a small otosphenoidal crest and a paired exit for the nerves X, XI and XII. The pterygoid bears 15 to 19 teeth, which are smaller than the marginal ones.

Mandible (Figs. 1, 2F). The dentary has a straight ventral border and a medial parapet half the heigth of the lateral one. It bears at least 19 teeth and has a long retrodental process. There is no rostrum. The splenial extends far anteriorly and exhibits a developed notched dorsomedial process (Fig. 2F). The splenial-angular joint is simple. The angular has no dorsomedial wing. The surangular has a small coronoid articulation surface and there is no coronoid buttress. It is exposed medially ventral to the coronoid. The coronoid is gently curved with a weak posteromedial process and without medial wing. The prearticular-articular are fused into a single bone. The glenoid cavity is formed by the articular only. The retroarticular process is obliquely oriented.

Marginal teeth (Fig. 1). The marginal teeth are about twice the size of the pterygoid ones. They are long and slender fangs, strongly posteromedially recurved and slightly laterally compressed. The crowns have an elliptical basal cross-section and no carinae. The enamel is either smooth or ornamented (in larger specimens) with minute ridges located on the lower half of the crown. The base of the teeth is ankylosed to the jaw bone (pleurodont insertion) and bears a posterolingual resorption pit (see [22]).

Vertebral column (Fig. 2G-M). The vertebral formula is unknown. The condyles and cotyles of precaudal vertebrae are obliquely oriented and elliptical in shape. Strong zygosphene-zygantrum articulations are present and lateral to the zygosphenes are large parazygosphenal foramina (Fig. 2I, pzf). Zygapophyses are probably present up to the first caudal vertebrae. Ventral to the zygapophyses are large paracotylar foramina (Fig. 2I, pcf). The cervicals bear triangular hypapophyseal peduncles and anteriorly located synapophyses which extend ventrally below the centrum ventral surface (Fig. 2G). The caudal centra are longer than high (Fig. 2M). The haemal arches are free. (Fig. 2M)

Appendicular skeleton (Fig. 2N-Q). The pectoral girdle elements are not fused but probably loosely sutured with small interdigitations. The scapula is very narrow and smaller than the coracoid (Fig. 2N). The coracoid has no anterior neck and exhibits one anterior emargination (Fig. 2O). The humerus has distally an ectepicondylar groove and small ectepi- and entepicondyles (Fig. 2P). The pelvic girdle bones are loosely in contact but not sutured (Fig. 2Q). The ilium is posteriorly oriented, as in aigialosaurs and terrestrial varanoids. Distally, it bears an articulation surface, probably for sacral rib contact. The distal part of the pubis remains very plesiomorphic, being fan-shaped and perpendicular to the body long axis. The pubis tubercle is large and located far from the acetabulum. The femur exhibits distally confluent articular facets. The fibula is long and slender, without posterodistal process. The metapodials are long and slender.

4. Discussion

Tethysaurus nopcsai shares most of the synapomorphies of pythonomorphs (*sensu* [15]), such as the occurrence of four or less premaxillary teeth, large and recurved pterygoid teeth, a highly mobile mandibular symphysis, an intramandibular joint (splenial-angular), a zygosphene-zygantrum complex and pelvic elements not sutured [5,15].

Fig. 2. *Tethysaurus nopcsai* gen. et sp. nov., referred specimens MNHN GOU 2 (B-D, F) and 3 (A, E, G-Q). A, frontal in dorsal view; B, parietal in dorsal view; C, right quadrate in medial view; D, basicranium in posterior view; E, left jugal in lateral view; F, right splenial in medial view; G-H, cervical vertebra in anterior and left lateral views; I-K, dorsal vertebra in anterior, left lateral and ventral views; L, pygal vertebra in anterior view; M, posterior caudal vertebra in left lateral view; N, right scapula in medial view; O, right coracoid in medial view; P, distal right humerus in medial view; Q, left ilium and pubis in lateral view. Scale bars: 2 cm but M (1 cm). Abbreviations: pcf, paracotylar foramen; pzf, parazygosphenal foramen.

Fig. 2. *Tethysaurus nopcsai* gen. et sp. nov., spécimens rapportés MNHN GOU 2 (B-D, F) et 3 (A, E, G-Q). A, frontal en vue dorsale ; B, pariétal en vue dorsale ; C, carré droit en vue médiale ; D, basicranium en vue postérieure ; E, jugal gauche en vue latérale ; F, splénial droit en vue médiale ; G-H, vertèbre cervicale en vues antérieure et latérale gauche ; I-K, vertèbre dorsale en vue antérieure, latérale gauche et ventrale ; L, vertèbre pygale en vue antérieure ; M, vertèbre caudale postérieure en vue latérale gauche ; N, scapula droite en vue médiale ; O, coracoïde droit en vue médiale ; P, extrémité distale d'humérus droit en vue médiale ; Q, ilium et pubis gauches en vue latérale. Barres d'échelle : 2 cm sauf M (1 cm). Abréviations : pcf, foramen paracotylaire ; pzf, foramen parazygosphénien.

Among Pythonomorpha, *Tethysaurus* exhibits most of the synapomorphies of Mosasauroidea (Aigialosauridae + Mosasauridae *sensu* [5,15]), among them a premaxillae-frontal contact, vestigial or absent nasal, elongated snout and retracted nares, fused frontals taking part into the naris margins, fused postfrontal and postorbital, jugal extending anteriorly past orbital rim, quadrate with large tympanic conch and curved suprastapedial process, more than thirteen marginal teeth and no zygapophyses nor transverse processes in distal caudal vertebrae [5,15].

Recent cladistic analyses show Aigialosauridae (*sensu* [15]) forming an unresolved polytomy with respect to the well-defined Mosasauridae [2,4,6,7,9]. The aigialosaurid record includes mainly taxa from the Adriatic Region, that are *Aigialosaurus dalmaticus* and *Opetiosaurus bucchichi* (Cenomanian-Turonian transition [13] of Slovenia) [10,12]; *Carsosaurus marchesetti* and the « Trieste aigialosaur » (Late Cenomanian [13] of Croatia) [9,10,12]; and probably *Haasiasaurus gittelmani* from the Early Cenomanian of Middle-East [18] and the « Dallas aigialosaur » (unpublished) from the Middle Turonian of Texas [2]. Synonymies have been suggested between *Carsosaurus* and the « Trieste aigialosaur » [9], and between *Aigialosaurus* and *Opetiosaurus* [9,10], but these opinions have been challenged [18].

In order to establish the phylogenetic relationships of *Tethysaurus nopcsai* within Mosasauroidea, a cladistic analysis has been conducted including this taxon in the data matrix of Caldwell [7] (see Appendix). The data matrix, composed of 66 osteological characters and 13 ingroup taxa (six mosasaurids, three aigialosaurids, two species of *Coniasaurus, Dolichosaurus* and *Tethysaurus*), was analysed using the Branch and Bound and Heuristic algorithms of PAUP 3.1.1 [20]. Characters were treated as unordered and without weight assignements. Eighteen most parsimonious trees have been generated (131 steps, C.I. = 0.611, H.I. = 0.397, R.I. = 0.643).

The topology of the strict consensus tree supports *Tethysaurus* as the sister-group of the monophyletic Mosasauridae (*Halisaurus* (other mosasaurids)), a result obtained in all the trees if the Majority Rule Consensus Tree (50%) is performed (Fig. 3). The clade *Tethysaurus* + Mosasauridae is supported by synapomorphies such as thick and fan-shaped basipterygoid process of basisphenoid, horizontal parietal suspensorial rami, jugal with posteroventral process, medial parapet of dentary raised to median height, and scapula smaller than the coracoid [6,7]. *Tethysaurus* lacks derived characters of Mosasauridae such as premaxilla-maxilla suture ending posterior to fourth maxillary tooth, less than nineteen dentary teeth, haemal arches fused to caudal vertebrae, fan-shaped scapula with deeply concave posterior emargination and not fused to coracoid [6,7].

Finally, *Tethysaurus* differs from all mosasauroids by the combination of autapomorphies listed in the diagnosis. Among them, it should be noted that the presence of paracotylar foramina is common in snakes although its significance remains unknown; moreover, the occurrence of parazygosphenal foramina is very rare in squamates (J.C. Rage, pers. com.). *T. nopcsai* exhibits a mosaic of plesiomorphic characters on the skull, mandible and postcranial skeleton (see Appendix), the most notable are those observed on the girdles (e.g., very small and narrow scapula, posteriorly oriented ilium bearing a distal articulation, pubis with a fan-shaped distal part perpendicular to the body axis).

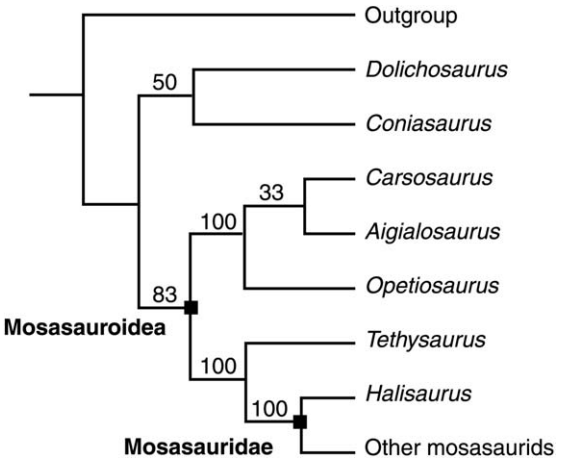

Fig. 3. Majority rule consensus tree (50%) of 18 cladograms (131 steps) obtained using data matrix from Caldwell [7] and showing the phylogenetical relationships of *Tethysaurus nopcsai* among Mosasauroidea. Numbers refer to percentage of most parsimonious trees showing that branching pattern.

Fig. 3. Arbre de consensus majoritaire (50 %) des 18 cladogrammes (131 pas) obtenu en utilisant la matrice de données de Caldwell [7] et montrant les relations phylogénétiques de *Tethysaurus nopcsai* au sein des Mosasauroidea. Les nombres indiquent le pourcentage d'arbres plus parcimonieux montrant cet arrangement.

5. Conclusion

Tethysaurus fills the gap between the aigialosaurids (Middle-East and Adriatic region, mainly Cenomanian in age) [10,12,13,18] and the mosasaurids (earliest records from the Middle Turonian of North America and the Late Turonian of Colombia and Angola) [3,17,21], from palaeobiogeographical, stratigraphical and even phylogenetical aspects. Its distribution in the Early Turonian of Northern Africa is in keeping with the paleobiogeography of marine organisms in the Cenomanian-Turonian, which can be correlated to reconstructed patterns of palaeo-currents from east to west through the Tethys seaway (see [8]).

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Appendix

Data matrix used in the analysis relies on the 66 characters scored by Caldwell [7] for nine mosasauroid taxa (three aigialosaurids and six mosasaurids), together with *Dolichosaurus* and the two *Coniasaurus* species. The characters score for *Tethysaurus nopcsai* are indicated below.

Matrice de données utilisée dans l'analyse, basée sur les 66 caractères codés par Caldwell [7] pour neuf mosasauroïdes (trois aigialosauridés et six mosasauridés), *Dolichosaurus* et les deux espèces de *Coniasaurus*. Ci-dessous, les caractères codés pour *Tethysaurus nopcsai*.

01?1? 11200 11000 100?0 00100 00?01 10100 00?0/10 0??01 ??010 01??? ?1??? ???0? 0

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