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The largest thalattosuchian (Crocodylomorpha) supports teleosaurid survival across the Jurassic–Cretaceous boundary

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ABSTRACT

A new teleosaurid from the Lower Cretaceous of Tataouine (Tunisia), *Machimosaurus rex* sp. nov., definitively falsifies that these crocodylomorphs faced extinction at the end of the Jurassic. Phylogenetic analysis supports its placement closer to *M. hugii* and *M. mosae* than *M. buffetauti*. With the skull length up to 160 cm and an estimated body length of 10 m, *M. rex* results the largest known thalattosuchian, and the largest known crocodylomorph at its time. This giant thalattosuchian probably was an ambush predator in the lagoonal environments that characterized the Tethyan margin of Africa during the earliest Cretaceous. Whether the Jurassic Cretaceous mass extinction was real or artefact is debated. The discovery of *M. rex* supports that the end Jurassic crisis affected primarily Laurasian biota and its purported magnitude is most likely biased by the incomplete Gondwanan fossil record. The faunal turnovers during the J–K transition are likely interpreted as local extinction events, triggered by regional ecological factors, and survival of widely distributed and eurytypic forms by means of habitat tracking.

1. Introduction

The Jurassic Cretaceous (J–K) transition has been considered a complex phase of global extinctions in both terrestrial and marine faunas, which affected rates of lineage diversification and morphological evolution during the Early Cretaceous (Bakker, 1978, 1998; Sepkoski, 1984; Bardet, 1994; Benton, 2001; Upchurch and Barrett, 2005; Lu et al., 2006; Benson et al., 2010). Whether this event was real (i.e., a complex combination of clade specific extinction patterns driven by physical and biotic factors) or represents an artefact remains unresolved (Gasparini et al., 2004; Bambach, 2006; Benson et al., 2010; Ruban, 2012; Newham et al., 2014). Among speciose clades of Jurassic marine reptiles, teleosaurid crocodylomorphs stand as the sole that supposedly went extinct at the Jurassic Cretaceous boundary (Young et al., 2014a), with all purported Cretaceous remains reinterpreted as belonging

to other reptilian clades, in particular, to the other thalattosuchian clade, Metriorhynchoidea (Young et al., 2014a,b). From a palaeogeographic perspective, Teleosauroidea is known largely from Europe (Vignaud, 1995), with Gondwanan remains rare, often limited to problematic or extremely fragmentary specimens (e.g., Martin et al., 2015; Young et al., 2014a).

In December 2014, the articulated remains of a giant crocodylomorph were found during prospecting activities at the Touil el Mhahir locality, Tataouine Governorate, Tunisia (Figs. 1, 2). In this study, we describe this new specimen and determine its affinities and stratigraphic placement. The results of our analyses support the erection of a new species of thalattosuchian teleosaurid, *Machimosaurus rex*. Furthermore, we discuss the implications of this new African taxon in the debate on the end Jurassic biotic crisis.

2. Material and methods

Specimens collected at the Touil el Mhahir locality in 2014 are housed in the Musée de l'Office National Des Mines (Ministère de l'Industrie et de la Technologie, Tunis), under the accession

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numbers ONM NG 1–25, 80, 81, and 83–87. Microvertebrate fossils, field notes and locality coordinates, and the 3D data are housed at the Museo Geologico Giovanni Capellini (MGGC, Bologna, Italy). Assemblage data were interpreted from the final quarry map as well as from field notes: all elements were mapped using a 1 m² grid box. Following the discovery of small elements from the surface of the outcrop, a total of 2.5 kg of sandy and clayish sediments were collected from both the excavation site and the matrix surrounding the skull for screen washing. Samples were soaked with water and H₂O₂ (5%) and screened using progressive sieves of 1 mm, 200 μm, and 63 μm. With 100% of collected matrix screened and sorted, a total of 231 specimens were identified. The collected specimens were primarily identified and compared with those described and illustrated by Cuny et al. (2004), Cuny et al. (2010) (Early Cretaceous of southern Tunisia), and Pouech et al. (2015) (Berriasian of France). Furthermore, during the preparation of the skull, four displaced osteoderms lying slightly imbricated on the snout were recovered and prepared (ONM NG 14 17).

2.1. Taxonomy

The taxonomic content of the genus level ranked clade *Machimosaurus* von Meyer, 1837, is controversial. Young et al. (2014a,b) recognised four species of *Machimosaurus*: *M. buffetauti* Young et al., 2014b, *M. hugii* von Meyer, 1837, *M. mosae* Sauvage and Liénard, 1879, (all from Europe) and *M. nowackianus* (von Huene, 1938) (from Ethiopia). Martin et al. (2015) challenged the distinction among the first three species suggested by Young et al. (2014a,b), referring all European *Machimosaurus* to *M. hugii*, and considered *M. nowackianus* as a *nomen dubium*. We follow the distinction among the species of *Machimosaurus* as suggested by Young et al. (2014b) since both morphological and stratigraphic

disparities among the three European morphotypes support a species level distinction among them, and tested whether the inclusion of the new Tunisian material in a phylogenetic analysis of Telesauroidea further supports or challenges a taxonomic distinction among the European *Machimosaurus*.

2.2. Phylogenetic analysis of *Thalattosuchia*

In order to analyse the evolutionary affinities of the Tunisian thalattosuchian, we performed Bayesian inference methods integrating the morphological and stratigraphic data with BEAST (Rambaut and Drummond, 2009; Drummond et al., 2012) following the method of Lee et al. (2014). The morphological dataset is based on Young (2014) and modified by Cau (2014) after the *a priori* exclusion of all non thalattosuchian taxa. As branch duration estimation and cladogenesis timing using Bayesian inference requires sampling among both constant characters and autapomorphies of terminal taxa – not solely among synapomorphies of internodes (Lee et al., 2014) – we retained all characters of the dataset of Young (2014), including those resulted phylogenetically uninformative by the *a priori* removal of most crocodyliform taxa from the ingroup. The ingroup was consequently expanded by the inclusion of *Machimosaurus buffetauti* (based on Martin and Vincent, 2013, and Young et al., 2014b) and the new Tunisian thalattosuchian. One Triassic pseudosuchian closely related to Crocodylomorpha (*Post osuchus* Chatterjee, 1985) and one basal crocodyliform (*Protosuchus* Brown, 1934) were used as outgroups – with the former set as root of the trees – according to the recent revision of thalattosuchian affinities by Wilberg (2015) indicating a non crocodyliform placement for Thalattosuchia. Stratigraphic data and age constraints for each terminal were obtained primarily from the Paleobiology Database (<http://paleobiodb.org/>) and from the literature, using

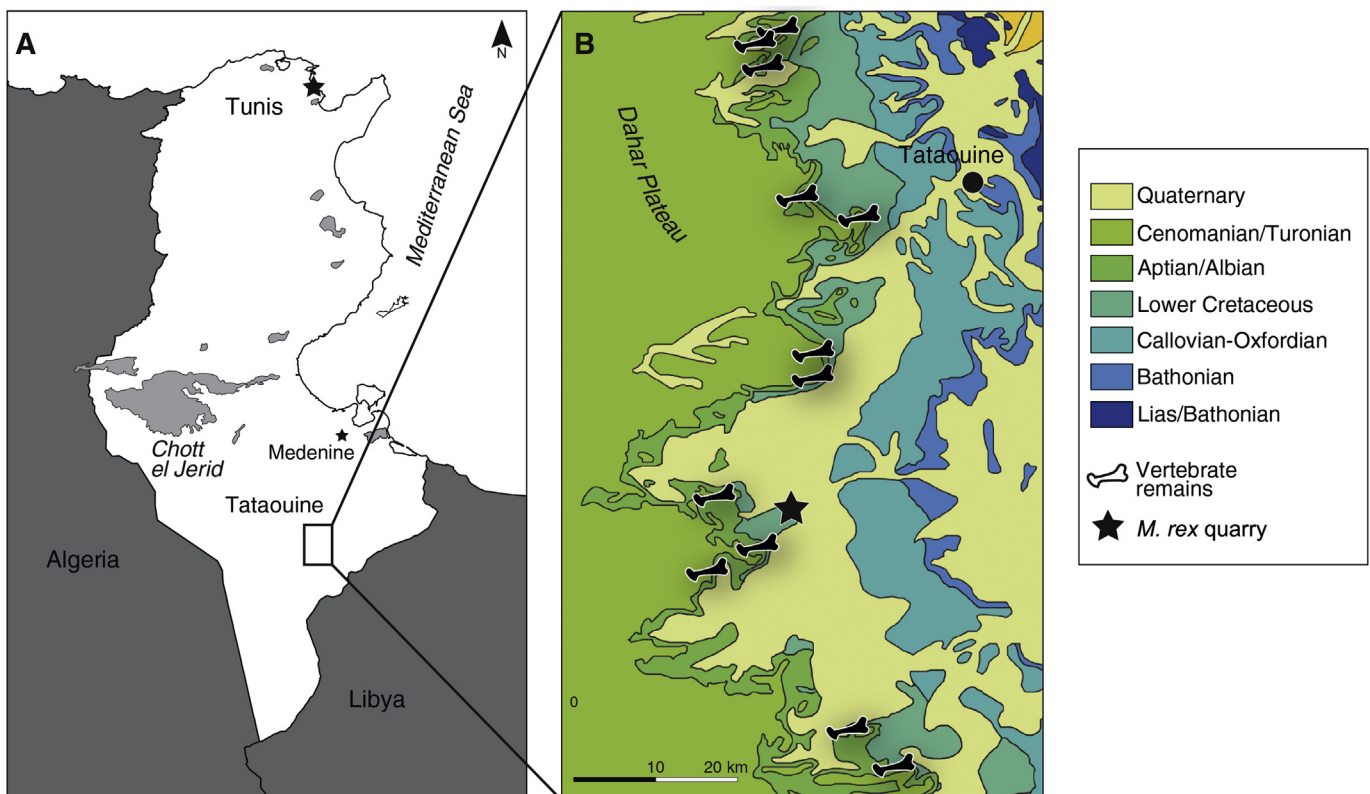


Fig. 1. (A) Geographic location and type locality of *M. rex*. (B) Simplified geological map of the Tataouine basin of southern Tunisia showing the Touil el Mhahir locality.

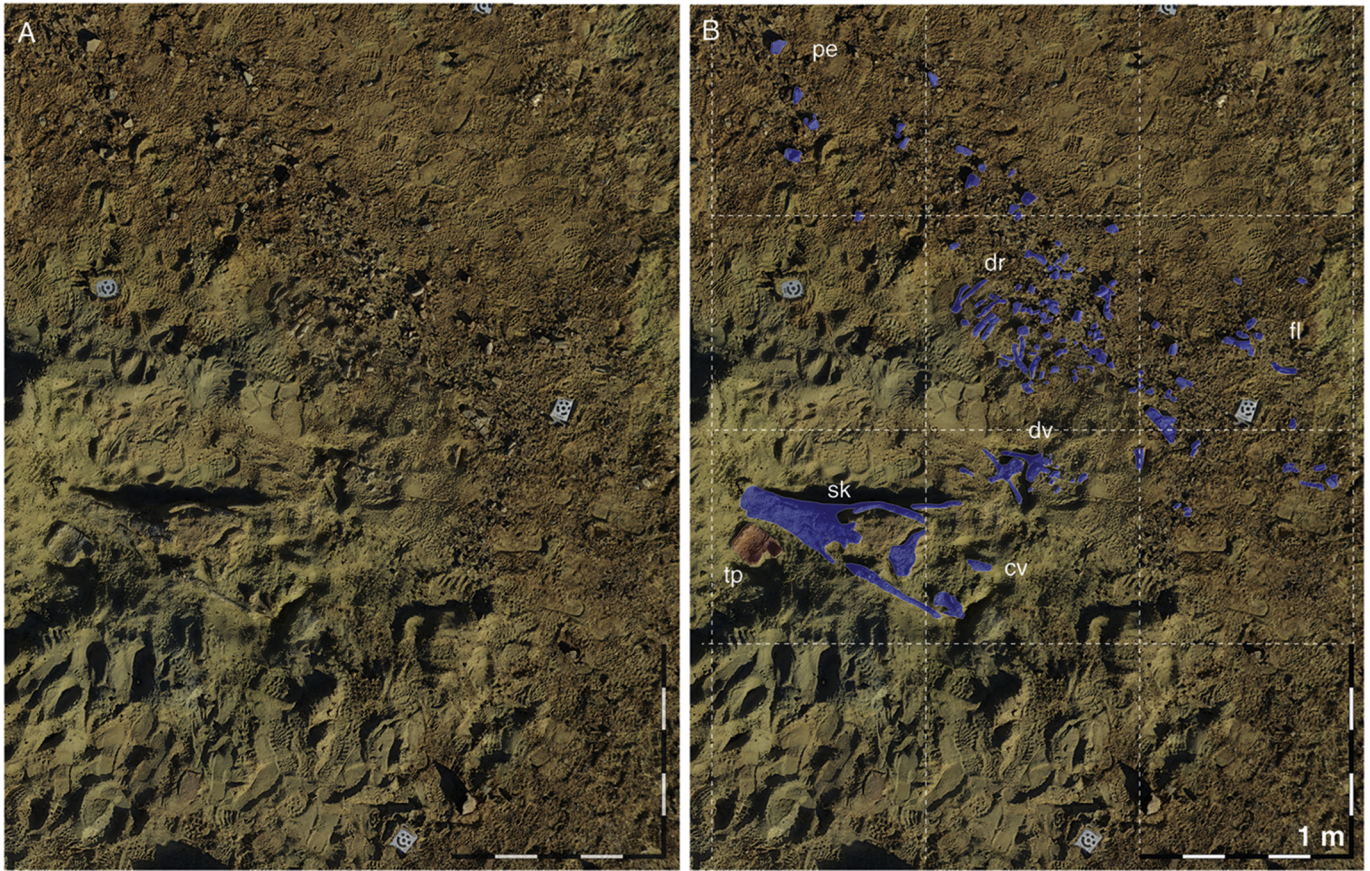


Fig. 2. *Machimosaurus rex* quarry map. Orthographic images of the 3D photogrammetry-based model of the main quarry in natural light (A) and with superimposed collected elements (B). Abbreviations: cv, cervical vertebrae; dr, dorsal ribs; dv, dorsal vertebrae; fl, forelimb bones; pe, pelvic elements; sk, skull; tp, turtle hyoplastron.

provided geochronological ages for the formations in which the taxa were found or the mean of the geologic stages associated with those formations. The root age prior (i.e., the maximum age of the last common ancestor of all included taxa) was set along a uniform range between 218 Mya (the age of the oldest terminal included, *Postosuchus*) and 252 Mya (the Permian Triassic boundary). The latter was considered as a 'loose' hard constraint that consistently pre dates the age of the oldest potential crocodylomorphs and basal loricatans. In the analysis, rate variation across traits was modelled using the gamma parameter, and rate variation across branches was modelled using an uncorrelated relaxed clock. The analyses used four replicate runs of 40 million generations, with sampling every 4000 generations. Burnin was set at 20%, and the Maximum Clade Credibility Tree (MCCT) of the merged four post-burnin samples was used as framework for phyletic reconstruction.

2.3. 3D photogrammetry and modelling

During the last decade, the development of Structure from Motion (SfM) techniques has been dramatically improved allowing accurate reconstruction of 3D structures processing 2D images (Koenderink and Doorn, 1991; Beardsley et al., 1996; Trucco and Verri, 1998; Dellaert et al., 2000; Haming and Peters, 2010; Fanti et al., 2013; Engel et al., 2014; Fanti et al., 2015). We acquired digital models of the *Machimosaurus* quarry, the skull (both dorsal and ventral views), and the prepared dorsal vertebrae, using high resolution photogrammetry. We used Agisoft PhotoScan Professional, and Meshlab for this technique. The models were built as in the following procedure: 1. positioning of coded targets so that 70% of photos frame at least one target (actual distances between

targets will serve to include accurate measurement tools in the model); 2. proper preparation of the light so that variations in the enlightenment are minimal; 3. prearrangement of a photo-shooting path. In order to properly perform the metric reconstruction in the 3D model, it was mandatory to work with a camera with a fixed focal length lens. The lens profile for Agisoft Photoscan was set using the software Agisoft lens. Automatic check of images verified the complete coverage of selected objects before proceeding with the alignment of frames that originated the first point cloud based on corresponding points recognized in different photos. Once the consistency of the generated surface were verified, a photographic texture was generated.

3. Stratigraphy and age

The Touil el Mhahir locality (the exact locality data can be obtained upon request) is located less than 50 km to the south west of the city of Tataouine and about 25 km to the north west of Remada (Fig. 1). Substantial erosion resulted in a badland like morphology that exposed the basal beds of the Douiret Formation, and in particular of the Douiret Sand Member. In the Tataouine Basin, the Douiret Formation uncoformably overlays the Boulouha Formation which has been assessed a Barremian age based on the occurrence of the Cretaceous brachiopod *Loriolithyrus russillensis* (De Loriol, 1866), in the upper beds of the unit (Peybernes et al., 1996; Ouaja et al., 2004; Bodin et al., 2010). However, recent re evaluation of stratigraphic and biostratigraphic data in southern Tunisia and western Lybia (Cuny et al., 2010; Le Loeuff et al., 2010; Fanti et al., 2012) placed the lower, sandy deposits of the Douiret Formation in the Barremian. Specifically, the age of the Douiret Formation has

been assessed primarily through a detailed, basin scale revision of the stratigraphic occurrence and lateral variability of fossil bearing strata (Fanti et al., 2012). The occurrence of the hibodontid *Eger tenodus* Maisey, 1987, and *Gyrodus* Agassiz, 1833, in the Douiret Formation supports an Hauterivian Barremian age for this unit. In fact, Rees and Underwood (2008) indicate the latest ascertain record of *Eger tenodus* in the Barremian of Spain, and Kriwet and Schmitz (2005) note the youngest record of *Gyrodus* in the Hauterivian of Germany. Therefore, although a pre Hauterivian age of the lower Douiret beds cannot be excluded, based on 1) the Early Cretaceous age of the Boulouha Formation, and 2) stratigraphic and biostratigraphic data provided by Cuny et al. (2010), Le Loeuff et al. (2012), and Fanti et al. (2012), we conservatively consider the age of the Touil el Mhahir locality as Hauterivian Barremian.

The deposits are characterized by repeating, fining up sequences of fine grained sand and clay, capped by an alternating sequence of clay and dolostone or dolomitized sandstone. The *M. rex* quarry is located approximately 20 m above the fossil rich conglomerate that, on a basin scale, marks the base of the Douiret Formation (Fanti et al., 2012). Furthermore, we report isolated teeth of *Machimosaurus* sp. occurring in several localities from the Douiret Formation deposits along the Dahar Escarpment (i.e. El Hmaima, Jebel Haddada, Boulouha localities; Fanti et al., 2012) of southern Tunisia, supporting that this genus is a representative of this formation.

4. Taphonomy and paleoecology

The type specimen of *Machimosaurus rex* represents the first articulated vertebrate from the Douiret Formation and the second Mesozoic archosaur skeleton collected in Tunisia (Fanti et al., 2012, 2013, 2015). The skeleton lies on its ventral side with the head rotated clockwise toward the right side of the body (Figs. 2–4). Only three teeth were found preserved in the alveoli (Fig. 5), whereas seven were shed along the snout. Although preserved elements show no evidence of major pre burial transportation (Figs. 2–8A), the overall posture (i.e. the body lying on its ventral side and the head curved on the right side of the body) combined with displacement of osteoderms and the missing anterior end of the snout strongly suggest that there was some influence from paleocurrents (paleoflow from the south east). In addition, the right side of the skull is laterally compressed (see also the taphonomic model of Syme and Salisbury, 2014). The dorsal part of the skeleton was found partially eroded with the exception of the skull, which lay slightly below ground level. Large turtle plastron elements were collected near the skull (Fig. 7E). The skull, two dorsal vertebrae, several dorsal rib and gastralia fragments, a partial humerus and osteoderms were collected during the excavation. The remaining part of the quarry was mapped and isolated elements littering the ground were collected.

The *M. rex* holotype was collected in association with abundant, disarticulated elements from large turtle carapaces, plastrons and vertebrae. The largest turtle elements, including a 25 cm long hyoplastron associated with the skeleton (Fig. 7E), suggest an individual close to 1 m in body length. Because most of the turtle elements were slightly above the type skeleton of *M. rex*, these elements can be attributed to a subsequent depositional event. Microvertebrate remains are representative of brackish and marine taxa and include elasmobranchs, actinopterygians, dipnoans and rare pterosaur teeth. Bivalves, gastropods, fragmentary echinoids shell and spines, and scaphopods are also abundant.

In terms of relative percentage, fish elements (teeth, scales and centra) represent 71% of the isolated elements; crocodylian (teeth and osteoderms) 10%; invertebrates (gastropods, bivalves, and echinoderms) 4%; elasmobranchs 3%; and the remaining 12%

consists of unidentifiable bony elements and teeth. Significantly, several teeth less than 5 mm in apicobasal length and a 4 mm wide osteoderm are otherwise morphologically similar to those described for *Machimosaurus*; the teeth are referred to the latter taxon based on shared presence of blunt apex and anastomosing apicobasal ridges on tooth crown. In addition, a partial dentary with *in situ* teeth referable to a juvenile individual of *Machimosaurus* was recovered in association with the type skull of *M. rex*. Prospecting activities in the area revealed the presence of four additional crocodylomorph individuals comparable in size and overall preservation to the *M. rex* holotype within 200 m from the main quarry.

The lower beds of the Douiret Formation are also rich in megaplant remains, including large gypsified and sporadic hematized trunks reaching 8 m in length. Remarkable fossil abundance in the area and recurrent tree trunks indicate high rates of sediment supply and accumulation: however, the lack of *in situ* plant roots and organic components in the sediments combined with gypsified fossils and dolomitized sandstones indicate arid to xeric environments subject to evaporitic conditions. Overall, *facies* analysis and faunal assemblage are interpreted as a vast lagoonal system with both marine and terrestrial influences.

5. Systematic paleontology

Crocodylomorpha Hay, 1930

Thalattosuchia Fraas, 1901

Teleosauridae Saint Hilaire, 1831

Machimosaurus von Meyer, 1837

***Machimosaurus rex* sp. nov.**

(ZooBank code: LSID urn:lsid:zoobank.org:act:1A11E9B9 0B1C 4557 92B7 165168658C17)

(ZooBank code: LSID urn:lsid:zoobank.org:pub:74F1DA00 4482 4398 A69B 144969210627)

Etymology. The species name *rex*, Latin for “king”, refers to its majestic size among known *Machimosaurus* and all thalattosuchians.

Holotype. ONM NG NG 1–25, 80, 81, and 83–87 (Figs. 2–7D; Table 1).

Locality and horizon. Touil el Mhahir, Tataouine Governorate, Tunisia; Douiret Sand Member, Douiret Formation, Hauterivian, Lower Cretaceous.

Diagnosis. Teleosaurid differing from other species by unique combination of: adult basicranial length >155 cm (Fig. 5); rostrum ornamented by densely arranged, parallel longitudinal ridges; orbit elliptical; interorbital space narrow (one fifth length of skull posterior to orbit); anteromedial margin of supratemporal fossae round; frontal not extended anteriorly to orbit and with reduced orbital margin; relatively large maxillary alveoli; anterior dorsal neural spine height less than centrum height; dorsal osteoderms with tightly packed pits that are round centrally and ellipsoid peripherally.

Differential diagnosis. Among the genus *Machimosaurus* (Fig. 8), *M. rex* differs from *M. buffetauti* (Fig. 8A) in having relatively larger and more closely spaced alveoli, and in bearing apicobasally aligned enamel ridges immediately adjacent to the apical anastomosed region of crown teeth that are closely packed on both labial and lingual sides; from *M. hugii* (Fig. 8C) in showing more developed ornamentation on maxillae and nasals, elliptical orbits, narrower interorbital space, and dorsal osteoderms with more closely spaced pits that become more elongate peripherally; from *M. mosae* (Fig. 8B) in bearing elliptical orbits and shallower and unkeeled

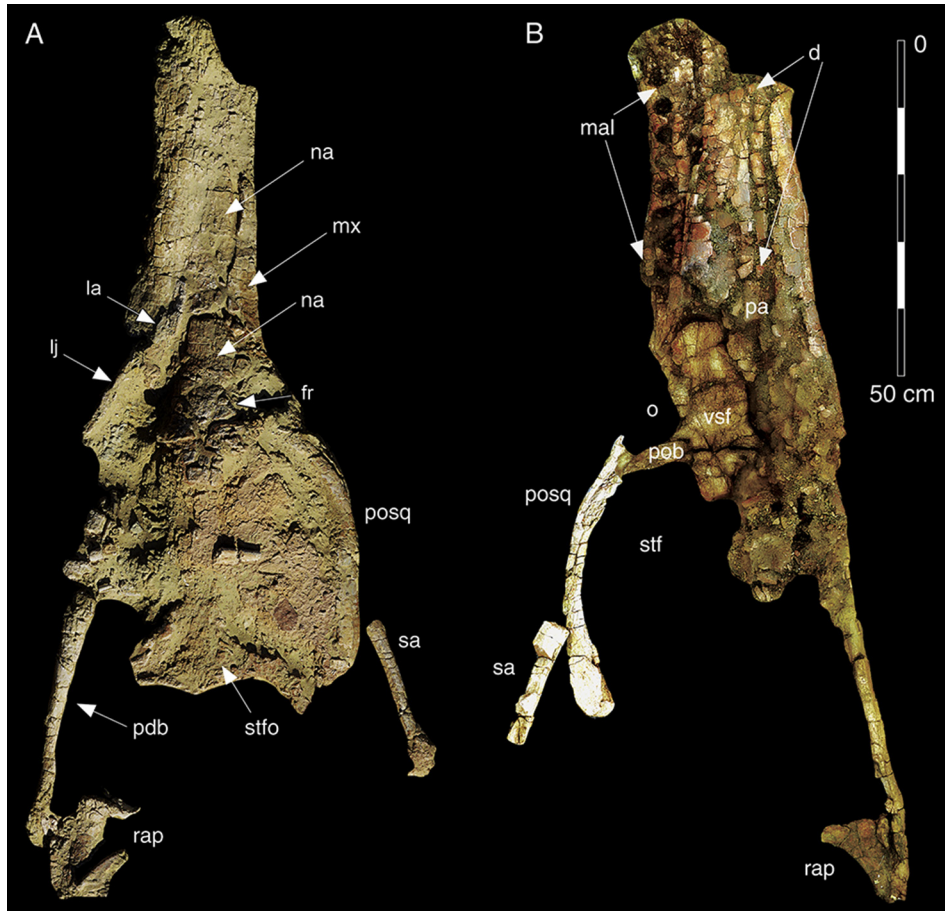


Fig. 3. *Machimosaurus rex* type skull. (A) dorsal view, (B) ventral view. Abbreviations: d, dentary; fr, frontal; lj, left jugal; la, lacrimal; mal, maxillary alveoli; mx, maxilla; na, nasal; pa, palatal element; pdb, postdentary bones; posq, postorbital-squamosal bar; rap, retroarticular process; sa, surangular; stfo, floor of supratemporal fossa. Scale bar 50 cm.

ventral osteoderms. There is currently no overlapping material between *M. nowackianus* and *M. rex* for a direct morphological comparison. Although stratigraphic placement alone cannot be used as a taxonomic criterion, based on stratigraphic separation between the two type localities of *M. nowackianus* and *M. rex* (the former is Oxfordian Kimmeridgian in age, see Young et al., 2014b), we consider likely these two African species as distinct.

6. Description of *Machimosaurus rex* type specimen

6.1. Skull and mandible (Figs. 3–7A)

The anterior end of the snout is missing. Based on comparison with other specimens of *Machimosaurus* (Hua, 1999; Martin and Vincent, 2013; Young et al., 2014a,b), we estimate that approximately posterior two thirds of the maxillae are intact. The preserved parts are ornamented with a dense pattern of lightly developed longitudinal ridges (Fig. 5A). Eight alveoli are preserved in the right maxilla (Fig. 5C). They are relatively large, their diameter being up to one sixth of snout width, and are closely spaced (Martin and Vincent, 2013; Young et al., 2014b). The interalveolar space is regular, as in the mid and posterior part of the maxilla of *M. hugii* and *M. mosae*. The nasal is subtriangular in dorsal view and ornamented by a finely developed pattern of longitudinal ridges. It does not reach the narial region anteriorly. The periorbital region is poorly preserved, with only fragmentary prefrontals and lacrimals present. Nevertheless, the preserved outline indicates elliptical

orbits, more like that in *M. buffetauti*, differing from the more quadrangular shape observed in both *M. hugii* and *M. mosae* (Young et al., 2014b). The lateral margins of the orbits are at the level of the anteromedial corners of the supratemporal fossae, relatively much closely placed than in *M. hugii* (Young et al., 2014b, fig. 41). The nasofrontal suture is at the level of the anterior margin of the orbit. The anterior end of the dorsal interfenestral bar is preserved, but most of the bar, including the parietal, is lost. The anterior margin of the supratemporal fossa is gently rounded. The posterior floor of the supratemporal fossae is partially preserved. The postorbital is robust and elongate posteriorly. Only the lateral part of both squamosals is preserved. The occipital region of the skull is preserved in numerous fragments. Nevertheless, the occipital condyle was preserved *in situ*, allowing an accurate estimation of the preserved basicranial length. The occipital condyle (Fig. 7A) consists exclusively of the basioccipital, as in other species of *Machimosaurus* (Young et al., 2014b). The posterior ends of both dentaries are preserved in articulation with the postdentary bones. The external mandibular fenestra is elongate anteroposteriorly. Both the left and right surangulars are articulated with the glenoid region. The angulars are in fragments. The retroarticular processes are elongate posteriorly and triangular in dorsal view. The teeth (Fig. 6) have several diagnostic features for *Machimosaurus* (Young et al., 2014c). The relatively low crowns are blunt apically and slightly curved apicodistally. No carinae are present, suggesting that all preserved teeth belong to the posterior half of the tooth row. The crowns are ornamented with tightly packed ridges oriented apicobasally. As in *M. hugii*, and differing from *M. buffetauti* (Young et al., 2014c), these

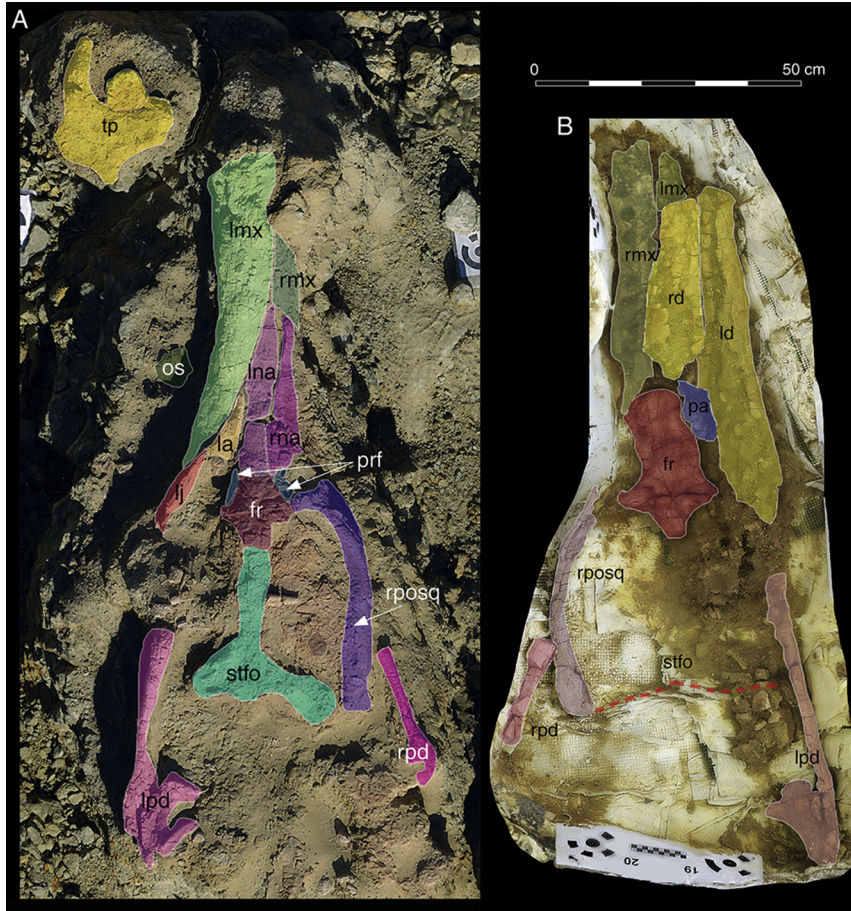


Fig. 4. *Machimosaurus rex* type skull, (A) *in situ* photograph showing dorsally exposed preserved bones, (B) prepared ventral surface. Abbreviations: fr, frontal; lj, left jugal; la, lacrimal; ld, left dentary; lmx, left maxilla; ina, left nasal; lpd, left postdentary elements; lposq, left postorbital-squamosal bar; os, osteoderm; pa, palatal element; rd, right dentary; rmx, right maxilla; rna, right nasal; rpd, right postdentary elements; rposq, right postorbital-squamosal bar; stfo, floor of supratemporal fossa; tp, turtle plastron element. Scale bar 50 cm.

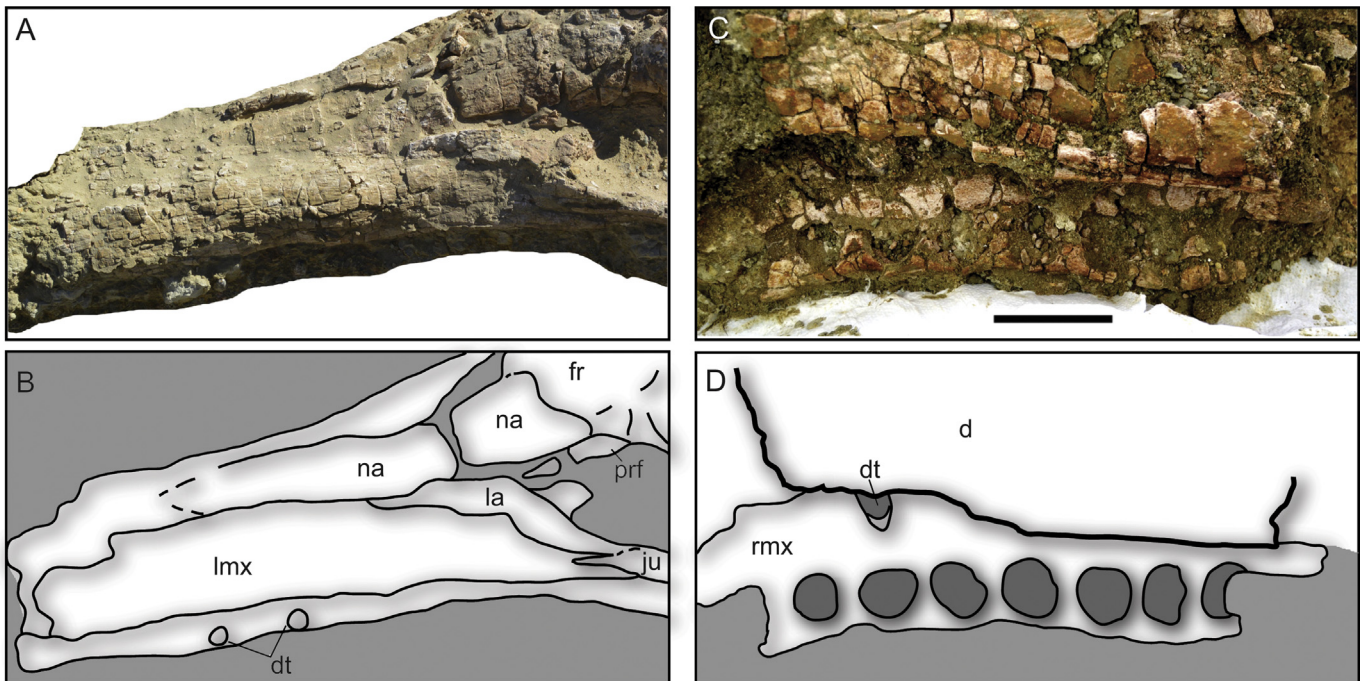


Fig. 5. Detail of *M. rex* type snout in dorsal (A, B) and ventral (C, D) views. Abbreviations: d, dentary; dt, dentary tooth; fr, frontal; ju, jugal; la, lacrimal; lmx, left maxilla; na, nasal; prf, prefrontal; rmx, right maxilla. Scale bar in C 5 cm.

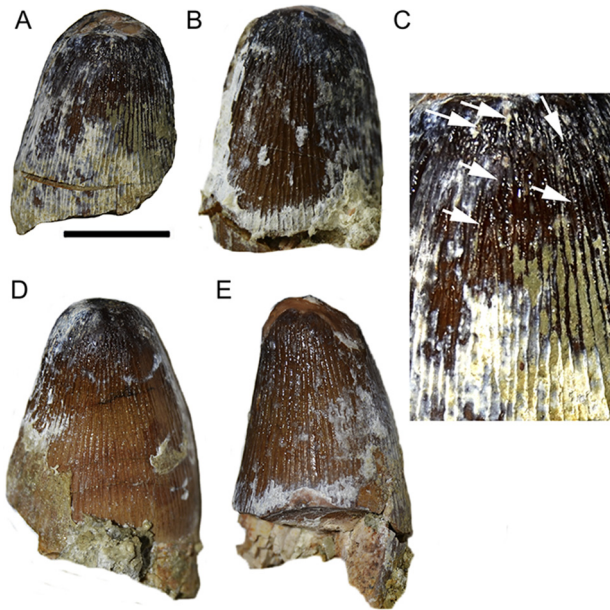


Fig. 6. Dentition of *M. rex* type. Isolated tooth crowns in labial (A, D) and lingual (B, E) views; (C) detail of enamel close to apex. Arrows indicate tubercle-like ornamentation of ridges. Scale bar = 5 cm.

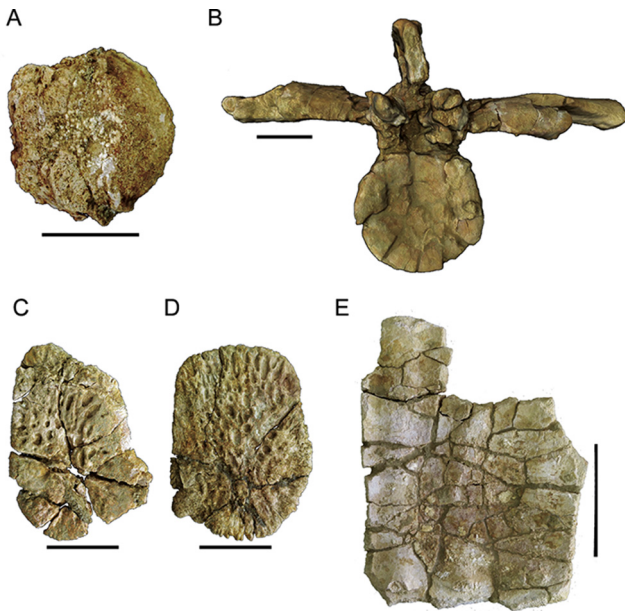


Fig. 7. Skeletal anatomy of *M. rex* sp. nov. type specimen and associated turtle remains. (A) Occipital condyle in dorsal view. (B) Anterior dorsal vertebra in anterior view. (C, D) Osteoderms in dorsal views. (E) Turtle hyoplastron in visceral view. Scale bars A, D = 5 cm; E = 10 cm.

ridges are closely packed on both labial and lingual sides of the crown. The ridges are irregularly undulated, but not producing distinct pseudo tubercles as in *M. hugii* (Young et al., 2014a,b). The ridges are anastomosed in the apical third of the crowns, forming a complex network as in other species of *Machimosaurus*. Most teeth show a distinct (macroscopical) apical wear.

6.2. Postcranial skeleton (Figs. 2, 7B–D)

The cervical series is poorly preserved. Few fragments of the atlas axis complex were recovered adjacent to the occipital region

of the skull. Two well preserved anterior dorsal vertebrae have massive centra that are as wide as tall in anterior view (Fig. 7B). The articular facet of the centra are subcircular and moderately concave. The lateral surfaces of the centra are both dorsoventrally and anteroposteriorly concave, due to the marked lateral rims of the articular facets. The neural arch is transversely wide and low dorsoventrally and has closely joined diapophyses and parapophyses that are oriented subhorizontally. The parapophyses extend laterally to half the extent of the diapophyses, with their articular surfaces facing posterolaterally. The dorsal surface of the transverse process is anteroposteriorly convex. The ventrolateral surfaces of the neural arches are moderately concave centrally. The neurocentral suture is obliterated, suggesting a mature individual. The zygapophyses are stout and moderately projected anteroposteriorly, being placed lateral to the neural canal and medial to the centrum outline in anterior/posterior views. The neural spine is robust, lower dorsoventrally than the height of the centrum and moderately expanded transversally at its apex. Several dorsal ribs and gastralia were found in articulation, although extremely fragmented.

Appendicular elements include fragments of the left forelimb, interpreted as the humeral shaft, and worn elements that, based on *in situ* placement posterior to the dorsal ribs series, are interpreted as belonging to the hindlimb.

6.3. Osteoderms (Fig. 7C, D)

Isolated osteoderms were found adjacent to the lower jaws. As the skull is turned backward relative to the presacral vertebral column, the osteoderms are interpreted as pertaining to the dorsal region. The osteoderms are quadrangular, with poorly developed anterolateral processes. Osteoderm ornamentation includes a tightly packed pattern of rounded pits in the central part of the dorsal surface, surrounded peripherally by radially elongate pits that reach the margin of the osteoderm; this pitting pattern differs from the more irregular pattern reported by Young et al. (2014b) for *Machimosaurus hugii*. Furthermore, none of the recovered osteoderms bears the marked thickening and the distinct keel both diagnostic of *Machimosaurus mosae* (Hua, 1999).

7. Results

7.1. Phylogenetic analysis

The MCCT of Thalattosuchia resulted by the Bayesian phylogenetic analysis (Fig. 9) agrees in overall topology with previous analyses of the same dataset using parsimony as tree search strategy (e.g., Young 2014). The analysis strongly supports the monophyly of *Machimosaurus* (posterior probability: 97%) and the inclusion of the new Tunisian taxon in that genus. *Machimosaurus buffetauti* resulted the basalmost member of the genus, excluded from the clade including *M. rex* and the other European species (posterior probability: 63%). The analysis therefore supports the distinction of *M. buffetauti* from other *Machimosaurus* suggested by Young et al. (2014a). Cladogenetic timing estimated by the Bayesian analysis places the divergence of the lineage leading to *M. rex* from the other *Machimosaurus* lineages at about 155 Mya.

8. Size of *Machimosaurus rex*

8.1. Skull length

The skull of the type specimen of *M. rex* lacks the anterior end of maxillae and the premaxillae. The basicranial length of the preserved skull is 114 cm, the length of the preserved skull from the

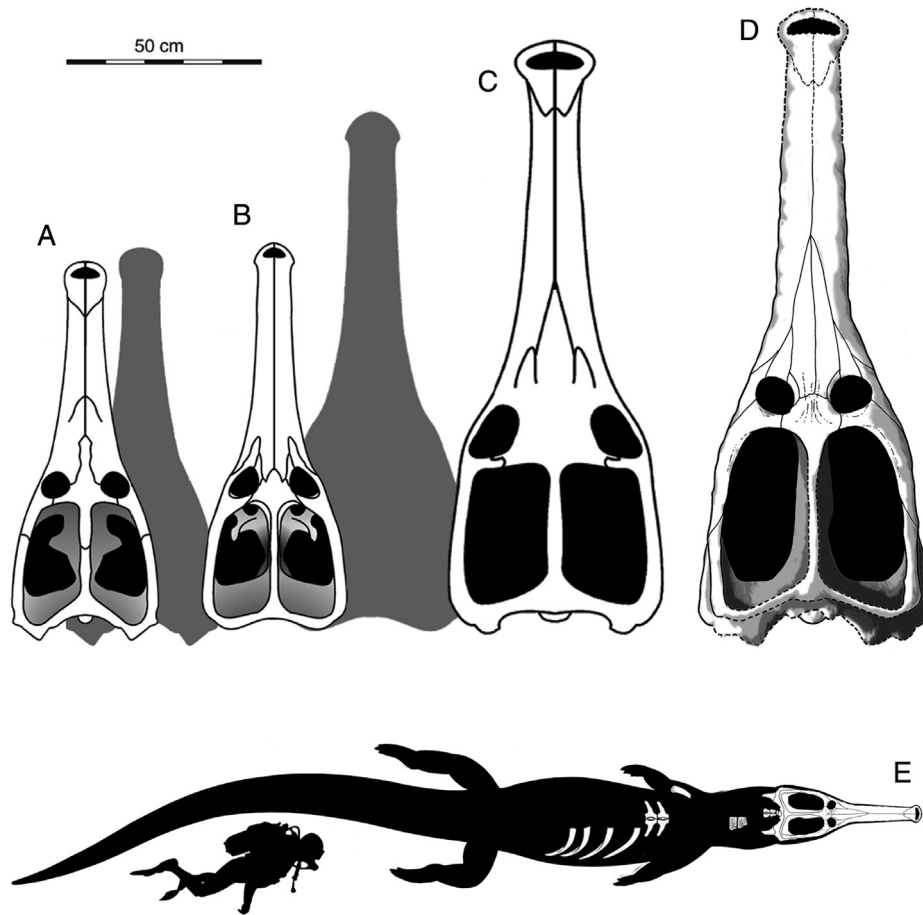


Fig. 8. Comparison among skulls of *Machimosaurus*. (A) holotype of *M. buffetauti*, (B) neotype of *M. mosae*, (C) estimated size of the 'Leira specimen' of *M. hugii*, (D) holotype of *M. rex*. Dashed areas in (A) and (B) indicate size of largest known individuals of those species. (E) Reconstruction of *M. rex* body based on preserved elements. Figures (A) (C) modified from Young et al. (2014b).

anterior end to the left mandibular glenoid is 134 cm. The length of the skull from occiput to the anterior end of the orbits ('post snout' length) is 65 cm. In a complete skull of *M. buffetauti* with a basicranial length of 93.5 cm (Kimmeridgian, Germany; Martin and Vincent, 2013; Fig. 8A), the equivalent part of the skull is 39 cm long (42% of basicranial length). In other specimens of *Machimosaurus*, the snout length of the skull is approximately 58% of the basicranial length, a value that is considered as an autapomorphy of *Machimosaurus* (Hua, 1999; Young et al., 2014b; Fig. 8B). That implies a 'post snout' length of about 42% of the skull length in this taxon (see also Martin and Vincent (2013), table 6). Assuming that the proportions of the complete skull of *M. rex* holotype were comparable to those observed in other *Machimosaurus* species, we estimate a minimum total basicranial length for the Tunisian taxon of 155 cm. Prior to this discovery, the largest size of *Machimosaurus* was based on a fragmentary skull of *M. hugii* (the "Leira specimen" of Young et al. 2014b, see Krebs (1967), Fig. 8C) with the basicranial length estimated between 141 cm (Hua, 1999) and 149 cm (Young et al., 2014b). Nevertheless, the "Leira specimen" lacks most of the orbital and temporal regions, and no measurements of the preserved elements are available, thus preventing any testable estimation of its actual size (see Krebs, 1967).

A comparison between the size of the alveoli in *M. rex* type specimen and other *Machimosaurus* individuals further supports the giant size of the Tunisian taxon. In the skull of *M. buffetauti* type specimen (Martin and Vincent, 2013), the mesiodistal diameter of the alveoli at mid length of the maxilla is between 15 and 18 mm.

In the neotype of *M. mosae*, the middle maxillary alveoli diameter ranges between 18 and 25 mm (Hua, 1999). In the type specimen of *M. rex*, the mesiodistal diameter of the middle maxillary alveoli ranges between 30 and 43 mm, a value 200% or more than those of *M. buffetauti* holotype, and about 166–173% larger than those in the *M. mosae* neotype. The latter range confirms that the basicranial length of the Tunisian specimen is at least 166% larger than that of the *M. mosae* neotype. Since the type skull of *M. rex* is also estimated about 165–170% the size of the *M. buffetauti* type skull (Martin and Vincent, 2013), the Tunisian species shows proportionally larger alveoli than in *M. buffetauti*.

8.2. Total body length

Young et al. (2014b) used the well preserved neotype specimen of *M. mosae* to estimate the total body length of various specimens of *Machimosaurus* from their basicranial lengths, assuming a body length to basicranial length ratio of about 6.22. Assuming isometry among the various *Machimosaurus* individuals, and using the same relationships of Young et al. (2014b), the total body length of *M. rex* type is estimated at least as 9.6 m. Compared to the neotype of *M. mosae*, the alveoli in *M. rex* holotype are about 166% larger than the same element in the French specimen (Hua, 1999). Therefore, assuming isometry in body proportions, based on both cranial and dental comparisons with the best preserved specimen of *Machimosaurus mosae* (Hua, 1999) the total body length of the Tunisian

Table 1
Selected measurements of *Machimosaurus rex* type specimen.

| | Measurements (cm) | |
|--|-------------------|------|
| <i>Skull</i> | | |
| Preserved basicranial length | 114 | |
| Left side, from preserved anterior end to mandibular glenoid | 134 | |
| Right side, distance from mandibular glenoid to anterior orbit | 64 | |
| Width of snout anterior to orbits | 25 | |
| Internal supratemporal fenestra length | 33 | |
| Distance between five maxillary alveoli | 22 | |
| Estimated total length of maxillary tooth row (range) | 80–97 | |
| Preserved snout length | 49 | |
| Postorbital skull length | 65 | |
| Interorbital width | 11.5 | |
| Occipital condyle width | 6.2 | |
| <i>Postcranial</i> | | |
| Anterior dorsal centrum height | 8.5 | |
| Anterior dorsal vertebra total height | 17.6 | |
| Anterior dorsal vertebra width across diapophyses | 24.3 | |
| Maxillary Alveoli ^a | MD | LL |
| 1 | 29.6 | 35.2 |
| 2 | 29.5 | 28.8 |
| 3 | 34.4 | 28.2 |
| 4 | 32.6 | 26.1 |
| 5 | 33.6 | 29.9 |
| 6 | 43.4 | 34.7 |
| 7 | 38.9 | 29.9 |
| 8 | n.d. | 32.4 |

MD, mesiodistal diameter; LL, labiolingual diameter, in mm.

^a Numeration refers to position along the preserved maxilla and not to the inferred position in the complete tooth row.

individual is estimated at about 10 m (166% of 6 m, see Young et al., 2014b; Fig. 8E).

9. Discussion

9.1. Hypothetical lifestyle

The skull of *M. rex* bears a platyrostral snout, longitudinally oriented ornamentations on the skull roof, elongate subrectangular supratemporal fossae and blunt crowned teeth with anastomosed apical enamel ornamentation (Figs. 1, 2), all synapomorphies of derived teleosaurids (Young et al., 2014b). With the skull length up to 160 cm and an estimated body length around 10 m (Fig. 8E), the new Tunisian species is the largest known thalattosuchian, and was the largest known crocodylomorph from the Triassic until the Aptian Albian (see Young et al., 2014b, Johnson et al., 2015). As in other *Machimosaurus* (in particular, *M. hugii*, Young et al., 2014b,c), the low crowned, sub globidont dentition of *M. rex* supports a generalist durophagous feeding ecology. The abundance of turtle remains in the *M. rex* quarry, including large bodied forms with length approaching 1 m, suggests that chelonians were a significant part of the diet also in the Tunisian taxon.

Krebs (1967) and Hua (1999) discussed the hypothetical life styles of *M. hugii* and *M. mosae* respectively (see also the review by Young et al., 2014b). The former was interpreted as well adapted to an open sea environment, whereas the latter resulted better adapted to high energy, coastal conditions. Based on extant analogues among crocodylians showing an inverse relationships between dermal ornamentation and aquatic adaptation, the relatively reduced ornamentation in both skull roof and osteoderms of *Machimosaurus hugii* has been suggested as additional functional adaptation to a pelagic lifestyle (Young et al., 2014b). Similarly, the thick and keeled ventral osteoderms of *M. mosae* are interpreted as adaptations to a high energy/turbulent environment (Hua, 1999;

Young et al., 2014b). In *M. rex*, both skull roof ornamentation and extent of pitting on the osteoderms are more developed than in *M. hugii*. The relatively shallower osteoderms lacking a keel suggest that the Tunisian species was not adapted to a high energy environment as that inferred for *M. mosae*. This interpretation is consistent with the paleoecology of the *M. rex* type locality (see above) indicating a lagoonal environment with significant terrestrial influences.

In analogy with modern semi aquatic crocodylians, we suggest that *M. rex* was an ambush predator that preyed on both aquatic and terrestrial vertebrates. Since *Machimosaurus* bite marks on a sauropod dinosaur bone are already known (Young et al., 2014b), we predict that *M. rex* included mid to large bodied dinosaurs in its diet.

9.2. Implications for teleosaurid extinction

Unlike their survival into the Cretaceous of southern Tethys, teleosaurids did not cross the J K boundary in the northern realm (Young et al., 2014a,b). The Late Jurassic species of *Machimosaurus* occur from Portugal to Germany to Ethiopia in lagoonal to shallow marine settings (Young et al., 2014b). These environmental conditions existed well into Cretaceous times in southern Tunisia, where lagoonal to tidal flats deposits straddle the J K transition and dominate the Lower Cretaceous sedimentary successions (Benton et al., 2000; Barale and Ouaja, 2002; Ouaja et al., 2004; Anderson et al., 2007; Ouaja et al., 2011; Fanti et al., 2012). Conversely, the end Jurassic transition in Europe is characterized by rapid climatic oscillations (alternation of ‘greenhouse’ conditions and cooling events) and concomitant extension of pelagic environments with dramatic loss of shallow marine and coastal ecosystems (Adatte et al., 1996; Cecca, 1999; Cecca et al., 2001; Dromart et al., 2003; Lécuyer et al., 2003; Cecca et al., 2005; Husinec and Jelaska, 2006; Ruban, 2011; Martin Garin et al., 2012). Reduction of these habitats most likely resulted in local extinction of teleosauroids across the J K boundary of Europe. Among macropredatory marine reptiles, as many as nine ichthyosaurian, three plesiosaurian and at least four metriorhynchoid lineages crossed the J K boundary, and morphological disparity of these clades maintained the pre-boundary levels through Early Cretaceous (Fischer et al., 2012, 2013, 2014; Benson and Druckenmiller, 2014; Young et al., 2014a; Chiarenza et al., 2015). Our study adds teleosauroids to the list of the reptilian lineages that crossed the Jurassic Cretaceous boundary.

10. Conclusion

Machimosaurus rex sp. nov. is based on the articulated skeleton of a giant crocodylomorph from the Hauterivian of Tunisia. This taxon represents the first indisputable Cretaceous teleosauroid, and the first member of this clade from Africa based on well preserved remains. With a basicranial length approaching 160 cm (and a partial skeleton indicating a total body length around 10 m), *M. rex* is the largest known thalattosuchian. Both paleoecological data and morphological features suggest that this species was an ambush generalist predator with an ecology comparable to extant semi-aquatic crocodylians. The discovery of *M. rex* falsifies a global mass extinction event at the J K transition (i.e., teleosauroid extinction), thereby highlighting the problem of sampling bias in the reconstruction of large scale patterns in the geological record. The new Tunisian teleosaurid points to a conservative interpretation of faunal turnovers during the J K transition: local extinction events triggered by regional ecological factors and survival of widely distributed and eurytypic forms by means of habitat tracking.

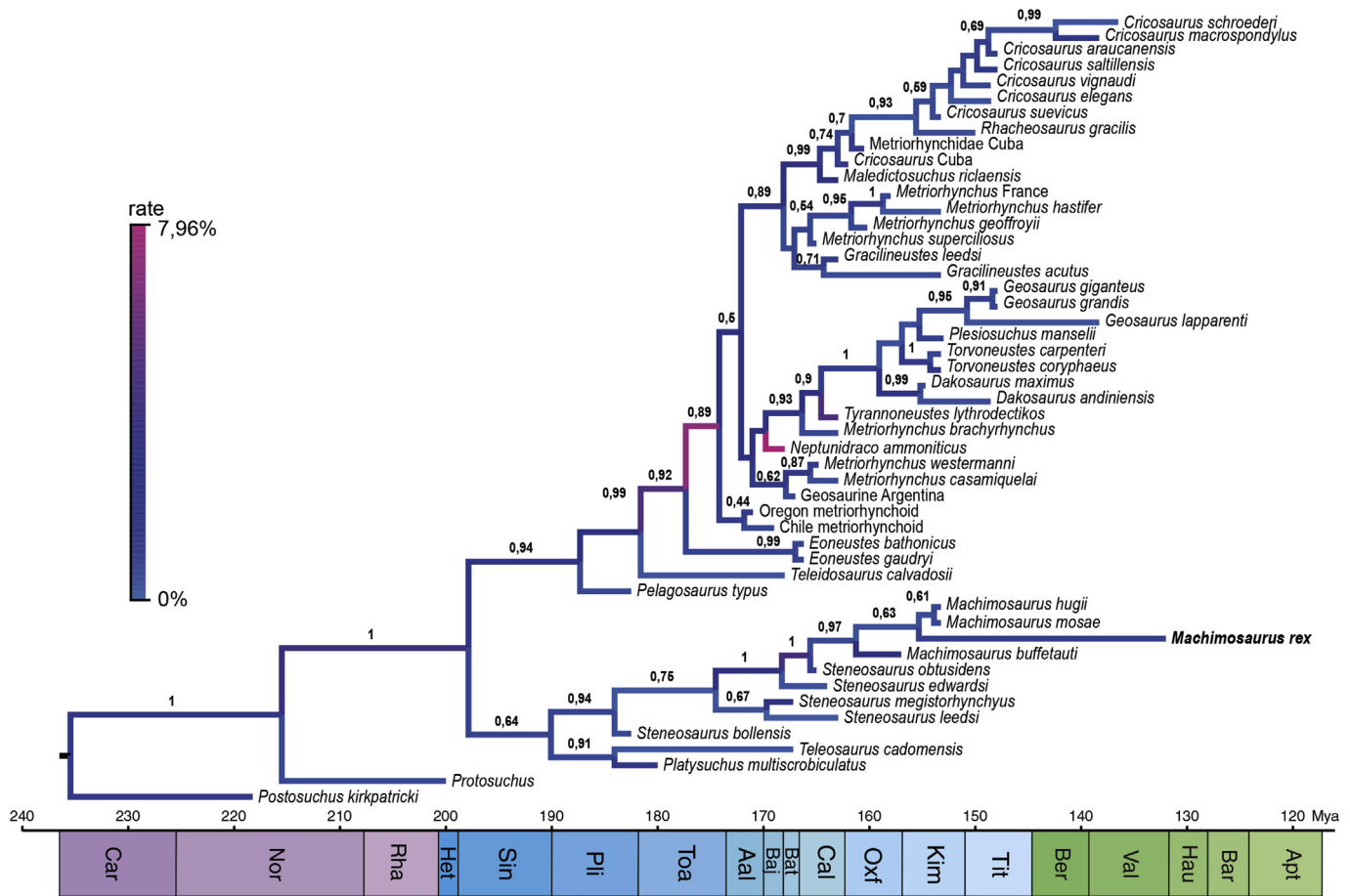


Fig. 9. Maximum Clade Credibility Tree of thalattosuchian evolution with divergence rates indicated by colored branches. Values at nodes indicate posterior probability values >0.5. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.cretres.2015.11.011>.