

Systematic Palaeontology (Vertebrate Palaeontology) / Paléontologie systématique

A new thalattosuchian crocodyliform from the Tithonian (Upper Jurassic) of northeastern Mexico

Marie-Céline Buchy ^{a,*}, Patrick Vignaud ^b, Eberhard Frey ^c, Wolfgang Stinnesbeck ^a, Arturo H. González González ^d

^a *Geologisches Institut, Universität Karlsruhe, Postfach 6980, 76128 Karlsruhe, Germany*

^b *Laboratoire de géobiologie, biochronologie et paléontologie humaine, UMR CNRS 6046, UFR-SFA, université de Poitiers, 40, avenue du Recteur-Pineau, 86022 Poitiers cedex, France*

^c *Geowissenschaftliche Abteilung, Staatliches Museum für Naturkunde, Erbprinzenstrasse 13, 76133 Karlsruhe, Germany*

^d *Museo del Desierto, Saltillo, Coahuila, Mexico*

Received 11 July 2005; accepted after revision 2 March 2006

Available online 02 May 2006

Abstract

Recent fieldwork in the Early Tithonian of northeastern Mexico has yielded the partial cranium and associated fragmentary postcranial elements of a thalattosuchian. The specimen is described and referred to a new species of the genus *Geosaurus* characterised by elongated, narrow, oval supratemporal fenestrae, and a prefrontal that excludes the frontal from the centre of the dorsal margin of the orbits; the cranium is gracile and was probably more longirostrine than occurs in other members of this genus. The new taxon represents the second occurrence of the genus *Geosaurus* in the Mexican Gulf and is in agreement with the partial isolation of the area during the Late Jurassic, which was previously suggested by the microfossil and invertebrate assemblages. **To cite this article:** *M.-C. Buchy et al., C. R. Palevol 5 (2006).*

© 2006 Académie des sciences. Published by Elsevier SAS. All rights reserved.

Résumé

Un nouveau crocodyliforme thalattosuchien du Tithonien (Jurassique supérieur) du Nord-Est du Mexique. Une récente campagne de terrain dans le Tithonien inférieur du Nord-Est du Mexique a livré le crâne partiel d'un thalattosuchien, ainsi que des fragments mal préservés de son squelette post-cranien. Ce spécimen est ici décrit et rapporté à une nouvelle espèce du genre *Geosaurus*, caractérisée par ses longues fenêtres supratemporales ovales et son préfrontal excluant le frontal du centre de la marge dorsale de l'orbite. Le crâne est gracile et était probablement longirostre pour un membre de ce genre. Le nouveau taxon représente le second représentant du genre *Geosaurus* décrit dans le golfe du Mexique et conforte l'hypothèse d'un isolement partiel de ce dernier au Jurassique supérieur, proposée à partir des assemblages de microfossiles et d'invertébrés. **Pour citer cet article :** *M.-C. Buchy et al., C. R. Palevol 5 (2006).*

© 2006 Académie des sciences. Published by Elsevier SAS. All rights reserved.

Keywords: Thalattosuchia; *Geosaurus saltillense* sp. nov.; Mexico; Tithonian; Palaeobiogeography

Mots clés : Thalattosuchia ; *Geosaurus saltillense* nov. sp. ; Mexique ; Tithonien ; Paléobiogéographie

* Corresponding author.

E-mail address: mcbuchy@myway.com (M.-C. Buchy).

¹ Current address: Museo del Desierto, Saltillo, Coahuila, Mexico.

Version française abrégée

Introduction

Si les thalattosuchiens sont assez bien connus dans le Jurassique supérieur d'Europe et de Russie [20,25,26], ils montrent une moindre diversité taxonomique en Amérique du Sud et à Cuba [13,16,21,27]. Ils participent de la faune de reptiles marins peuplant le corridor caraïbe qui reliait l'archipel Européen et la marge Pacifique des Amériques depuis le Jurassique moyen [13,27]. Le Nord-Est du Mexique faisait partie du domaine marin à l'époque où furent déposés les sédiments deltaïques et de plate-forme interne de la formation La Casita et ceux de la plate-forme externe de la formation contemporaine La Caja [1,17]. Les assemblages de microfossiles et d'invertébrés semblent cependant indiquer l'isolement partiel du golfe du Mexique, à la fois de l'archipel Européen et du Pacifique, peut-être dû au soulèvement de la Floride [1,2]. Au cours du Jurassique supérieur, cette région était probablement divisée en bassins, en raison de l'activité tectonique régionale [18]. Les reptiles marins du Nord-Est du Mexique font l'objet de description systématique depuis peu [5,6,11]. Un premier membre mexicain du genre *Geosaurus*, *G. vignaudi* Frey et al., 2002 avait conforté l'hypothèse de l'isolement partiel du golfe du Mexique au Jurassique supérieur. Un nouveau spécimen du Tithonien inférieur du Nord-Est du Mexique, comprenant crâne et squelette post-crânien partiels, est rapporté ici à une nouvelle espèce du même genre et renforce encore cette hypothèse.

Abréviations institutionnelles

MUDE: Museo del Desierto, Saltillo, Mexique; SMNK: Staatliches Museum für Naturkunde Karlsruhe, Allemagne; SMNS: Staatliches Museum für Naturkunde Stuttgart, Allemagne.

Paléontologie systématique

Thalattosuchia Fraas, 1901

Metriorhynchidae Fitzinger, 1843

Geosaurus Cuvier, 1824

Geosaurus saltillense sp. nov.

Holotype. Crâne et squelette post-crânien partiels, CEP1823, MUDE (Figs. 2 et 3).

Locus typicus. Sierra de Buñuelas, près de Gomez Farías, Coahuila, Mexique (Fig. 1).

Stratum typicum. Section de la formation La Caja datée du Tithonien inférieur (Jurassique supérieur).

Derivatio nominis. Du comté de Saltillo, dont dépend le village de Gomez Farías.

Diagnose. Un membre du genre *Geosaurus*, caractérisé par ses fenêtres supratemporales très longues et étroites, dont la longueur atteint environ 2,5 fois leur largeur dans leur partie caudale. Le sillon marquant les marges latérales de la partie supraorbitale du frontal suggère que cet os était séparé par le préfrontal du centre de la marge dorsale de l'orbite. Les marges latérales de la barre intertemporale sont droites, sauf pour l'étroite table pariétale, située vers le milieu de la barre intertemporale.

Discussion

Paléontologie comparative. CEP1823 est attribué au genre *Geosaurus*, en raison de son crâne gracile et non ornementé, de l'angle de 40 à 45° formé par les processus latéraux de son frontal, de son arcade supratemporale située en contrebas de la barre intertemporale [11,26].

Parmi les autres membres du genre *Geosaurus*, *G. giganteus* (Soemmering, 1816) est une forme massive mal connue, ne comprenant que l'holotype fragmentaire [26]. Le crâne de CEP1823 est plus gracile, avec des fenêtres supratemporales plus longues et plus étroites, que *G. gracilis* (Meyer, 1830), *G. araucanensis* Gasparini & Dellapé, 1976 et *G. vignaudi* Frey et al., 2002 [10,11,13,26]. Les fenêtres supratemporales très longues et ovales de *G. suevicus* Fraas, 1901, reconstituées par Fraas [10], semblent similaires à celles de CEP1823. Cependant, le crâne sur lequel cette reconstitution est basée ([10]: spécimen A, SMNS 9808, M.-C.B. pers. obs.) est cassé dans sa portion caudodorsale, et ni la longueur, ni la forme des fenêtres supratemporales ne peut être correctement déterminée. D'après la position de la cavité glénoïde de la mandibule préservée en occlusion, la longueur de la fenêtre supratemporale de SMNS 9808 était proche de celle de *G. vignaudi*.

Vignaud [26] a montré que, dans le genre *Geosaurus*, les juvéniles sont caractérisés par une fenêtre supratemporale subcirculaire, devenant ovale chez l'adulte. CEP1823 représente donc une forme adulte de ce point de vue. La suture interfrontale est oblitérée sur CEP1823, alors qu'elle est visible chez de nombreux métriorhynchides juvéniles ainsi que chez les adultes de *G. araucanensis* [26]. De plus, la portion préservée du crâne de CEP1823 a la même taille que

la portion équivalente de spécimens adultes de *G. araucanensis* et *G. suevicus* [10,13,26], et du crâne adulte holotype de *G. vignaudi* [11]. CEP1823 ne peut donc pas représenter une forme juvénile de l'un de ces taxons.

Sur CEP1823 comme chez *G. araucanensis* [13,26], les marges médiorostrales des palatins divergent et un processus caudal du maxillaire s'insère entre les deux processus palatins. La face palatine est cependant très mal préservée, ou n'est pas visible, chez la plupart des autres membres du genre [26].

La forme et l'extension du préfrontal et son contact avec le frontal chez *G. araucanensis* et d'autres métriorhynchides sont variables indépendamment de l'ontogénie, comme l'a montré Vignaud [26] ; cependant, l'architecture et les proportions du crâne, en particulier des fenêtres supratemporales, ne sont pas modifiées significativement par la variation des os crâniens. De plus, l'aire périorbitaire de *Geosaurus* est encore trop mal connue pour juger de l'impact taxonomique de l'extension latérale et caudale du préfrontal de CEP1823. L'architecture et les proportions du crâne diffèrent de celles de tout autre thalattosuchien décrit. La création d'une seconde espèce du genre *Geosaurus*, *G. saltillense*, dans le Tithonien du golfe du Mexique est donc justifiée.

Paléobiogéographie. Le genre *Geosaurus* comprend trois espèces dans le Tithonien inférieur de l'archipel Européen, qui apparaît comme un centre d'origine probable du genre [26] ; une seule espèce a été décrite jusqu'ici dans le Tithonien inférieur à moyen du bassin de Neuquén en Argentine, alors que les marges Pacifiques de l'Amérique du Sud n'ont pas livré d'autres restes déterminables (Fig. 4) [12–14,26,27]. *G. vignaudi*, du Tithonien moyen du golfe du Mexique, présente des similarités à la fois avec *G. suevicus* et *G. araucanensis* [11,26], alors que *G. saltillense* représente une forme gracile, probablement longirostre (d'après ses fenêtres supratemporales longues et étroites, voir [26]), dont les affinités sont encore obscures. Il ajoute à notre connaissance de la diversité de l'assemblage particulier de reptiles marins du golfe du Mexique au Jurassique supérieur [6]. La poursuite du travail de terrain clarifiera le contexte géologique et la taphonomie de cette découverte.

1. Introduction

Late Jurassic thalattosuchians are well known from western Europe and Russia [20,25,26]. They were comparatively seldom reported from South and Central

America, where they have a lower taxonomical diversity [13,16,21,27]. Thalattosuchians are part of the marine reptile fauna that populated the Caribbean corridor linking the European Archipelago and the Pacific margin of the Americas since the Middle Jurassic [14,16]. Northeastern Mexico was part of the marine realm during the Late Jurassic when the deltaic and inner shelf conglomerates, sandstones and siltstones of the La Casita Formation were deposited; shales, siltstones and phosphorites characterize the more distal outer shelf sediments of the contemporaneous La Caja Formation [1, 17]. However, according to the microfossil and invertebrate assemblages, the Mexican Gulf was at that time partly isolated from both the European Archipelago and the Pacific, with the Florida uplift possibly forming a barrier between the European Tethys and the Mexican Gulf [1,2]. Moreover, at the time that the La Casita/La Caja Formations were deposited, northeastern Mexico experienced large-scale tectonic activity and sea-level fluctuations, leading to irregular sea floor topography and causing variable restrictions or subdivision of basins [18].

Thalattosuchians and other marine reptiles have been known from the La Casita/La Caja Formations of northeastern Mexico for some time [3,19,22,24], but have only recently been formally described [5,6,11]. The occurrence of at least one distinct species of *Geosaurus* (*Geosaurus vignaudi* Frey et al., 2002) in the Middle Tithonian of Puebla State (Central–East Mexico) appears to support the hypothesis that the Mexican Gulf was partially isolated during the Late Jurassic, as has been suggested on the basis of the invertebrate assemblages [1,2]. Recent field work in the Early Tithonian section of the La Caja Formation in southernmost Coahuila, northeastern Mexico (Fig. 1) yielded the partial cranium and postcranium of a thalattosuchian here referred to a new species of *Geosaurus*.

2. Institutional abbreviations

MUDE: Museo del Desierto, Saltillo, Mexico; SMNK: Staatliches Museum für Naturkunde Karlsruhe, Germany; SMNS: Staatliches Museum für Naturkunde Stuttgart, Germany.

3. Systematic Palaeontology

Thalattosuchia Fraas, 1901 [9]

Metriorhynchidae Fitzinger, 1843 [8]

Geosaurus Cuvier, 1824 [7]

Geosaurus saltillense sp. nov.

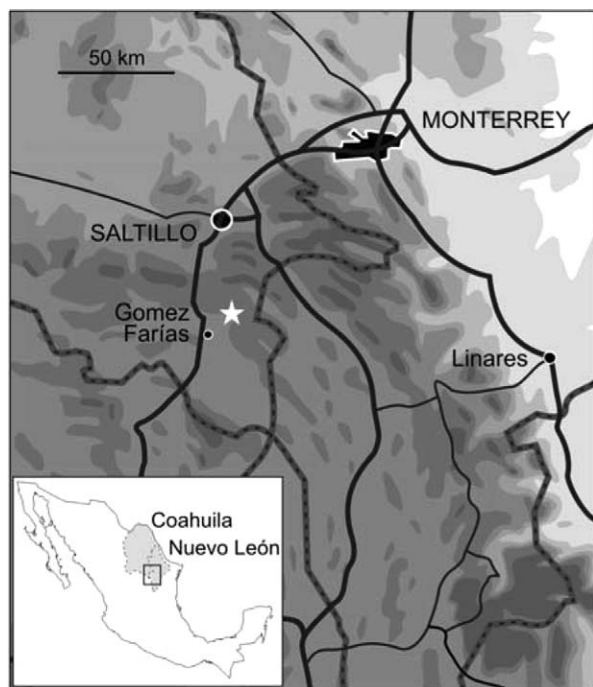


Fig. 1. Map of Mexico (insert) and detail of southeastern Coahuila and south Nuevo León; the area of the find is shown by a star.

Fig. 1. Carte du Mexique (insert) et détail du Sud-Est du Coahuila et du Sud-Est du Nuevo León ; l'étoile marque la zone de la découverte.

Holotype. Partial cranium and postcranium, CEP1823, MUDE (Figs. 2,3).

Locus typicus. Sierra de Buñuelas, near Gomez Farías, Coahuila, Mexico (Fig. 1).

Stratum typicum. Early Tithonian (Upper Jurassic) section of the La Caja Fm.

Derivatio nominis. From the county of Saltillo, upon which the village of Gomez Farías depends.

Diagnosis. A member of the genus *Geosaurus* characterised by its extremely long and narrow supratemporal fenestra, the length of which reaches about 2.5 times its caudal width. The lateral margins of the supraorbital portion of the frontal are grooved, suggesting that this bone was excluded from the centre of the dorsal margin of the orbit by the prefrontal. The lateral margins of the intertemporal bar are straight, except for the narrow parietal table located in the middle area of the bar.

Preservation and taphonomy. Of the cranium of CEP1823, the frontal, intertemporal bar, occiput and quadrates, and the caudal-most portions of both supratemporal bars are preserved in articulation (Figs. 2 and 3). The rostral-most portion of the frontal (see § *Description*) was separated from the main portion of cranium by a 5- to 10-mm-thick vein of calcite and matrix,

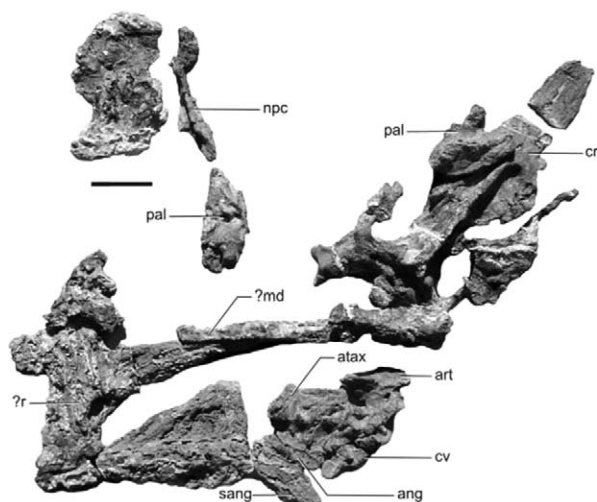


Fig. 2. CEP1823, *Geosaurus saltillense*, sp. nov., holotype as preserved with the main portion of cranium in dorsal view. Abbreviations: abo: basioccipital apophysis; ang: angular; art: articular; atax: atlas/axis complex; bsp: basisphenoid; cr: main portion of cranium; crf: cranioquadrate foramen; cv: cervical vertebrae; eo: exoccipital; fint: median intertympanic foramen; fm: foramen magnum; fr: frontal; hy: hyoid; j: jugal; md: mandible; npc: nasopharyngeal canal; oc: occipital condyle; olfb: olfactory bulb; olft: olfactory tractus; pal: palatine; par: parietal; porb: postorbital; pro: prootic; pt: pterygoid; q: quadrate; qj: quadratojugal; r: rib; scp: sclerotic plate; sq: squamosal; stf: supratemporal fenestra; IX/X/XI: foramina for cranial nerves IX, X and XI. Scale bar: 50 mm.

Fig. 2. CEP1823, *Geosaurus saltillense*, sp. nov., holotype tel qu'il est préservé avec la partie principale du crâne en vue dorsale. Abréviations : abo : apophyse basioccipitale ; ang : angulaire ; art : articulaire ; atax : atlas/axis ; bsp : basisphénoïde ; cr : partie principale du crâne ; crf : foramen craniocarré ; cv : vertèbres cervicales ; eo : exoccipital ; fint : foramen intertympanique médian ; fm : foramen magnum ; fr : frontal ; hy : hyoïde ; j : jugal ; md : mandibule ; npc : canal nasopharyngien ; oc : condyle occipital ; olfb : bulbe olfactif ; olft : tractus olfactif ; pal : palatin ; par : pariétal ; porb : postorbital ; pro : prootique ; pt : ptérygoïde ; q : carré ; qj : quadratojugal ; r : côte ; scp : plaque sclérotique ; sq : squamosal ; stf : fenêtre supratemporale ; IX/X/XI : foramen des nerfs crâniens IX, X et XI. Échelle : 50 mm.

indicating that it was most likely broken prior to fossilisation. The occipital portion of the cranium suffered from dorsoventral compression, as the articular processes of the quadrates are now sub-horizontal. A pair of elements is tentatively identified as the rostral-most portion of the palatine, including the palatine part of the prefrontal pillar. Both palatines lack their caudal portion and were compressed dorsoventrally. The left one is preserved upside down upon the left lateral process of the frontal, the ascending process facing rostrally (Figs. 2 and 3). The right palatine is lying about 100 mm to the left of the main portion of the cranium, resting dorsal side up (Fig. 2). About 10 mm rostral to the right palatine fragment and in line with it, an 85-

mm-long grooved element is identified as part of the (presumably right) nasopharyngeal duct. The surface of this element is very poorly preserved, and the bones that comprise it cannot be determined. Adjacent to the nasopharyngeal duct, some additional bone substance is preserved, not entirely freed from matrix, and cannot be further identified (Fig. 2). Inside and to the right of the right supratemporal fenestra, portions of the supra- and infratemporal bars and the caudal-most part of a quadratojugal are preserved, together with probable portions of the hyoid apparatus and possibly of a pterygoid (Fig. 3). A seemingly triradiate bone preserved lying dorsal to the right quadrate could represent a postorbital. However, in ventral aspect, it is covered by a long element that most likely is part of the mandible (Figs. 2 and 3B, see below); in dorsal aspect, it is obscured by matrix and remains of a rib and a seemingly flat bone, having the outline of two adjacent semicircles (Fig. 3A). A similarly looking element was identified in the same area of the holotype of *G. vignaudi* as a possible sclerotic plate [11]. However, as it is located, this element might also belong to the mandible (Fig. 2). The mandibular rami are preserved caudal to the main portion of cranium (Fig. 2); their surface is so heavily corroded that no individual bone can be identified with certainty, with the notable exception of the massive left articular and most likely the caudal-most portion of the articulated right angular and surangular (Fig. 2). No tooth, and indeed no alveolus, could be identified. The partly preserved atlas, the axis, ribs pertaining to the atlas and axis and the three articulated succeeding cervical vertebrae are preserved adjacent to the left articular. Of the rest of the postcranium, several thoracic ribs can be identified, but their numbers are uncertain; more corroded, intermeshed, unidentified bones or bone fragments are present (Fig. 2).

Either the frontal and parietal were fused, or their sutural contact was running where a break affects the intertemporal bar just rostral to the parietal table (Fig. 3). Frontal and nasals are possibly fused (see § Discussion). The ascending process of the palatines, if correctly identified, were not fused to the descending process of the prefrontals. Apparent fusion of the bones of the occipital face can possibly result from dorsoventral compression. The neurocorporal sutures of the preserved cervical vertebrae on the other hand are clearly visible. The individual age of the specimen is therefore difficult to assess, although it is probably safe to assume that it was not a fully mature adult [4].

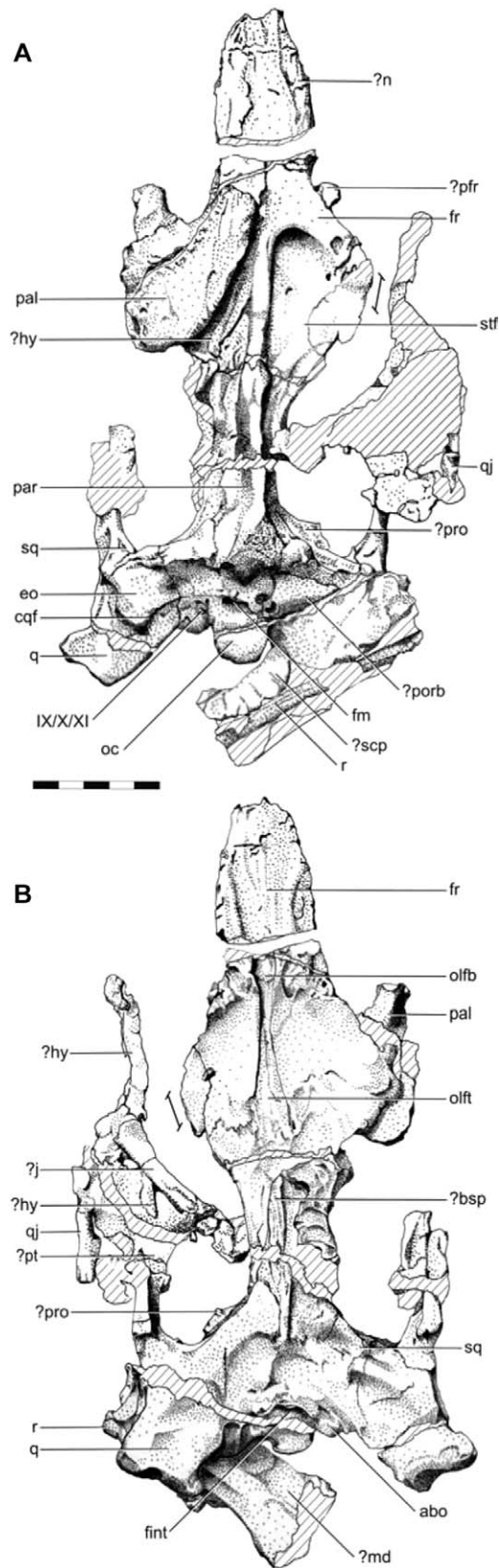
CEP1823 was collected during a field campaign in March 2004 and mechanically prepared in the SMNK.

The ventral side of the cranium was exposed when discovered, showing the olfactory tract; according to our observations of the local geology, this indicates that the cranium rested on its dorsal side. However, the dorsal portion of the caudal-most part of the parietal is weathered so that the spongiosa is exposed (Figs. 2 and 3A). The cranium therefore probably rested for some time on its ventral side. Several subcircular holes or deep depressions could be attributable to scavengers or represent bite marks (Fig. 3); the heavily corroded condition of the mandible and postcranial bones, though, suggests that these elements were dissolved. Several isolated bones from the same locality (MUDE undescribed specimens) lack a proper cortical layer and appear dissolved as well, as if having been exposed to an acidic environment. However, the surface of the main portion of the cranium of CEP1823 is smooth, showing no such trace of dissolution. The identical relative location of the articular in relation to the atlas/axis and cervical vertebral column in the holotype of *G. vignaudi* [11] and CEP1823 (Fig. 2) hints at a similar displacement of the neck and caudal portion of the mandible when still connected by muscles, ligaments and skin. The taphonomical history of the specimen is thus complex, combining agents mighty enough to tilt the skull, break or disarticulate and displace the brain case, temporal bars, prefrontals, rostrum and mandible, and still leave in place, e.g., the broken rostral-most portion of the frontal or portions of the supra- and infratemporal bars. Further geological and sedimentological studies of the finding site are necessary to understand the taphonomy of CEP1823.

Description. The rostral-most portion of the interorbital area is most likely formed mainly by the frontal (Figs. 2 and 3). The nasal, however, might form its lateral part; on the right side, an elevated linear area of bone running rostromedially on the dorsal surface could then mark the location of the suture with the frontal (Fig. 3A). In ventral aspect, no potential nasofrontal suture is visible (Fig. 3B).

No other suture is clearly visible on the cranium; when necessary in what follows, we designate the bones according to Fraas [10] and Vignaud [26].

In its narrower portion, both lateral surfaces of the frontal show conspicuous grooves extending caudally until the level of the rostral margin of the supratemporal fenestra; these grooves probably mark the contact of the frontal with the prefrontal. The ventral surface of the rostralateral-most portion of the frontal on the main cranium fragment (Fig. 3B) exhibits a wrinkled area lateral to the olfactory bulb imprint on both sides, where most



likely the prefrontal underlaid the frontal. It thus appears that the prefrontal formed the rostral and central portions of the dorsal margin of the orbit and extended caudally until level with the rostral margin of the supratemporal fenestra. The lateral extent of the prefrontal and its original dorsal exposure, however, cannot be determined. A square fragment of bone sitting in the right frontal lateral groove might represent part of the prefrontal (Fig. 3).

The lateral processes of the frontal form together an angle of 40 to 45°. The rostral margin of the supratemporal fenestra is rounded; at least in its rostral fourth, delimited medially by the intertemporal bar and laterally by the lateral process of the frontal, it is triangular (Fig. 3A). The caudal part of the supratemporal fenestra is subrectangular, the posttemporal bar being oriented laterocaudally, and the preserved portion of the supratemporal arch rostrally. A possible fragment of the proötic may be preserved in the caudomedial corner of the right supratemporal fenestra (Fig. 3). The length of the supratemporal fenestra is about 2.5 times its preserved maximal width (in its caudal portion, Fig. 3A). Owing to the breakage of the lateral portions of the lateral processes of the frontal and missing (or disarticulated) postorbitals, the actual extent of the supratemporal fossa can only be estimated: it might have occupied about half the surface, in any case about half the length measured along its midline of the supratemporal fenestra (Fig. 3A). The medial margin of both supratemporal fossae is genuine and clearest on the right; it smoothly curves caudomedially until it merges with the intertemporal bar. The intertemporal bar is presumably formed rostrally by the frontal and caudally by the parietal; it has straight, vertical margins, until the weak enlargement in its middle area forming an ill-defined parietal table. The margins of the intertemporal bar slightly converge caudal to the parietal table. The squamosal appears to form most of the caudal margin of the supratemporal fenestra.

The caudal-most portions of the supratemporal arches (presumably formed by the squamosal) show a sharp dorsal margin and a flat ventral articular surface for the quadratojugal. Of the infratemporal arch, only the caudal-most portion of a quadratojugal is identified, displaced to the right (Fig. 3). Its shaft emerges at low angle from its rectangular articular surface for the squa-

mosal (Fig. 3B); it is sub-circular in cross-section, about 5 mm in diameter.

The osteological composition of the occiput is obscured by compression and/or fusion of the bones (see § *Preservation*); it generally agrees with the description by Vignaud [26] of undistorted, juvenile metriorhynchids. The parietal forms the median dorsal-most part of the occipital face, bordered lateroventrally by the exoccipital; the supraoccipital cannot be identified and was presumably fused to the adjacent elements (Fig. 3A). The ventral half of the occipital face comprises the basioccipital forming the occipital condyle, and the quadrate laterally (Fig. 3B). Few foramina of the occipital face are identifiable: the foramen magnum, the caudal aperture of the cranioquadrate canal and two of the foramina for cranial nerves IX, X and XI on the dorsal half of the occiput (Fig. 3A); the median intertympanic foramen on its ventral half (Fig. 3B). The occipital part of the basisphenoid cannot be distinguished from the basioccipital apophyses; the rostral portion of the basisphenoid, however, might be present close to its original position, i.e. ventral to the median portion of the intertemporal bar (Fig. 3B).

The articular condyle of the quadrate is transversely elongate, oval, concave in its middle portion, convex laterally and medially (Figs. 2,3).

Provided the palatines are correctly identified, their caudal process is not preserved (Figs. 2,3). Through comparison with the preserved dorsal width of the interorbital area and because the ventral surface of both palatines are identical in outline, the median margins might be close to original. They appear to diverge rostrally. The laterocaudal margin of the palatine (the medio-rostral margin of the palatine fenestra) smoothly curves rostrolaterally (Fig. 3A). The ascending process appears to emerge just rostral to the rostral-most margin of the palatine fenestra. However, dorsoventral compression renders the actual, 3-dimensional morphology of the area uncertain. Both processes are about 20-mm long, and preserve lateral and medial crests that extend respectively laterally and medially and presumably merged with the dorsal surface of the ventral portion of the palatine.

As mentioned, the mandible is poorly preserved. The ventrally concave suture between the right angular and surangular might be preserved in lateral aspect (Fig. 2),

Fig. 3. CEP1823, *Geosaurus saltillense*, sp. nov., holotype, drawing of the cranium in (A) dorsal view, (B) ventral view. Abbreviations as in Fig. 2. The brackets indicate the broken edge of the lateral processes of the right frontal that formed further laterally the rostral part of the supratemporal bar. Scale bar : 50 mm.

Fig. 3. CEP1823, *Geosaurus saltillense*, sp. nov., holotype, dessin du crâne en vue (A) dorsale, (B) ventrale. Abréviations : voir Fig. 2. Les crochets indiquent le bord cassé du processus latéral du frontal droit, qui formait latéralement la portion rostrale de la barre supratemporale. Échelle : 50 mm.

although possibly not with its original outline, owing to extensive weathering. The articular as preserved appears to form about the lateral two-thirds of the glenoid fossa. The latter is slightly convex mediolaterally; a sharp crest, higher laterally, bounds it caudally and delimitates the rostral margin of the retroarticular process. The rostral margin of the glenoid is less sharply defined; it is rounded and the bone surface smoothly curves rostroventrally to form the rostral process of the articular. The articular forms only the dorsolateral-most part of the retroarticular process, which is broken caudally.

The atlas/axis complex and succeeding cervical vertebrae are similar in size and morphology to what was described for e.g. *G. suevicus* or *G. vignaudi* with similar cranium size [10,11].

4. Discussion

Comparative palaeontology. CEP1823 is referred to the genus *Geosaurus* because of its gracile cranium lacking ornamentation; the 40 to 45° angle formed by the lateral processes of its frontal and its supratemporal arch, situated lower than the intertemporal bar [11,26].

Among the other members of the genus *Geosaurus*, *G. giganteus* (Soemmering, 1816), is poorly known by the fragmentary holotype cranium representing a massive form [26]. CEP1823 differs from *G. gracilis* (Meyer, 1830), *G. araucanensis* Gasparini & Dellapé, 1976 and *G. vignaudi* Frey et al., 2002 in its more gracile cranium and proportionately longer, narrower supratemporal fenestrae [10,11,13,26]. *Geosaurus suevicus* Fraas, 1901 was reconstructed by Fraas [10] as possessing long, oval supratemporal fenestrae looking similar to that of CEP1823. However, a crack runs caudoventrally through the caudal portion of the skull in the specimen upon which Fraas' reconstruction is based ([10]: specimen A, SMNS 9808, M.-C.B. pers. obs.); the extent and shape of the supratemporal fenestra cannot be judged properly. Based upon the location of the glenoid fossa on the occluding mandible, the length of the supratemporal fenestra in SMNS 9808 was close to that of *G. vignaudi* both relatively and absolutely.

Vignaud [26] showed that in thalattosuchians the width of the supratemporal fenestra compared to its length is subject to allometric growth during ontogeny. In all previously described species of *Geosaurus*, juveniles are characterised by a subcircular supratemporal fenestra, while it becomes oval in adults. CEP1823 therefore shows the adult configuration in this respect. Additionally, no interfrontal suture is present in CEP1823, as it is in many juvenile metriorhynchids

and adult *G. araucanensis* as well [26]. Moreover, the preserved portion of cranium of CEP1823 is of a similar size as the equivalent portion of adult specimens of *G. araucanensis* and *G. suevicus* [10,13,26, and specimens in the SMNS, M.-C.B. pers. obs.], and of the adult holotype and only known specimen of *G. vignaudi* [11]. CEP1823 therefore cannot represent a juvenile of any of these taxa.

CEP1823 approaches *G. araucanensis* in the diverging medio-rostral margins of its palatine, where a caudal process of the maxilla inserts in the latter taxon [13, 26]. However, the palatal area is very poorly preserved or exposed in most other members of the genus [26].

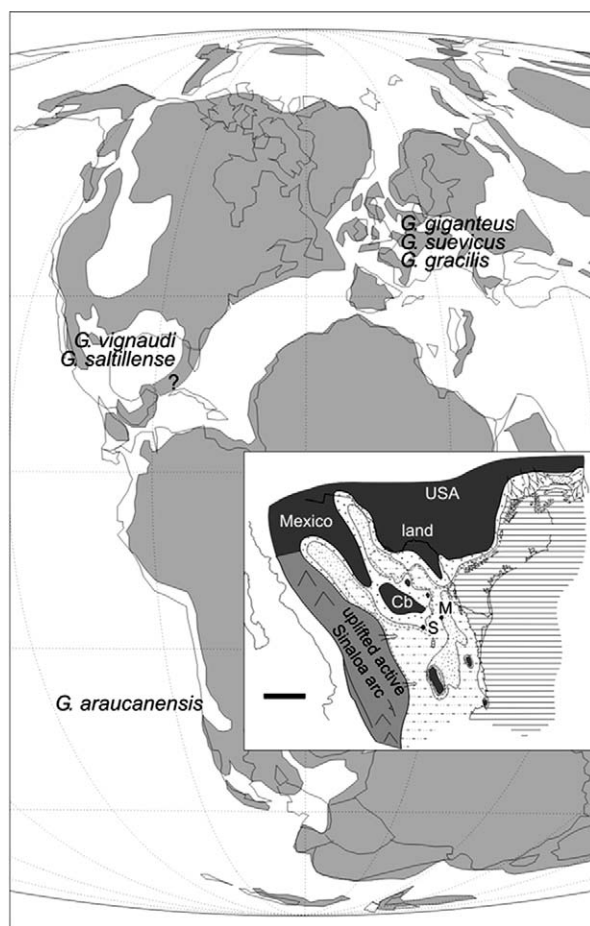


Fig. 4. Palaeogeographical map of the Late Jurassic (modified from [23]). Insert: palaeobiogeographical map of northeastern Mexico during the Tithonian; Cb: Coahuila block; M: Monterrey; S: Saltillo; scale bar 150 km (redrawn after [17]).

Fig. 4. Carte paléogéographique du Jurassique supérieur (modifiée d'après [23]). Insert : carte paléobiogéographique du Nord-Est du Mexique durant le Tithonien ; Cb : bloc du Coahuila ; M : Monterrey ; S : Saltillo ; échelle : 150 km (redessinée d'après [17]).

The shape, extent and contact with the frontal of the prefrontal of *G. araucanensis* and other metriorhynchids were shown by Vignaud [26] to be variable independent of ontogenetic stage; however, the skull architecture and proportions, especially of the supratemporal fenestrae, are not significantly modified in relation to the variation of the cranial bones. Moreover, the orbital area and its three-dimensional anatomy in *Geosaurus* are poorly known, due to inadequately preserved or prepared specimens. The taxonomical importance of the lateral and caudal extent of the prefrontal dorsal to the orbit in CEP1823 therefore cannot be judged properly, but the shape and proportions of its cranium are significantly different from those of any other described thalattosuchian. For that reason, we feel confident in erecting a second species of the genus, *G. saltillense*, from the Tithonian of the Mexican Gulf.

Palaeobiogeography. Three species of the genus *Geosaurus* are described from the Early Tithonian of the European Archipelago, and on this basis the area has been proposed as the likely centre of origin for the genus [26]; a single species is described at present in the Early to Middle Tithonian of the Neuquén Basin of Argentina, while the Pacific margins yielded no other diagnostic remains (Fig. 4) [12–15,26,27]. *G. vignaudi* from the Middle Tithonian of the Mexican Gulf shows similarities with both *G. suevicus* and *G. araucanensis* [11,26], while *G. saltillense* represents a gracile, probably longirostrine form (on behalf of its long and narrow supratemporal fenestrae, see [26]) of unclear affinities at present. It adds to our knowledge of the diversity of the peculiar tetrapod assemblage of the Late Jurassic Mexican Gulf [6]. Further fieldwork will clarify the geological context and taphonomy of the find.

Acknowledgements

Fieldwork was performed with the help of Jens Erdmann (Stuttgart, Germany), Elizabeth Jardon Nava, José López Espinoza (both MUDE), Franck Métayer (Strasbourg, France) and Jorge Velasco Segura (Linares, Mexico). All facilities in Gomez Farías were offered by Don Gregorio ‘Dinosaurio’ Sánchez and his family, the Comisariado Ejidal Guadalupe Lara, as well as the citizens of Gomez Farías. The specimen was excellently prepared by F. Wittler (Karlsruhe, Germany). Thanks are due to Rainer Schoch (SMNS) for access to specimens in his care and to Krister T. Smith (Yale) for discussion. Steven W. Salisbury made valuable comments upon the manuscript and straightened the language. Thanks are due to S. Jouve (Paris) and an anon-

ymous referee. We acknowledge financial support from the Deutsche Forschungsgemeinschaft (grant number FR 1314/9-1).

References

- [1] T. Adatte, W. Stinnesbeck, J. Remane, The Jurassic–Cretaceous boundary in Northeastern Mexico. Confrontation and correlations by microfacies, clay mineral mineralogy, calpionellids and ammonites, *Geobios* 17 (1994) 37–56.
- [2] T. Adatte, W. Stinnesbeck, J. Remane, H. Hubberten, The western end of the Tethys at the Jurassic–Cretaceous boundary: Evidence for a paleogeographic change in NE Mexico, *Cretaceous Res.* 27 (1996) 671–689.
- [3] F. Aranda-Manteca, W. Stinnesbeck, Reptiles marinos del Jurásico Superior (Kimmeridgiano) del Noreste de Mexico, *Soc. Mexicana Paleontol., IV Congreso Nacional* (October 1993), *Tagungsheft* (1993) 15–16.
- [4] C.A. Brochu, Closure of neurocentral sutures during crocodylian ontogeny: implications for maturity assessment in fossil archosaurs, *J. Vertebr. Paleontol.* 16 (1996) 49–62.
- [5] M.-C. Buchy, E. Frey, W. Stinnesbeck, J.G. López-Oliva, First occurrence of a gigantic pliosaurid plesiosaur in the Late Jurassic (Kimmeridgian) of Mexico, *Bull. Soc. geol. France* 174 (2003) 271–278.
- [6] M.-C. Buchy, E. Frey, W. Stinnesbeck, J.G. López-Oliva, An annotated catalogue of the Upper Jurassic (Kimmeridgian and Tithonian) marine reptiles in the collections of the Universidad Autónoma de Nuevo León, Facultad de Ciencias de la Tierra, Linares, Mexico, *Oryctos* (in press).
- [7] G. Cuvier, Sur les ossements fossiles de crocodiles, in: *Recherche sur les ossements fossiles*, 2^e édition, 5 (2), Dufour and D’Occagne, Paris, 1824, pp. 143–160.
- [8] L. Fitzinger, *Systema Reptilium*, Braumüller and Seidel, Vienna, Austria, 1843.
- [9] E. Fraas, Die Meerkrokodile (*Thalattosuchia* n.g.) eine Sauriergruppe der Juraformation, *Jahr. Ver. vaterl. Naturk. Wuerntemb.* 57 (1901) 409–418.
- [10] E. Fraas, Die Meer-Crocodylier (*Thalattosuchia*) des oberen Jura unter specieller Berücksichtigung von *Dakosaurus* und *Geosaurus*, *Palaeontographica* 49 (1902) 1–79.
- [11] E. Frey, M.-C. Buchy, W. Stinnesbeck, J.G. López-Oliva, *Geosaurus vignaudi* n. sp. (Crocodylia, Thalattosuchia), first evidence of metriorhynchid crocodylians in the Late Jurassic (Tithonian) of central-east Mexico (State of Puebla), *Can. J. Earth Sci.* 39 (2002) 1467–1483.
- [12] Z. Gasparini, Marine reptiles of the Circum-Pacific region, in: G.E.G. Westermann (Ed.), *The Jurassic of the Circum-Pacific*, *World Reg. Geol.* 3 (1992) 361–364.
- [13] Z. Gasparini, D. Dellapé, Un nuevo cocodrilo marino (*Thalattosuchia*, *Metriorhynchidae*) de la Formación Vaca Muerta (Jurásico, Tithoniano) de la Provincia de Neuquén (República Argentina), *Actas 1e Congreso Geológico Chileno*, Santiago, Chile (1976) 1–22.
- [14] Z. Gasparini, M. Iturralde-Vinent, Metriorhynchid crocodylians (*Crocodyliformes*) from the Oxfordian of Western Cuba, *N. Jahrb. Geol. Paläontol. Monatsh.* 9 (2001) 534–542.
- [15] Z. Gasparini, P. Vignaud, G. Chong, The Jurassic *Thalattosuchia*, (*Crocodyliformes*) of Chile: a paleobiogeographic approach, *Bull. Soc. geol. France* 171 (2000) 657–664.

- [16] Z. Gasparini, N. Bardet, M. Iturralde-Vinent, A new cryptoclidid Plesiosaur from the Oxfordian (Late Jurassic) of Cuba, *Geobios* 35 (2002) 201–211.
- [17] R.K. Goldhammer, Mesozoic sequence stratigraphy and paleogeographic evolution of North East Mexico, in: C. Bartolini, J.L. Wilson, T.F. Lawton (Eds.), *Sedimentary and tectonic history of North-Central Mexico*, *Geol. Soc. Am., Spec. Pap.* 340, 1999, pp. 1–31.
- [18] R.K. Goldhammer, C.A. Johnson, Middle Jurassic–Upper Cretaceous paleogeographic evolution and sequence-stratigraphic framework of the Northwest Gulf of Mexico Rim, in: C. Bartolini, R.T. Buffler, A. Cantu-Chapa (Eds.), *The Western Gulf of Mexico Basin – Tectonics, Sedimentary Basins, and Petroleum Systems*, *A.A.P.G. Mem.* 75 (2001) 45–82.
- [19] W. Hähnel, Hallazgo de restos de dinosaurio en Aramberri, N.L., Mexico, *Actas Fac. Cien. Tierra UANL Linares* 3 (1988) 245–250.
- [20] S. Hua, P. Vignaud, V. Efimov, First record of Metriorhynchidae (Crocodylomorpha, Mesosuchia) in the Upper Jurassic of Russia, *N. Jahrb. Geol. Paläontol. Monatsh.* 8 (1998) 475–484.
- [21] M. Iturralde-Vinent, M.A. Norell, Synopsis of Late Jurassic Marine Reptiles from Cuba, *Am. Mus. Novit.* 3164 (1996) 1–17.
- [22] D. Schumann, Observaciones paleoecológicas en secuencias del Kimmeridgiano/Tithoniano (Formación La Casita) de Nuevo León, Noreste de México, *Actas Fac. Cien. Tierra, UANL Linares* 3 (1988) 43–59.
- [23] A.G. Smith, D.G. Smith, B.M. Funnel, *Atlas of Mesozoic and Cenozoic coastlines*, Cambridge University Press, Cambridge, 1994 (99 p).
- [24] W. Stinnesbeck, T. Adatte, J. Remane, Mazatepec (Puebla, México) – Reevaluación de su valor como estratotipo del límite Jurásico–Cretácico, *Rev. Esp. Micropaleontol.* 25 (1993) 63–79.
- [25] G.W. Storrs, M.S. Arkhangel'skii, V.M. Efimov, Mesozoic marine reptiles of Russia and other former Soviet republics, in: M.J. Benton, M.A. Shishkin, D.M. Unwin, E.N. Kurochkin (Eds.), *The age of dinosaurs in Russia and Mongolia*, Cambridge University Press, Cambridge, 2000, pp. 187–210.
- [26] P. Vignaud, *Les Thalattosuchia, crocodiles marins du Mésozoïque : systématique phylogénétique, paléoécologie, biochronologie et implications paléogéographiques*, unpublished Ph.D. thesis, University of Poitiers, France, 1995 (271 p.)
- [27] P. Vignaud, Z. Gasparini, *Dakosaurus andiniensis* n. sp. (Crocodylia, Thalattosuchia), first record of *Dakosaurus* in the Upper Jurassic of Argentina, *C. R. Acad. Sci. Paris, Ser. IIA* 322 (1996) 245–250.