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

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ABSTRACT – We present an annotated catalogue of the Late Jurassic marine reptiles held in the collections of the Universidad Autónoma de Nuevo León, Facultad de Ciencias de la Tierra, in Linares, Mexico (UANL-FCT). Most of the specimens are fragmentary because they were collected in the frame of geological surveys. The collections comprise the holotype of the recently described thalattosuchian *Geosaurus vignaudi*, from the Tithonian (Late Jurassic) of Puebla State. The collections of the UANL-FCT additionally document a new marine reptile assemblage from the Kimmeridgian (Late Jurassic) of north-eastern Mexico, which represents groups hitherto unknown from the Late Jurassic Mexican Gulf. The assemblage comprises thalattosuchians, ichthyosaurs, pliosaurs, and a single elasmosaur vertebra. Most of the diagnostic specimens are endemic to at least the species level, confirming the partial isolation of the Mexican Gulf during the Late Jurassic, as suggested on the basis of invertebrate assemblages. The composition of this new tetrapod assemblage is compared to the Late Jurassic marine tetrapod assemblages of Europe and South America.

Key words: *Thalattosuchia, Ichthyosauria, Plesiosauria, Late Jurassic, Mexico, palaeobiogeography*

Catalogue commenté des reptiles marins du Jurassique supérieur (Kimméridgien et Tithonien) des collections de l'Universidad Autónoma de Nuevo León, Facultad de Ciencias de la Tierra, Linares, Mexique – Nous présentons un catalogue commenté des collections de reptiles marins du Jurassique supérieur de l'Universidad Autónoma de Nuevo León, Facultad de Ciencias de la Tierra, Linares, Mexique (UANL-FCT). Les spécimens sont fragmentaires parce que collectés surtout dans le cadre d'explorations géologiques. Les collections de l'UANL-FCT comprennent l'holotype du thalattosuchien récemment décrit *Geosaurus vignaudi*, provenant du Tithonien (Jurassique supérieur) de l'État de Puebla. Les collections de l'UANL-FCT livrent aussi un nouvel assemblage de reptiles marins du Kimméridgien (Jurassique supérieur) du nord-est du Mexique, livrant des groupes jusqu'ici inconnus dans le Jurassique supérieur du Golfe du Mexique. Cet assemblage comprend thalattosuchiens, ichthyosaures, pliosaures et une vertèbre isolée d'élasmosaure. La majorité des spécimens diagnostiques sont endémiques, au moins au niveau spécifique, et confirment l'isolement partiel du Golfe du Mexique durant le Jurassique supérieur suggéré par les assemblages d'invertébrés. La composition de ce nouvel assemblage de tétrapodes est comparée aux assemblages du Jurassique supérieur d'Europe et d'Amérique du Sud.

Mots clés: *Thalattosuchia, Ichthyosauria, Plesiosauria, Jurassique supérieur, Mexique, paléobiogéographie*

INTRODUCTION

Marine vertebrates are known to occur in the La Casita / La Caja Formations of eastern and north-eastern Mexico (figs 1, 2), but this vertebrate assemblage was only briefly mentioned by Michalzik (1988), Schumann (1988)

Figure 1 (above) – Map of Mexico, and detailed road maps of south Nuevo León and north-east Puebla States. Fossiliferous localities are shown by an asterisk; SelMP: Sierra El Montelongo Pedregoso, Nuevo León. On the general map, scale bar represents 200 km. On road maps, scale bar represents 20 km.

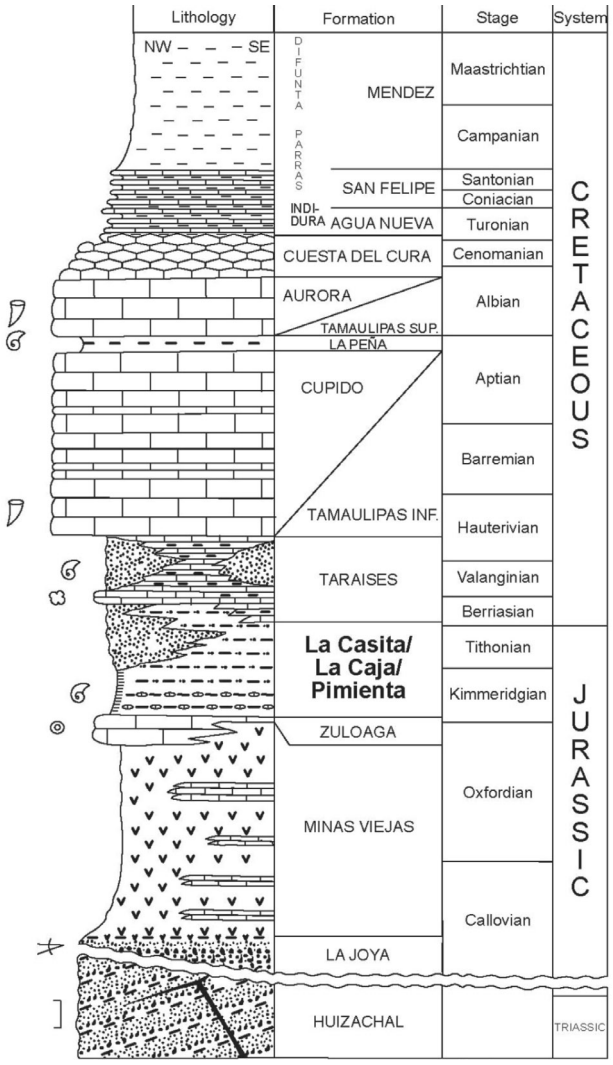

Figure 2 (right) – Stratigraphical units of the Mesozoic in the northern Sierra Madre Oriental (north-eastern Mexico), between Monterrey and Saltillo. Redrawn after Michalzik, 1988 and Götte, 1990. Scale bar represents 100 m.

and Aranda-Manteca & Stinnesbeck (1993), as the collection of vertebrate remains was mainly conducted during geological survey. Our examination of the collections of the Universidad Autónoma de Nuevo León, Facultad de Ciencias de la Tierra, Linares, Mexico (UANL-FCT) resulted in the formal description of a new thalattosuchian crocodilian (*Geosaurus vignaudi*, Frey *et al*., 2002; specimen UANL-FCT-R1), and the discovery of the largest pliosaur described to date (Buchy *et al*., 2003; specimen UANL-FCT-R2). Further remains of marine reptiles from the La Casita Formation are kept in the UANL-FCT (Table 1), and are described here for the first time, revealing a rich assemblage of marine reptiles. North-eastern Mexico appears a promising area for further finds, being intermediate both in time and space between the known European and Pacific marine vertebrate assemblages (e.g. Bardet, 1995; Gasparini *et al*., 2000; Frey *et al*., 2002).

GEOLOGY

In north-eastern Mexico the Late Jurassic represents a time of gradual transgression (figs 2, 3). Marine deposition began during the Oxfordian as the result of widespread rifting caused by the opening of the Gulf of Mexico. Evaporites of the Minas Viejas Formation underlie the Oxfordian to Lower Kimmeridgian limestones of the Zuloaga Formation which were deposited in shallow water environments of a carbonate ramp. Upsection, lithologies and fossil content indicate increased terrigenous influence, probably from the Coahuila Peninsula north and west of Saltillo, Coahuila (e.g., Michalzik, 1988; Götte, 1990; Adatte *et al*., 1994; Goldhammer, 1999). Extensive deltaic and inner shelf conglomerates, sandstones and siltstones of the La Casita Formation developed from late Early Kimmeridgian to Valanginian stages in the proximal southern vicinity of the Coahuila block, whereas the La Caja Formation consists of shales, siltstones and phosphorites and characterizes more distal outer shelf settings further to the south (fig. 3). This latter unit only reaches as high as Early Berriasian and underlies pelagic limestones and marls of the Taraises Formation with a gradual contact (Adatte *et al.*, 1994; 1996). Both the La Casita and La Caja Formations are characterized by block tectonics leading to rapid lateral changes in facies

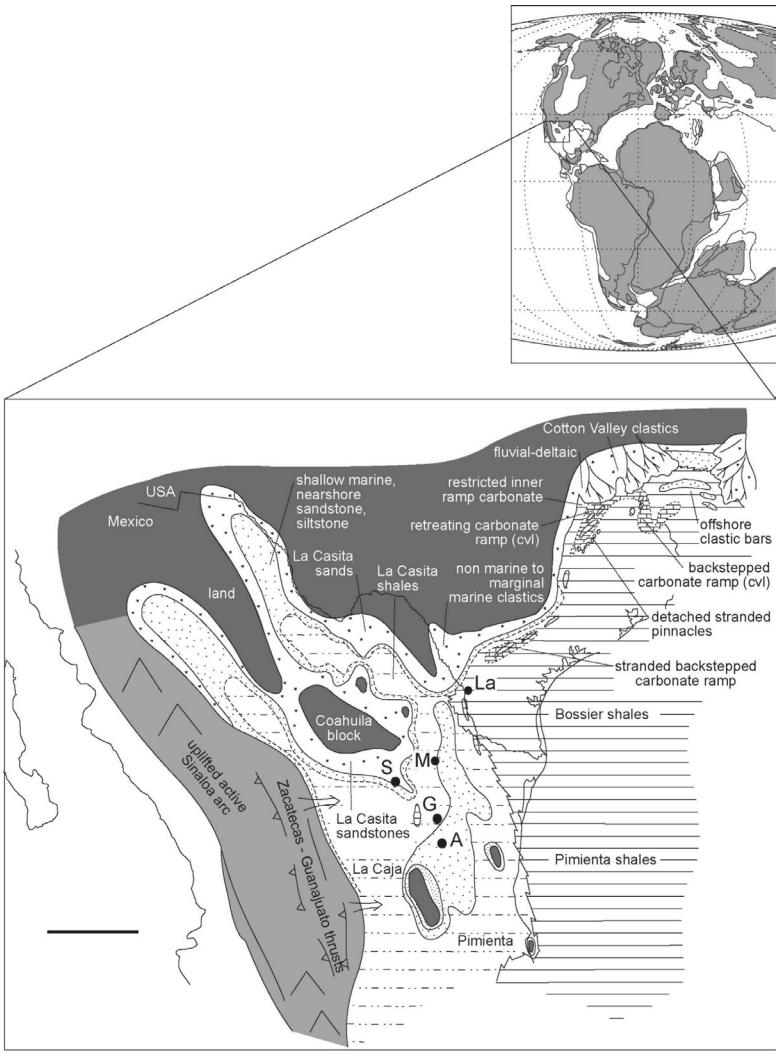

Figure 3 – Palaeogeographical map of the world during the Tithonian (after Smith *et al*., 1994), and a detailed map of northern Mexico during the same period (redrawn from Goldhammer, 1999). A: Aramberri, Nuevo León; G: Galeana, Nuevo León; La: Laredo, Texas; M: Monterrey, Nuevo León; S: Saltillo, Coahuila. Scale bar represents 100 km.

and abrupt variations in thickness, from 40 m to more than 500 m (Wilson, 1990; Salvador, 1991; Goldhammer & Johnson, 2001). The Upper Jurassic sediment sequence was later covered by between 1000 m and more than 2000 m thickness of Cretaceous sediments. In the Sierra Madre Oriental foldbelt outcrops of Upper Jurassic sediments are thus found only in the center of anticlines and diapiric domes.

Both the La Casita and the La Caja Formations are well known for their abundant and diverse invertebrate remains. Fossils are usually flattened in the siltstones and shales but are preserved 3-dimensionally in limestones and calcareous concretions which reach a few centimeters to more than 2 m in diameter. Diverse assemblages of ammonites were described and allow a detailed assignation of biostratigraphic zones (Castillo & Aguilera, 1895; Burckhardt, 1906; 1930; Imlay, 1939; 1984; Cantú-Chapa, 1963; 1968; 1971; Verma & Westermann, 1973; Adatte *et al*., 1994, 1996; Olóriz *et al*., 1999; Villaseñor *et al*., 2000). In addition, belemnites, bivalves, brachiopods, and serpulids are also present, as well as radiolarians and calpionellids.

All except one of the vertebrates described here come from the lower part of the La Casita / La Caja Formations. Ammonites collected in the same sediments (e.g., *Idoceras, Glochiceras, Haploceras, Procraspedites*) indicate a late Early to early Late Kimmeridgian age (Olóriz *et al*., 1999; Villaseñor *et al*., 2000). Only the holotype of *Geosaurus vignaudi* Frey *et al*., 2002 (UANL-FCT-R1), from the hamlet of Mazatepec in the State of Puebla (fig. 1), was discovered in sediments of undisputedly Tithonian age.

CATALOGUE OF SPECIMENS

Crocodyliformes Benton & Clark, 1988
Mesoeucrocodylia Whetstone & Whybrow, 1983
Neosuchia Benton & Clark, 1988
Thalattosuchia Fraas, 1901
Thalattosuchia indet.
UANL-FCT-R11

Material: One isolated and fragmentary neural arch.
Origin: The neural arch was discovered during the excavation of the pliosaur UANL-FCT-R2, at Aramberri, Nuevo León (fig. 1). The age of the La Caja deposits at this site, as

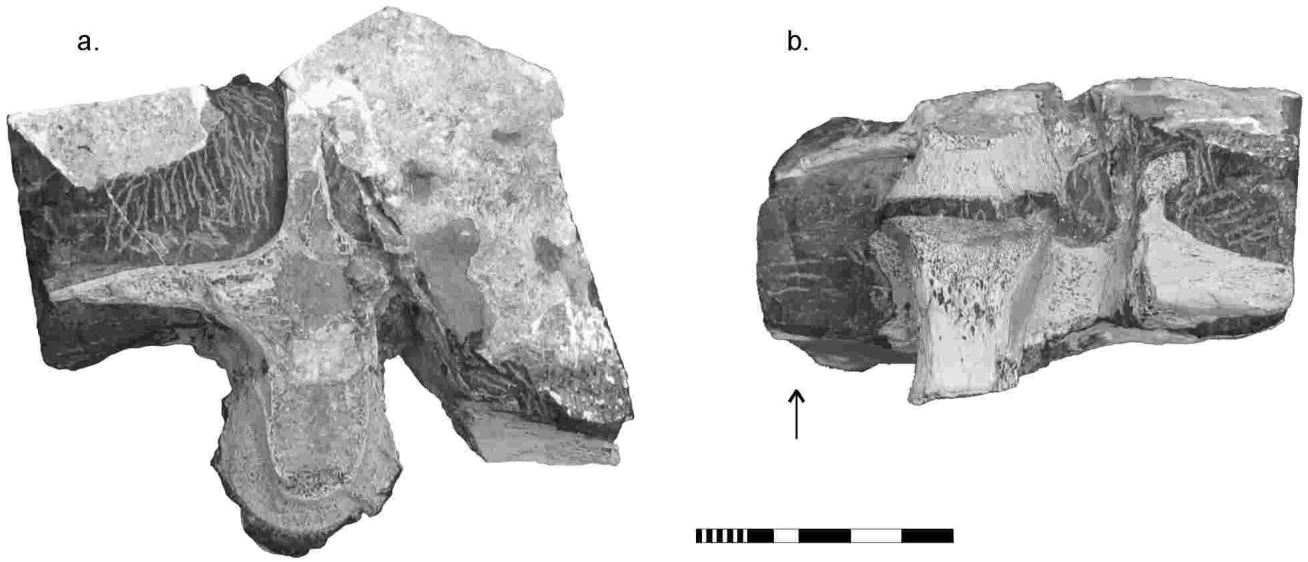

Figure 4 – UANL-FCT-R15, in a/ cranial and b/ ventral views. Arrow in b/ points cranially. Scale bar represents 50 mm.

determined by the ammonite assemblage, is late Early to early Late Kimmeridgian (see Buchy *et al*. 2003).
Description: The fragment comprises the proximal two thirds of a neural spine and the almost complete right transverse process, which shows a configuration of rib articulation facets typical for the thoracic vertebrae of Crocodyliformes (synapophyse). The marine off-shore environment and the Late Jurassic age of the fragmentary vertebra excludes any other known crocodyliform but thalattosuchians. Therefore we refer this specimen to an undetermined thalattosuchian genus.

UANL-FCT-R15 (fig. 4)
Material: One thoracic vertebra with the proximal fragment of the right rib, and the caudal half of the preceding vertebra.
Origin: late Early to early Late Kimmeridgian La Casita Formation, determined from the matrix. The exact origin of the specimen is unclear: probably either Galeana, or Iturbide, Nuevo León (fig. 1).
Description: The caudal articular surface of the vertebra is missing and the compacta is preserved only in the left dorsal part of the corpus, which shows a ventral keel. The unfused neurocorporal suture and the horizontal orientation of the transverse process is diagnostic of Crocodyliformes (e.g. Kälin, 1955). The laterally oriented proximal fragment of a rib belonging to this vertebra is seen in ventral view only and articulates with a short lateral process, which represents the parapophysis. This indicates that the two rib articulations are situated in a dorsoventral plane. Such a configuration is indicative of the prothoracic region. Of the cranially following vertebra, only the cranial half is preserved, including the neural spine and a fragmentary transverse process, which extends further laterally than the preceding parapophysis. The lack of osteoderms, which may have been expected in articulated specimens, indicates that the vertebrae might come from a metriorhynchid thalattosuchian, but this can only be clarified by further preparation.

UANL-FCT-R25
Material: Two fragmentary thoracic vertebrae.
Origin: late Early to early Late Kimmeridgian La Casita Formation at Galeana, Nuevo León (fig. 1).
Description: The vertebrae are sitting in a concretion, and need additional preparation. Only the dorsal aspect of the transverse processes and the right bases of the neural spines are exposed. The transverse process of the best preserved vertebra shows the horizontally aligned articular surfaces for a thoracic rib (synapophysis). The lateral extension of the transverse processes indicates a large thalattosuchian crocodilian, of about 3 m in length.

Metriorhynchidae Fitzinger, 1843
Metriorhynchinae Fitzinger, 1843
Metriorhynchinae indet.

UANL-FCT-R13
Material: Fragment of a rostrum comprising a fragmentary mandible around the caudal terminus of the symphysis including the dentition, and the crowns of the maxillary teeth aligned with the endocast of the internal cavity of the nasal duct of the maxillary rostrum. The interdigitating maxillary and mandibular teeth show that the jaws are in occlusion.
Origin: late Early to early Late Kimmeridgian La Casita Formation, as determined from the matrix. The specimen probably comes from either Galeana or from Iturbide, Nuevo León (fig. 1).
Description: The rostrum as preserved is 120 mm long.

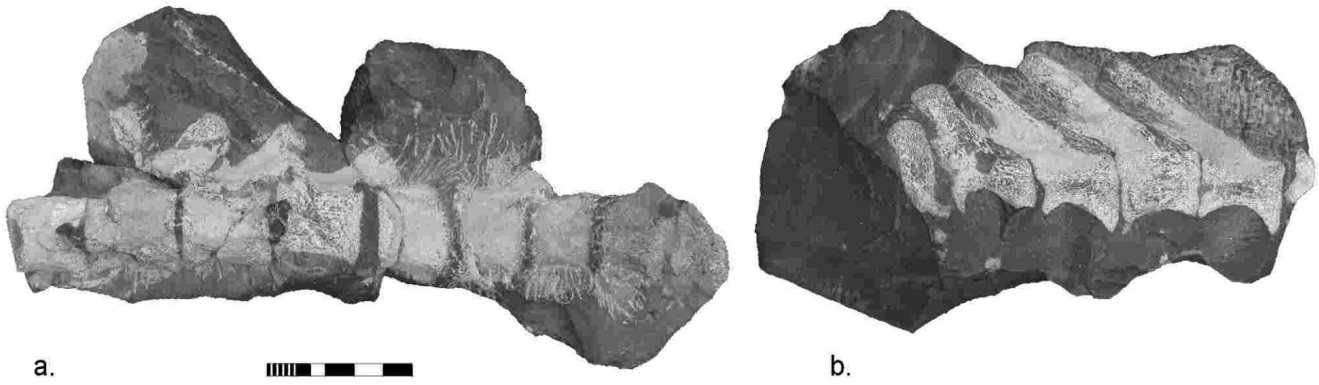

Figure 5 – a/ UANL-FCT-R16, in right lateral view; b/ UANL-FCT-R17, in left lateral view. Scale bar represents 50 mm.

On the right side six tooth positions of the maxilla and mandible are visible, on the left side only the two rostral most preserved dentary ones; the rest is obscured by matrix. As far as is visible, the teeth are slightly longitudinally oval in cross-section and slightly re-curved. The surface of the enamel shows faint canellation, but no carinae. The external surface of the mandibular part of the rostrum also lacks any sculpture. These features hints at either *Geosaurus* or, more likely, *Metriorhynchus*. The endocast of the maxillary rostrum shows fine, transversely running wrinkles, which probably represent imprints of the internal lining of the nasal cavity. Following further preparation, the specimen will most probably reveal further diagnostic features, as well as details of the internal cranial anatomy, and will therefore add substantially to our knowledge of Mexican metriorhynchids.

UANL-FCT-R16 (fig. 5a)
Material: Nine articulated caudal vertebrae.
Origin: late Early to early Late Kimmeridgian La Casita Formation, at Galeana, Nuevo León (fig. 1).
Description: All the vertebrae are seen from the left side, while the right side is still embedded in matrix. Only vertebrae one to three and five to seven, as preserved, are virtually complete, while vertebra four lacks its left half, and vertebrae eight and nine are missing both sides of the corpus. Only in vertebrae two to six are the neural spines preserved. They are inclined about 50° to the horizontal in terminal direction and rapidly decline in height towards the terminus of the tail. This, and the lack of any trace of transverse processes, shows that the fragment comes from the terminal third of the tail, shortly cranial of the tail bend of a metriorhynchine crocodylifrom.

UANL-FCT-R17 (fig. 5b)
Material: Four articulated caudal vertebrae, neural spine of a cranially adjacent vertebra, and cranial portion of the corpus of a caudally adjacent one.
Origin: late Early to early Late Kimmeridgian La Casita Formation, at Galeana, Nuevo León (fig. 1).
Description: All vertebrae are visible from the left side while the right side is obscured by matrix. The cranial inclination of the neural spines and their height relative to the adjacent corpora demonstrates that the vertebrae come from the cranial most segment of the tail bend of a metriorhynchid crocodilian. All preserved vertebral corpora lack their left third and the two cranial neural spines, as preserved, are exposed in longitudinal section. The size of the vertebrae, as well as the colour and consistency of the matrix indicate that this specimen is consistent with UANL-FCT-R16, whose origin is identical, and may belong to the same individual, although the two fragments do not match.

Geosaurus Cuvier, 1824
Geosaurus vignaudi Frey *et al.*, 2002
UANL-FCT-R1
Material: Holotype skull and mandible, atlas, axis and 3 cervical vertebrae on a limestone slab.
Origin: Tithonian Pimienta Formation near Mazatepec, Puebla (fig. 1). In central-eastern Mexico, the Pimienta Formation is an open marine shelf equivalent of the La Caja Formation (figs 2, 3).
Description: The specimen comprises an almost complete, but partially disarticulated skull with the cranial part of the cervical vertebral column. The holotype and only known specimen, including comments on the palaeobiogeography was described in detail by Frey *et al*. (2002).

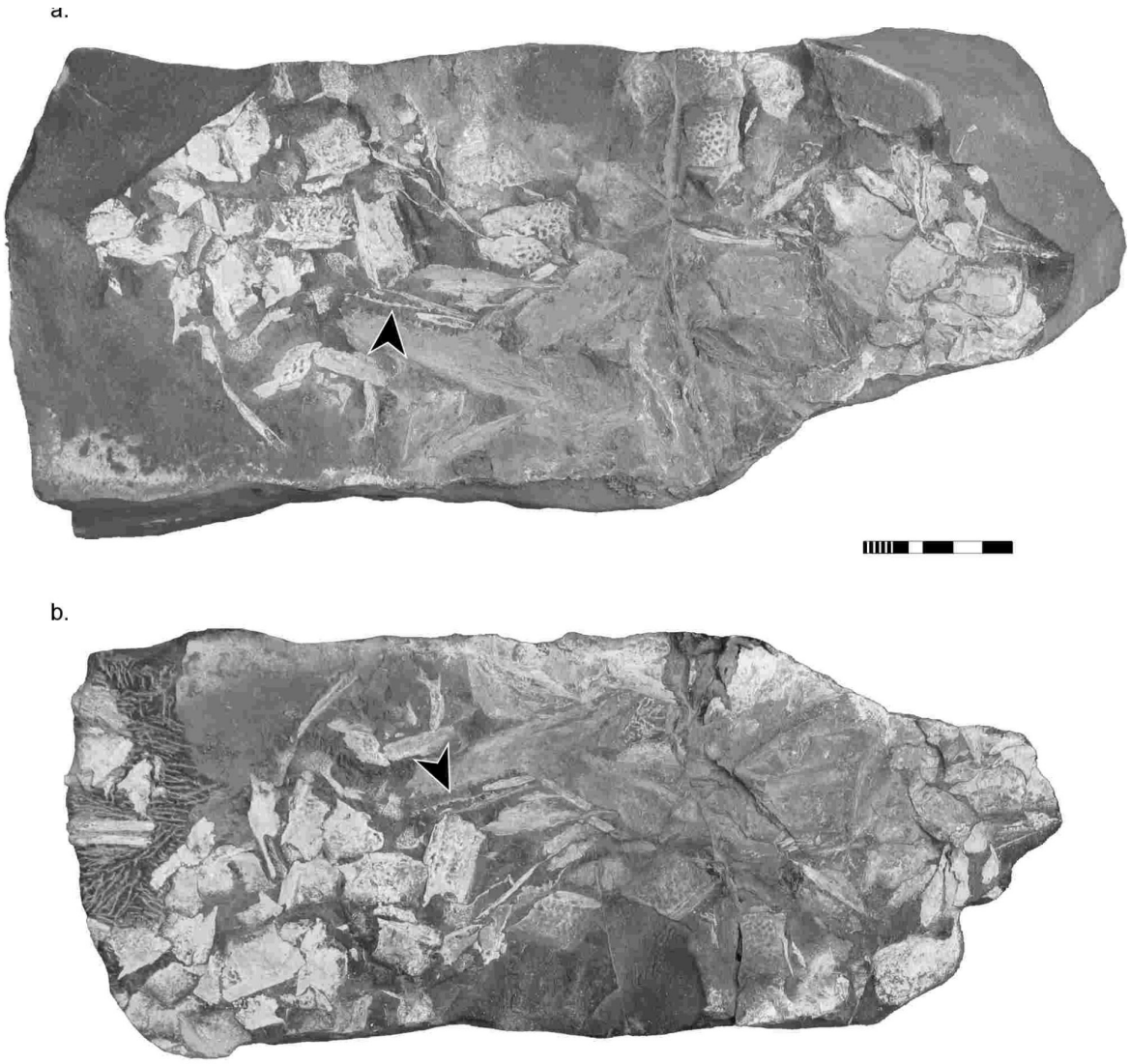

Figure 6 – a/ and b/ UANL-FCT-R12, both surfaces of the split concretion. Arrows point at the preserved jaw fragment. Scale bar represents 50 mm.

Thalattosuchia Fraas, 1901
Teleosauroidea Geoffroy Saint-Hilaire, 1831
Teleosauridae Geoffroy Saint-Hilaire, 1831
Teleosauridae indet.

UANL-FCT-R12 (fig. 6)
Former accession number: LCITØ / 1005
Material: Osteoderms, cranial and post-cranial fragments preserved on both surfaces of a split concretion.
Origin: late Early to early Late Kimmeridgian La Casita Formation, at Iturbide, Nuevo León (fig. 1).
Description: The specimen is preserved on an incomplete concretion and comprises the remnants of a disarticulated small teleosaurid less than one metre in length. The identification is based on the osteoderms which are about twice as wide as they are long and flat. The corners of the osteoderms are rounded and the cranially directed articular process is short and slightly curved medially, representing less than one fifth of the length of the osteoderm. The external sculpture consists of circular pits, and the unsculptured articular surface covers about one quarter of the external face of each osteoderm. If the remnants came from *Steneosaurus* Geoffroy Saint-Hillaire, 1825, or *Machimosaurus* Meyer, 1837, it would represent a very young individual or a new gracile form. This is the first evidence of the existence of this type of crocodilian in Mexico. Further details could be obtained following preparation of the specimen; a jaw fragment preserved on both slabs would certainly provide diagnostic features.

Ichthyopterygia de Blainville, 1835
Euichthyopterygia Motani, 1999
Euichthyopterygia indet.

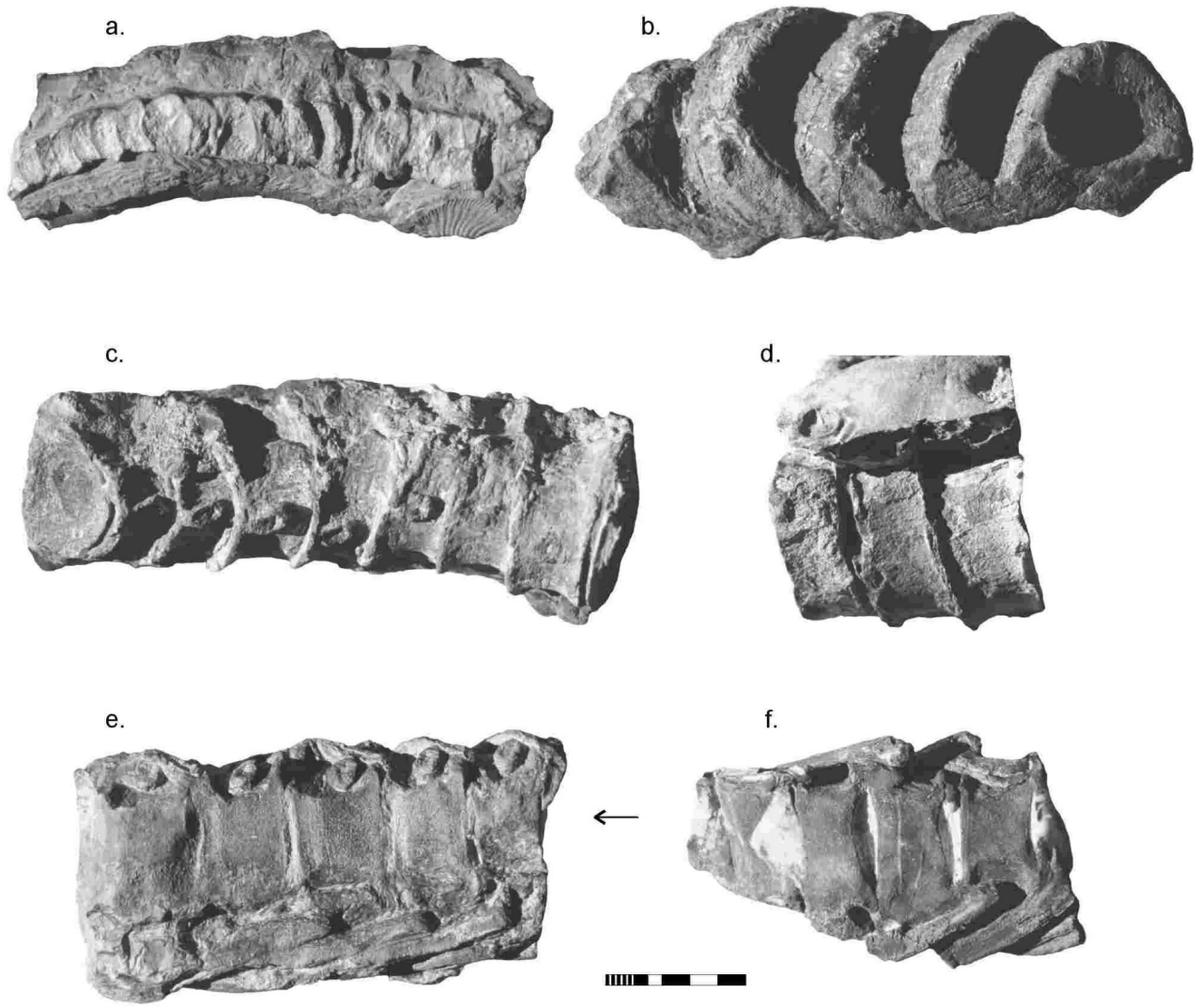

Figure 7 – a/ UANL-FCT-R18 in right lateral view; b/ UANL-FCT-R19 in caudolateral or craniolateral view; c/ UANL-FCT-R20 in right lateral view; d/ UANL-FCT-R21 in left lateral view; e/ UANL-FCT-R22 in ventral view; f/ UANL-FCT-R23 in ventral view. Arrow applies to e/ and f/ and points cranially. Scale bar represents 50 mm.

UANL-FCT-R18 (fig. 7a)
Former accession number: LCRPØ / 1003
Material: Portion of caudal vertebral column consisting of approximately 14 corpora.
Origin: late Early to early Late Kimmeridgian La Casita Formation, at Rio Pablillo, Nuevo León (fig. 1).
Description: The vertebral corpora are preserved on the surface of a nodule, and visible in right lateral view. They are articulated, and the ventral bend of the tail is preserved. The exposed surfaces of the corpora are very poorly preserved, and the distinction between the individual bones is difficult to determine with certainty. Approximately 7 corpora are preserved cranial to the tail bend and at least 7 caudal to it. The height of the cranial-most preserved corpus is 26 mm, its length is approximately 18 mm, and the height of the terminal-most preserved corpus is 14 mm, its length is 8 mm.

UANL-FCT-R19 (fig. 7b)
Former accession number: LCRPØ / 1002
Material: Five corpora; serial position undetermined.
Origin: late Early to early Late Kimmeridgian La Casita Formation, at Rio Pablillo, Nuevo León (fig. 1).
Description: The corpora are completely prepared out of the sediment. They are aligned but tilted and shifted from their original contacts, and, together with the poor preservation, this indicates that the specimen suffered decay prior to embedding. The articular surfaces of the corpora are subcircular; the height of the largest corpus is 83 mm, its length approximately 30 mm. The other corpora appear smaller in diameter, which could be the result of weathering. Due to poor preservation the serial position of the corpora in the vertebral column cannot be determined.

UANL-FCT-R20 (fig. 7c)
Former accession number: LCSLØ / 1001
Material: Seven articulated caudal corpora.
Origin: late Early to early Late Kimmeridgian La Casita Formation, at San Lucas, Nuevo León (fig. 1).
Description: The corpora are visible in right lateral aspect only, due to incomplete preparation. Their articular surfaces are subtriangular, with the dorsal portion narrower. The cranial-most preserved corpus has a maximal height of 70 mm, and a length of 30 mm. The maximal height of the caudal-most preserved corpus is 55 mm, its length approximately 20 mm. In lateral aspect, all corpora exhibit only a parapophysis, situated ventrally on their lateral margin. The specimen therefore represents the cranial portion of the tail.

UANL-FCT-R21 (fig. 7d)
Material: Three articulated corpora; serial position uncertain.
Origin: late Early to early Late Kimmeridgian La Caja Formation, at La Angostura, Nuevo León (fig. 1).
Description: The specimen is still partly embedded in matrix. The three corpora are visible only in ventral aspect. Their articular surfaces are subcircular, with a diameter of approximately 70 mm, and a length of 30 mm. Additional preparation is necessary to determine from which region of the vertebral column they come.

UANL-FCT-R22 (fig. 7e)
Material: Five articulated corpora and adjacent rib fragments.
Origin: late Early to early Late Kimmeridgian La Casita Formation, from 2 km south-east of San Lucas, Nuevo León (fig. 1).
Description: The corpora are visible in ventral and right ventrolateral aspect. Their articular surfaces are subcircular, with a width of approximately 60 mm, a length of 30 mm to 32 mm, and the parapophyses are situated on the ventral portion of the lateral margins. The dorsal portions of the corpora in both lateral views are obscured by matrix and ribs, and the presence of diapophyses cannot be proven. However, from their subcircular section these corpora are probably dorsals or sacrals. The ribs are fragmentary, approximately 10 mm diameter in cross-section.
These vertebrae come from the same locality and have a similar aspect and size to UANL-FCT-R23. They could belong to the same individual, though as no additional data are available two accession numbers were kept.

UANL-FCT-R23 (fig. 7f)
Material: Four articulated corpora and rib fragments.
Origin: late Early to early Late Kimmeridgian La Casita Formation, from 2 km south-east of San Lucas, Nuevo León (fig. 1).
Description: As in UANL-FCT-R22, the corpora are best viewed in ventral and ventrolateral aspects, though the ventral face of UANL-FCT-R23 has suffered from more intensive weathering than UANL-FCT-R22. Despite their poor preservation, the corpora are of similar size and morphology to UANL-FCT-R22, as are the rib fragments.

Sauropterygia Owen, 1860
Plesiosauria de Blainville, 1835
Plesiosauroidea Welles, 1943
Elasmosauridae Cope, 1869
Elasmosauridae indet.

UANL-FCT-R5 (fig. 8)
Former accession number: LCANØ / 1006
Material: Isolated dorsal corpus, with the ventral part of the neural arch and right transverse process.
Origin: late Early to early Late Kimmeridgian La Caja Formation, at La Angostura, Nuevo León (fig. 1).
Description: The bone surface is punctured and scratched due to preparation, therefore some uncertainties persist as to the actual morphology of the specimen. The articular surfaces of the corpus are subcircular, except the dorsal margins, which are concave level with the neural canal. The corpus is 85 mm long, platycelous, with poorly expressed lips on its ventral and lateral surfaces. The width of the articular surfaces is 95 mm and the corpus is 70 mm in minimal width, in its middle portion. The lateral and ventral surfaces of the corpus are concave. In ventral aspect, a longitudinal low keel is situated on the right side of the specimen, approximately 15 mm lateral to the middle line, rather than on the middle line itself (see e.g. Tarlo, 1960). One pair of rostrocaudally elongate nutritive foramina is visible on the ventral face. The neural arch is fused to the corpus. Its cranial margin rises vertically level with the cranial articular surface of the corpus. Its caudal margin gently slopes dorsally 20 mm cranial from the caudal articular surface of the corpus. The neural canal is subtriangular in cranial aspect and high oval in caudal aspect, possibly due to preparation damage; it is approximately 30 mm in maximal width.
The preserved diapophysis is a high oval in cross-section, 35 mm high and 25 mm long. It is inserted on the caudal portion of the neural arch, level with the middle of the corpus.
Due to the flat articular surfaces and the proportions (length to width) of the corpus, this vertebra is tentatively identified as belonging to an undetermined elasmosaur (Bardet, pers. comm.).

Pliosauroidea (Seeley, 1874a) Welles, 1943
Pliosauridae Seeley, 1874a
Pliosauridae indet.

UANL-FCT-R2
Material: Seven articulated pectoral vertebrae, rib fragments, and portions of the pectoral girdle mounted on a concrete stand; 9 cervical vertebrae; lost portion of rostrum; articular head of a femur. Additional material is in preparation and expected from ongoing excavations.

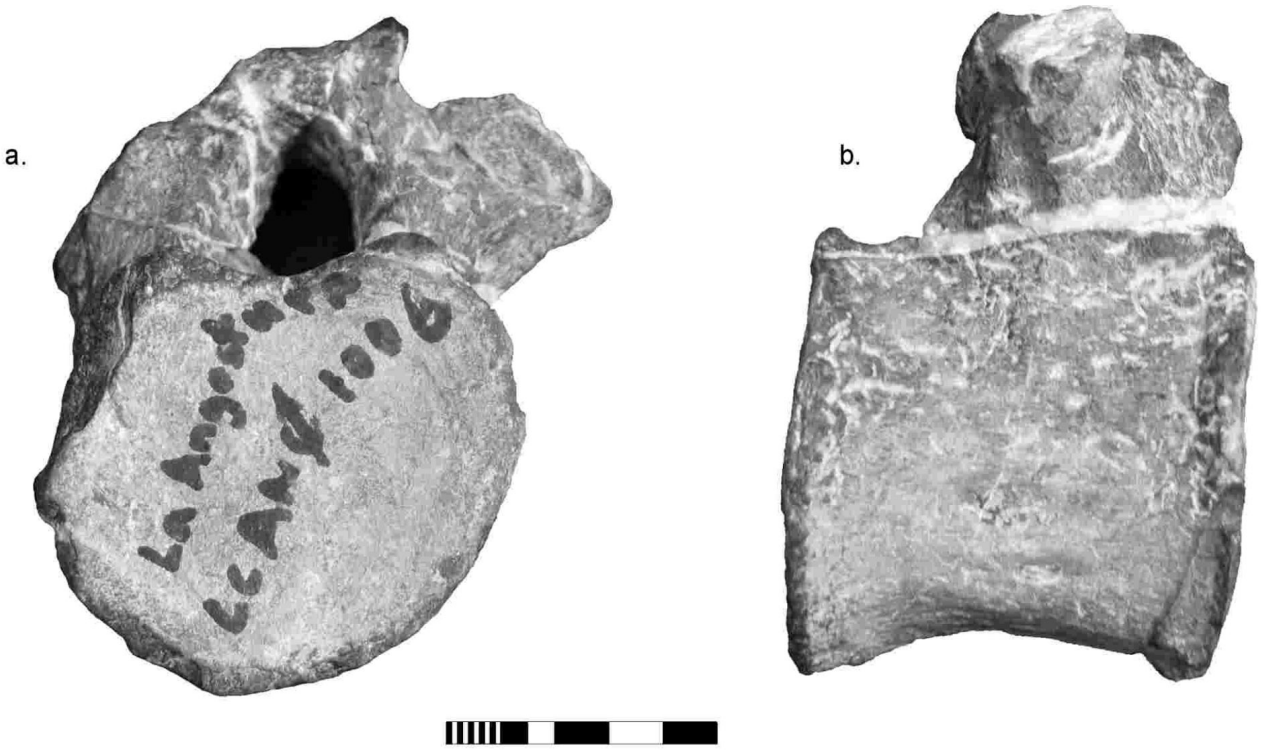

Figure 8 – UANL-FCT-R5 in a/ caudal and b/ right lateral views. Scale bar represents 50 mm.

Origin: Late Early to early Late Kimmeridgian La Caja Formation at Aramberri, Nuevo León (fig. 1).
We reported the history of this specimen, nicknamed "The Monster of Aramberri", and gave a description of the material mounted in the concrete stand (Buchy *et al*., 2003). Subsequently, excavations have been undertaken on the site at Aramberri, which yielded additional material, and may in the future allow recovery of the caudal portion of the animal. This juvenile pliosaur was certainly complete prior to weathering of the cranial half of the skeleton. Cranial fragments, currently under preparation, were found as isolated debris, and more are expected to be found during the next field campaign. The articular head of a femur was also discovered, aligned with portions of the pelvic girdle. This femoral head has a length of 450 mm, while the femoral head of a subcomplete, 5 meter long *Liopleurodon ferox* mounted in the Geological Institute in Tübingen, Germany (IGPT, uncatalogued specimen; Noé 2001: fig. 1) is 140 mm in length. The femoral head and all other fragments of UANL-FCT-R2 confirm our estimation of an animal at least 15 meters in length.
When excavation and preparation are complete, we shall report more fully upon this specimen.

Pliosauridae indet.

UANL-FCT-R3
Material: Adjacent portions of the maxillary and mandibular rostra with teeth. The preserved portion of the mandible represents the caudal part of the mandibular rostrum.
Origin: Late Early to early Late Kimmeridgian La Caja Formation. The specimen was collected in February 1988 by one of us (W.S.) and Martin Götte, then a PhD student, in the Sierra El Montelongo Pedregoso, Nuevo León (fig. 1).
Description: The maxillary rostrum is semicircular in cross-section. In dorsal aspect it exhibits a rostral prolongation of the parietal medial to the premaxillae until approximately level with the internal naris. The lateral margins of the mandibular and maxillary rostra are straight. The mandibular rostrum houses more than 5 tooth positions. The teeth are covered with smooth enamel, are strongly curved and trihedral in their apical half. This specimen will be described elsewhere (Buchy *et al*., in prep.). It is clearly belonging to Plesiosauria in its mesiolingual tooth replacement pattern, and referable to an undetermined pliosaur on the ground of its elongate mandibular symphysis and tooth size and morphology (e.g. Brown, 1981).

UANL-FCT-R7 (fig. 9)
Material: Four and a half caudal cervical corpora, and adhering portions of the coracoids.
Origin: late Early to early Late Kimmeridgian La Caja Formation, at La Angostura, Nuevo León (fig. 1), collected by Walter Hähnel in 1985.
Description: Three corpora are preserved in articulation, indicating a dorsal curvature of the neck. The fourth, and

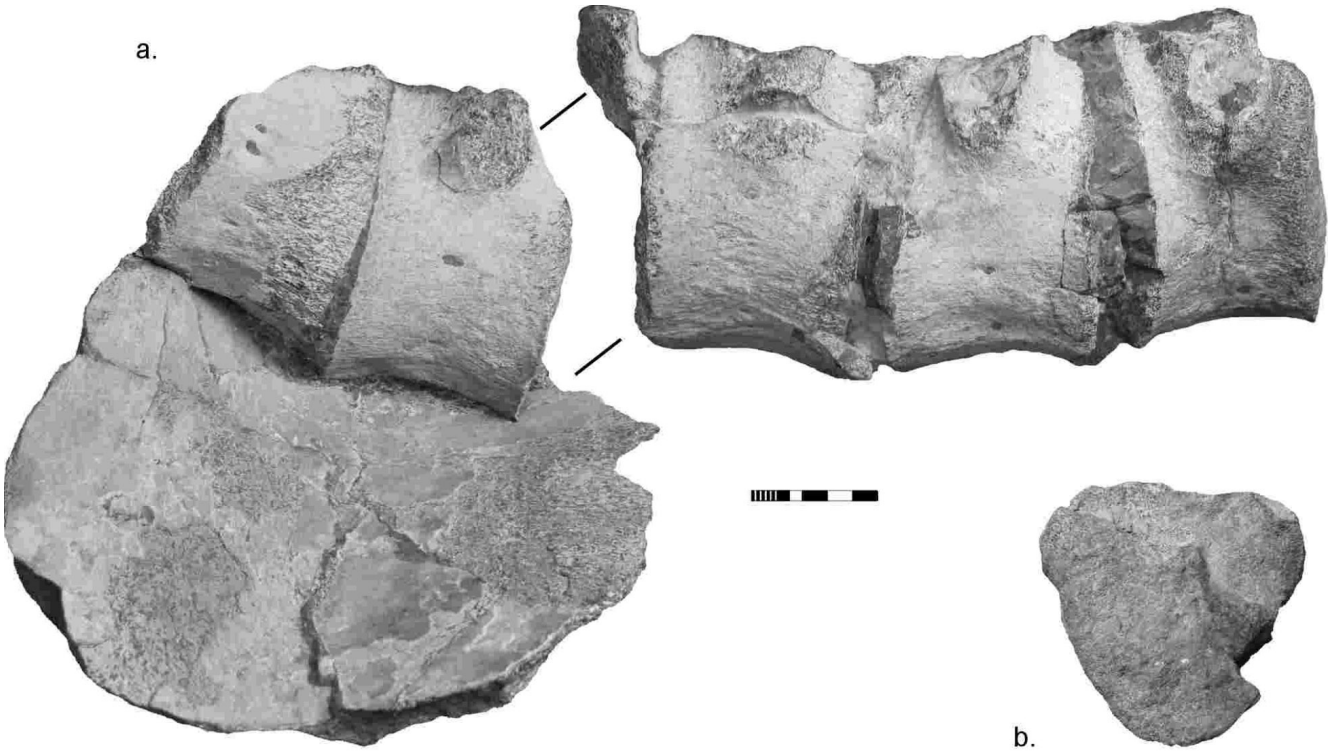

Figure 9 – UANL-FCT-R7 a/ in right lateral view; the black bar indicates the contact between the two fragments. b/ cranial view of the cranial-most preserved corpus. Scale bar represents 50 mm..

the preserved portion of the fifth vertebrae, rest on fragments of the coracoids. Both fragments match but have not been glued together. The individual corpora have a length of approximately 90 mm. The articular surface of the cranial-most corpus is heart-shaped, with a narrower ventral portion. Its median height is 145 mm, and its maximum width (level with the parapophysis) is 140 mm. The articular surfaces of the following corpora are subcircular, with a diameter of 135 mm to 140 mm. All visible articular surfaces are flat. The lateral surfaces of all corpora are concave, forming sharp angles with the articular surfaces, without lips. A faint median ventral keel is visible only on the third preserved corpus. The first preserved corpus exhibits one pair of nutritive foramina, the second and third, two pairs, and the fourth and fifth, three pairs. The foramina are rostrocaudally oval, and range from 2 mm to 9 mm in length. The parapophyses are poorly preserved. They originate in the middle of the corpora longitudinally. Medially, they contact the articular facets for the neural arches. The neural arches are entirely missing. They were lost prior to fossilisation, as the articular facets on the corpora are still partly obscured by matrix. In dorsal aspect, the neural canal is hour-glass-shaped.

The coracoids are not fused, and their contact is straight longitudinally. Of the left coracoid, only a small fragment is preserved. The preserved portion of the right coracoid is 250 mm wide, but no other original margin is preserved. At its craniolateral-most break, it is 5 mm thick. Its thickness increases to 20 mm at its medial margin, and up to 110 mm at its caudal-most break, toward the glenoid cavity.

The presence of the ventral foramina on the corpora indicates a member of Plesiosauria. The proportion of the corpora, whose length is smaller than their height and width, allows to refer this specimen to an undetermined pliosaur (e.g. Brown, 1981).

UANL-FCT-R8 (fig. 10)

Material: Fragmentary maxillary and mandibular rostra with teeth (fig. 10a).

Origin: late Early to early Late Kimmeridgian La Casita Formation. The material was collected by a shepherd in August 2002, about 1 km north-west of the hamlet of El Salitre, close to the city of Zaragoza, Nuevo León (fig. 1). It was subsequently bought by a private collector, who partly transferred it to the UANL-FCT. At least an isolated dorsal vertebra is still in the possession of this collector (fig. 10b, c). We collected additional bones and teeth when visiting the site in September 2003.

Description: The material is mostly unprepared, and various fragments do not match yet. The width of the maxillary rostrum is approximately 160 mm; it is subtriangular in cross-section. The width of the mandibular rostrum is approximately 140 mm. The mandibular rostrum comprises at least 6 teeth. Rostral to the third preserved dentary tooth, the lateral and ventral margins of the mandibular rostrum taper toward its rostral tip, the rostral-most two teeth being smaller than the following ones. The tooth crowns are

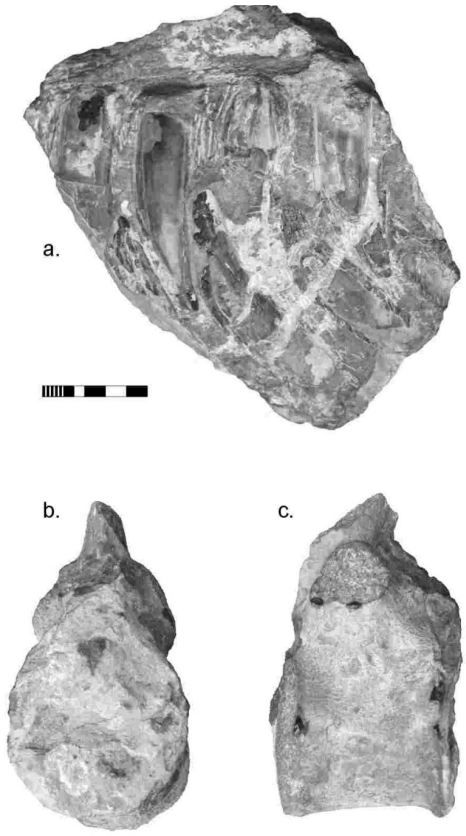

Figure 10 – a/ UANL-FCT-R8, one of the fragments of the rostrum in left lateral view. Dorsal vertebra in a private collection, supposedly found associated with UANL-FCT-R8 in b/ cranial and c/ right lateral views. Scale bar represents 50 mm.

elliptical in cross-section, and the rostral-most two pairs exhibit a mesial and a distal carina. The enamel is mainly preserved imprinted in the matrix; it is smooth or only faintly ornamented.

Together with the vertebra supposedly found at the site which yielded cranial material of UANL-FCT-R8, were two articulated ichthyosaur vertebrae, which were said by the owner to come from the same animal. It is therefore impossible to be sure, that the vertebra and the cranial remains belong together.

The transverse processes and neural arch of the vertebra are broken. The neural arch is fused to the corpus. The articular faces of the corpus are subcircular, with a diameter of 85 mm, with well-expressed lips. The lateral faces of the corpus are poorly concave. The corpus is approximately 80 mm long. A fuller description must await further preparation.

This specimen clearly belongs to a pliosaur on the ground of its tooth replacement pattern, mandibular symphysis length and tooth morphology, as UANL-FCT-R3.

DISCUSSION

Comparative palaeontology

Crocodilians

Five genera of thalattosuchian Crocodyliformes are reported from Upper Jurassic marine deposits: the teleosaurids *Steneosaurus* Geoffroy Saint Hilaire, 1825 and *Machimosaurus* v. Meyer, 1837 and the metriorhynchids *Metriorhynchus* v. Meyer, 1830, *Geosaurus* Cuvier, 1824 and *Dakosaurus* Quenstedt, 1856 (Vignaud, 1995). During the Upper Jurassic, the fossil record of *Steneosaurus* is restricted to the European archipelago. *Machimosaurus* is also mainly reported from Europe, but one specimen has been described from the Upper Oxfordian of Ethiopia (v. Huene, 1938; Bardet & Hua, 1996). *Metriorhynchus*, *Geosaurus* and *Dakosaurus* occur in Europe as well as in South America (Vignaud, 1995; Vignaud & Gasparini, 1996).

Of the Mexican crocodilians only one specimen to date is diagnostic to the species level: *Geosaurus vignaudi* Frey *et al*., 2002. This species shows neither affinities to the European forms, nor to the ones known from the Americas (Frey *et al*., 2002). *G. vignaudi* represents the northernmost diagnostic Metriorhynchinae known to date in the Americas.

The vertebrae UANL-FCT-R11, R15, and R25 are not palaeobiogeographically significant. UANL-FCT-R11 comes from an animal of about 2.5 m in length, while R15, and R25 are referable to animals exceeding 3 m in length.

The specimens UANL-FCT-R16 and R17, which comprise caudal vertebrae, are from a metriorhynchid about 3 m long. It is highly likely that the skull fragment UANL-FCT-R13 also comes from a metriorhynchid, but further preparation is needed in order to decide whether it should be referred to *Geosaurus* or *Metriorhynchus*. The fragment clearly does not belong to *Dakosaurus*, because the teeth are subcircular in cross-section and not mesiolingually

Accession number	Identification	Formation	Stage	Locality	References; figure
UANL-FCT-R1	Thalattosuchia, Metriorhynchidae, holotype of *Geosaurus vignaudi*	La Casita	Tth	Near Mazatepec, Puebla	Frey *et al*. (2002)
UANL-FCT-R2	Plesiosauria, Pliosauridae indet. "The Monster of Aramberri"	La Caja	Kim	Aramberri, Nuevo León	Hähnel (1988); Buchy *et al*. (2003)
UANL-FCT-R3	Plesiosauria, Pliosauridae indet.	La Caja	Kim	Sierra El Montelongo Pedregoso, Nuevo León	
UANL-FCT-R5	Plesiosauria, Elasmosauridae indet.	La Caja	Kim	La Angostura, Nuevo León	fig. 8
UANL-FCT-R7	Plesiosauria Pliosauridae indet.	La Caja	Kim	La Angostura	fig. 9
UANL-FCT-R8	Plesiosauria Pliosauridae indet.	La Casita	Kim	El Salitre, near Zaragoza, Nuevo León	fig. 10
UANL-FCT-R11	Thalattosuchia indet.	La Caja	Kim	Aramberri, Nuevo León	
UANL-FCT-R12	Thalattosuchia, Teleosauridae indet.	La Casita	Kim	Iturbide, Nuevo León	fig. 6
UANL-FCT-R13	Thalattosuchia, Metriorhynchinae indet.	La Casita	Kim	Galeana or Iturbide, Nuevo León	
UANL-FCT-R15	Thalattosuchia indet.	La Casita	Kim	Galeana or Iturbide, Nuevo León	fig. 4
UANL-FCT-R16	Thalattosuchia, Metriorhynchinae indet.	La Casita	Kim	Galeana, Nuevo León	fig. 5a
UANL-FCT-R17	Thalattosuchia, Metriorhynchinae indet.	La Casita	Kim	Galeana, Nuevo León	fig. 5b
UANL-FCT-R18	Ichthyopterygia indet.	La Casita	Kim	Rio Pablillo, Nuevo León	fig. 7a
UANL-FCT-R19	Ichthyopterygia indet.	La Casita	Kim	Rio Pablillo, Nuevo León	fig. 7b
UANL-FCT-R20	Ichthyopterygia indet.	La Casita	Kim	San Lucas, Nuevo León	fig. 7c
UANL-FCT-R21	Ichthyopterygia indet.	La Caja	Kim	La Angostura, Nuevo León	fig. 7d
UANL-FCT-R22	Ichthyopterygia indet.	La Casita	Kim	2 km SE of San Lucas, Nuevo León	fig. 7e
UANL-FCT-R23	Ichthyopterygia indet.	La Casita	Kim	2 km SE of San Lucas, Nuevo León	fig. 7f
UANL-FCT-R25	Thalattosuchia indet.	La Casita	Kim	Galeana, Nuevo León	

Table 1 – Late Jurassic marine reptiles in the collections of the UANL-FCT. Abbreviations: Kim: Kimmeridgian; Tth: Tithonian.

compressed.

UANL-FCT-R12 is referable to the Teleosauridae. It represents the western-most certain occurrence of Teleosauridae, and contradicts the assumption that teleosaurids had a restricted dispersal area due to poor swimming capabilities (e.g. Vignaud, 1995; Hua, 1997). Instead, the dominance of the Metriorhynchidae over the Teleosauridae in open seas should be examined in the light of the proximity of available breeding grounds and possible differences in post-hatchling behavior, which may determine preferential living areas closer to the shoreline.

No specimen can be referred to the metriorhynchid genus *Dakosaurus* in the Upper Jurassic of Mexico. This genus is reported from the European archipelago and the south-western Gondwanan coast during the Upper Jurassic (Vignaud & Gasparini, 1996), and therefore may be expected to have been present in the Mexican Gulf.

Ichthyosaurs

During the Late Jurassic, six ichthyosaur genera are known, all grouped by Motani (1999) together with the Cretaceous ubiquitous genus *Platypterygius* within the clade Ophthalmosauria (the family Ophthalmosauridae of Appleby, 1956). *Brachypterygius* von Huene, 1922 was described from

England and Russia (McGowan, 1997; Arkhangelsky, 1998); *Ophthalmosaurus* Seeley, 1874b, from England, France, Russia, Argentina, and North America (Kirton, 1983; Bardet *et al*., 1997; Gasparini & Fernandez, 1997; Fernandez, 2003); *Caypullisaurus* Fernandez, 1997 is known only in Argentina (Fernandez, 1997, 1998); *Nannopterygius* von Huene, 1922, only in England; *Paraophthalmosaurus* Arkhangelsky, 1997, and *Otschevia* Efimov, 1998, only in Russia. The Mexican ichthyosaurs are far too incomplete to assign them to any of these genera, or even to the Ophthalmosauria. However, the likelihood that these fragmentary remains represent a new, hitherto unknown high taxonomic rank group of ichthyosaurs is very low. Further field excursions are necessary to determine whether their incompleteness and poor preservation can be related to a distant living area, or is due to collection bias.

Pliosaurs and plesiosaurs

While pliosaurs are abundant and well-known during the Late Jurassic in Europe (Tarlo, 1960; Persson, 1963; Bardet, 1992; 1995), they are rare from the eastern margin of the Pacific, and were unknown in Mexico until the correct identification of UANL-FCT-R2 (Buchy *et al.*, 2003). A fragmentary rostrum from the Tithonian of Argentina was doubtfully attributed to *Liopleurodon macromerus* by Gasparini *et al.* (1982). However, as was pointed out by Noè (2001), in the light of his unpublished revision of the genus *Liopleurodon* which he restricts to the Callovian, this identification should be reassessed. Moreover, Noè *et al*. (2004) provisionally placed *'Liopleurodon' macromerus* back to the genus *Pliosaurus*. Other fragments from the Tithonian of the same area are reported by Gasparini & Fernandez (1997) and Gasparini *et al.* (1997) as belonging to *Pliosaurus* sp. and to an indeterminate member of Pliosauridae.

The collections of the UANL-FCT therefore substantially increase our knowledge of Late Jurassic pliosaurs. The material is fragmentary, mainly composed of vertebrae and partial rostra. The vertebrae are of little taxonomic validity within the Family. However, they provide hints at the ontogenetic age of the specimens, and allow us to estimate the overall length of the animal, through cautious comparison with complete mounted skeletons in the IGPT.

UANL-FCT-R2 is a juvenile giant pliosaur whose length is estimated to have reached at least 15 m (Buchy *et al*., 2003). UANL-FCT-R7 would have reached approximately 10 m in length, and is also a juvenile individual, raising the question as to whether it could represent a younger individual of the same species. In crocodiles, the neurocorporal suture closes very late in ontogeny, still being visible in individuals having long reached sexual maturity (Frey, 1988; Brochu, 1996). Therefore, it is possible that two juveniles *sensu* Brown, 1981 of the same pliosaur species differ by 5 m in length, although, the sutural surface between the corpus and the neural arch in pliosaurs is not a serrated suture as in crocodiles (e.g. Brochu, 1996). Instead, in pliosaurs the surface of the neurocorporal suture exhibits shallow pitting and numerous foramina. The load on the neural arch mainly presses it ventrally against the corpus in life (Frey, 1988), and in crocodiles lateral and longitudinal sliding is additionally avoided by the serrated suture. In crocodiles therefore the neural arch is always firmly held to the corpus even without co-ossification. In pliosaurs, lateral sliding of the neural arch was not prevented by the interdigitating suture found in crocodiles. This may hint at the closure of the neurocorporal suture earlier in ontogeny than in crocodiles, especially when considering the rigid trunk of plesiosaurs. This situation should be the subject of a proper biomechanical analysis, but we note as a first comment that the plate-like girdles and the well-developed gastral basket in close contact with the ribs form a cage-like trunk suspended from the vertebral column. This would apply lateral and torque forces at the suspension point of the rib and girdle system, i.e. on the transverse processes and neural arches. Early fusion of the neural arches to the corpora, and of the ribs to the transverse processes, appear necessary to counter-act these dislocating forces.

UANL-FCT-R2 and R7 also differ in their vertebral anatomy. The caudal-most cervical corpora in UANL-FCT-R2 are longitudinally compressed, their length being less than half their width, with well-expressed lips. In UANL-FCT-R7 the width of the corpora is only about 1.5 times their length, with no lateral lip, and their lateral margins shallowly concave. The relative proportions of the corpora in Plesiosauroidea were shown by Brown (1981) to be independent from the ontogenetic stage of the specimen. If this is also the case for pliosaurs, then UANL-FCT-R2 and R7 represent two different taxa.

The rostral prolongation of the parietal in UANL-FCT-R3 was only previously known in the Lower Cretaceous pliosaur *Kronosaurus queenslandicus* (M.-C. B. and E. F. pers. obs.; McHenry pers. comm.). On the other hand, the straight lateral margins of the mandibular and maxillary rostra, the length of the mandibular rostrum housing more than 5 tooth positions, and the trihedral teeth covered with smooth enamel, indicate that this pliosaur is closely related to the European genus *Pliosaurus* (Tarlo, 1960; Noè, 2001; Noè *et al.*, 2004).

UANL-FCT-R8 is another partial rostrum, that needs further preparation. However, it cannot yet be assigned to any previously described taxon, and most likely also differs from UANL-FCT-R3. The teeth of UANL-FCT-R8 are less curved than those of UANL-FCT-R3, subcircular in cross-section until the apex, and at least the rostral-most ones have a mesial and a distal carina. The maxillary rostrum of UANL-FCT-R3 is semicircular in cross-section, whilst in UANL-FCT-R8 it is subtriangular.

Size and individual age estimation is problematical based on fragmentary rostra, as they vary in relative size and morphology between taxa. Concerning UANL-FCT-R8, the presumed associated vertebra indicates a 6 m long animal, which appears coherent with the width of the rostrum when

compared with other taxa.

The overall size of UANL-FCT-R3 is difficult to assess. Its rostrum is smaller than the rostrum of UANL-FCT-R8. Both rostra indicate subtriangular skulls in dorsal aspect without the spatulate symphyseal area found e.g. in *Simolestes* (Noè, 2001). Therefore UANL-FCT-R3 was probably an animal smaller than UANL-FCT-R8.

Altogether, at least three, and probably four, different pliosaurs are documented in the collections of the UANL-FCT, ranging in size from less than 6 m long adults, to 15 m long juveniles, with an intermediate size juvenile class reaching about 10 m in length. These animals appear large, compared to the common pliosaurs from the Late Jurassic of Europe, which was also noticed for eastern Pacific Tithonian pliosaurs (Gasparini & Fernandez, 1997). However, this is probably a bias due to poor preservation of large carcasses in European palaeoenvironments at that time, as isolated pliosaur vertebrae, of approximately the size of the vertebrae of UANL-FCT-R2 are known from there (McHenry *et al*., 1996). An estimated 3 m long mandible, which would be the estimated length of the mandible of UANL-FCT-R2, is preserved in the Oxford University Museum (Specimen OUM.J. 10454; Tarlo, 1959; Noè *et al*., 2004). Additionally, a 3 m long mandible was recently found in the Kimmeridge Bay (Etches, pers. comm.).

None of these pliosaurs can be referred with certainty to any previously described taxon. UANL-FCT-R7 is too incomplete for determination beyond Family level. The size of UANL-FCT-R2 itself probably distinguishes it from hitherto described taxa; unfortunately comparative material of similar size class from Europe is too fragmentary. Moreover, additional material is awaiting further preparation and excavation. UANL-FCT-R3 and R8 probably represent hitherto unknown taxa. The former shows affinities with both the Upper Jurassic *Pliosaurus*, and the Lower Cretaceous *Kronosaurus* (M.-C.B. and E.F. pers. obs.). The latter needs additional preparation to clarify its anatomy and relationships.

UANL-FCT-R5 represents the first elasmosaur remains from Mexico. As in the case of the ichthyosaurs, further exploration, especially of the more proximal facies of the La Casita / La Caja Formations, are necessary to give greater significance to this isolated find.

Remark on collection bias

Most of the vertebrate specimens in the UANL-FCT (including fish remains which are not discussed here) were collected during geological surveys of the La Casita and La Caja Formations by geologists and/or students. In practice, that means that at each outcrop, virtually every visible concretion is hammered open, whatever its size. Ammonites, which are common fossils, are only collected when complete or unknown, but any unusual structure is examined during the process, and every bone-bearing concretion is collected. Outcrops are regularly visited as part of the students' education.

Miners and locals also explore the outcrops in order to collect ammonites for trading. Vertebrate specimens are recognised as rare compared to ammonites, and usually kept as curiosities. This was the case for UANL-FCT-R8, or e.g. ichthyosaur vertebrae used as ash trays (W.S. pers. obs.). When the opportunity arises for safe compensation via an authorised official, additionally helped by a law dealing with national treasures, the fossils are transferred to the UANL-FCT, as witnessed by the numerous offers for diverse mammal remains and artefacts we encountered while digging for UANL-FCT-R2.

The apparent collection bias is a consequence of the absence of large-scale exploration in search of vertebrates, and might not be actually as high as it might appear on first glance. As collection is made, only visible fragments are collected, and no systematic exploration of the area is conducted for further bones of the same fossil. As in the case of UANL-FCT-R2 and R8, re-examination of the sites still yields additional bones years after the first collection. These collection "methods" result in incomplete specimens, however they correspond to a large-scale sampling of the outcrops. We shall not argue that the status of the collections of the UANL-FCT reflects a statistical sample of the marine reptiles from the Late Jurassic in north-eastern Mexico, but that it represents a first hint at the composition of the assemblage in the explored outcrops of La Casita and La Caja Formations.

Upper Jurassic invertebrate assemblages of north-eastern Mexico: palaeobiogeographic considerations

The time of the La Casita / La Caja Formation in north-eastern Mexico was characterised by block tectonic and sea level fluctuations, leading to an irregular sea floor and causing variable restrictions or subdivision of basins (e.g. Michalzik, 1988; Götte, 1990; Goldhammer, 1999; Goldhammer & Johnston, 2001). Connections with open seas or oceanic waters of the Pacific and Mediterranean Tethys appear to have been limited, leading to variable degrees of endemism (Salvador *et al*., 1993; Adatte *et al.*, 1994; 1996). With regard to ammonites, correlations with both the Andean and Mediterranean assemblages are tenuous and difficult to achieve. Ammonite populations and species can easily be distinguished from those of peri-Gondwanian, European and Mediterranean regions (Salvador *et al*., 1993).

For the Tithonian and early Berriasian, this endemism of the eastern and north-eastern Mexican assemblages is, in addition, indicated by microfossils. Mediterranean faunal elements such as *Saccocoma, Chitinoidella*, and calpionellid associations of the Crassicollaria-zone are characteristically missing in northern and north-eastern Mexico (Adatte *et al.*, 1994; 1996). This absence most likely results from a palaeogeographic barrier formed by the southward moving of Yucatan and uplift of the Florida Straits block (e.g. Pindell, 1985; Salvador, 1991; Hay & Wold, 1992). In eastern Mexico, the Mediterranean influence is slightly stronger, but consists only of short-

lived incursions of Mediterranean faunal elements. Direct and long-term faunal exchange and transatlantic correlation was not achieved until the middle Berriasian (calpionellid zones B and C), as indicated by the appearance in eastern Mexico of abundant calpionellid assemblages and typically Mediterranean ammonites (Adatte *et al*., 1994, 1996).

Tetrapod assemblage from the La Casita / La Caja Formations

The tetrapod assemblage from the La Casita / La Caja Formations mainly consists of pliosaurs and thalattosuchians. All sufficiently preserved specimens appear to be endemic, which confirms the aforementioned palaeobiogeographical conclusions drawn on the basis of invertebrate assemblages. In addition to pliosaurs and thalattosuchians, the La Casita / La Caja Formations in north-eastern Mexico yield a few fragmentary ichthyosaurs, and a single plesiosaur vertebra. No turtle remain have yet been found.

Ichthyosaurs are more abundant in the northern-most sites (Rio Pablillo, San Lucas, La Angostura, figs 1, 3; table 1), but they are also reported from pliosaur-yielding sites further to the south (Zaragoza; material in private collection, see UANL-FCT-R8). Thalattosuchians show the same trend becoming rare in the south, while all pliosaurs come from distal shelf localities south of La Angostura (fig. 3). However, the sample is for now too restricted to be sure that an ecological segregation actually exists.

A wider sample would be necessary in order to compare the La Casita / La Caja assemblage to the Late Jurassic assemblages in Europe (Arkhangelsky, 1997; 1998; Bardet, 1992; 1995; Broin, 1994; Efimov, 1998; Hua, 1997; Hua *et al*., 1998; Vignaud, 1993; 1995; and references therein; Mazin *et al*., unpublished data) and eastern Pacific margin (Fernandez, 1997; Gasparini & Fernandez, 1997; Gasparini *et al*. 1995; 2000; Vignaud & Gasparini, 1996). An attempt to quantify the proportions of the different types of marine reptiles in western Europe was made by Mazin *et al*. (unpublished data). These authors consider the proportions of valid species in assemblages, which might not be the most ecologically significant data set, compared, for example, to the respective abundance of each taxon. The proportion of valid species is not directly available for the La Casita / La Caja assemblage. With this restriction, according to their results, the La Casita / La Caja Formations yield an assemblage similar to the Oxford Clay (Martill *et al*., 1994), with a high diversity of pliosaurs and thalattosuchians, few ichthyosaurs, and no turtles, excluding the rarity of plesiosaurs.

Cryptodiran turtles are known in the Kimmeridgian of Kazakhstan and western Europe, and from the Tithonian of western Europe and Argentina (Bardet 1992; 1995; Broin, 1994; Gasparini & Fernandez, 1997). The pleurodiran *Notoemys* comes from the Tithonian of the Neuquén Basin, in Argentina, but its relationships remain obscure (Fernandez & Fuente, 1993; Gasparini & Fernandez, 1997). Probably, turtles did not reach Mexico by the Kimmeridgian, which would explain their absence from the La Casita / La Caja sediments. The association of turtles and thalattosuchians as a marker of lagoonal environments suggested by Mazin *et al*. (unpublished data) was contradicted by the off-shore assemblage yielding turtles and thalattosuchians described by Gasparini & Fernandez (1997) from Argentina. In the case of the La Casita / La Caja Formations, thalattosuchians, including the reputed coastal-most teleosaurids, are associated with supposedly off-shore pliosaurs and ichthyosaurs. Probably, the habits and dispersal capacity of thalattosuchians, mostly determined on the basis of their swimming capacity (see e.g. Hua, 1997), should also be examined under other aspects e.g. availability of breeding areas.

The La Casita / La Caja Formations represent a specific palaeoenvironment, yielding a marine reptile assemblage whose peculiarities will only be clarified by further studies and additional finds.

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REFERENCES

Adatte, T., Stinnesbeck, W. & Remane, J. 1994. The Jurassic-Cretaceous boundary in Northeastern Mexico. Confrontation and correlations by microfacies, clay

mineral mineralogy, calpionellids and ammonites. *Geobios*, 17: 37-56.

Adatte, T., Stinnesbeck, W., Remane, J. & Hubberten, H. 1996. Paleooceanographic change at the Jurassic-Cretaceous boundary in the western Tethys, northeastern Mexico. *Cretaceous Research*, 17: 671-689.

Appleby, R. M. 1956. The osteology and taxonomy of the fossil reptile *Ophthalmosaurus*. *Proceedings of the Zoological Society of London*, 126: 403-447.

Aranda-Manteca, F. & Stinnesbeck, W. 1993. Reptiles marinos del Jurásico Superior (Kimmeridgiano) del Noreste de Mexico. *Sociedad Mexicana de Paleontología. IV Congreso Nacional* (Oktober 1993), Tagungsheft, 15-16.

Arkhangelsky, M. S. 1997. On a new Ichthyosaurian genus from the Lower Volgian Substage of the Saratov, Volga Region. *Paleontological Journal*, 31 (1): 87-90.

Arkhangelsky, M. S. 1998. On the ichthyosaurian fossils from the Volgian Stage of the Saratov Region. *Paleontological Journal*, 32 (2): 192-196.

Bardet, N. 1992. Evolution et extinction des reptiles marins au cours du Mésozoïque. Unpublished Ph.D. thesis, Université Paris VI.

Bardet, N. 1995. Evolution et extinction des reptiles marins au cours du Mésozoïque. *Paleovertebrata*, 24 (3-4): 177-283.

Bardet, N. & Hua, S. 1996. *Simolestes novackianus* Huene, 1938 from the Upper Jurassic of Ethiopia is a teleosaurid crocodile, not a pliosaur. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 2: 65-71.

Bardet, N., Duffaud, S., Martin, M., Mazin, J.-M., Pereda Suberbiola, X. & Vidier J.-P. 1997. Découverte de l'ichthyosaure *Ophthalmosaurus* dans le Tithonien (Jurassique supérieur) du Boulonnais, Nord de la France. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 205 (3): 339-354.

Benton, M. J. & Clark, J. M. 1988. Archosaur phylogeny and the relationships of the Crocodylia; pp. 295-338. *In* Benton, M. J. (ed.) *The phylogeny and classification of the tetrapods, 1: Amphibians, reptiles, birds*. Systematics association, Sp. Vol. 35A.

Blainville, H. D. de 1835. Description de quelques espèces de reptiles de la Californie, précédée de l'analyse d'un système général d'erpétologie et d'amphibiologie. *Nouvelles Annales du Muséum d'Histoire naturelle de Paris*, série 3, 4: 233-296.

Brochu, C. A. 1996. Closure of neurocentral sutures during crocodilian ontogeny: implications for maturity assessment in fossil archosaurs. *Journal of Vertebrate Paleontology*, 16 (1): 49-62.

Broin, F. de 1994. Données préliminaires sur les chéloniens du Tithonien inférieur des calcaires lithographiques de Canjuers (Var, France). *Geobios*, 16: 167-175.

Brown, D. S. 1981. The English Upper Jurassic Plesiosauroidea (Reptilia) and a review of the phylogeny and classification of the Plesiosauria. *Bulletin of the British Museum (Natural History), Geology*, 35 (4): 253-347.

Buchy, M.-C., Frey, E., Stinnesbeck, W. & López-Oliva, J. G. 2003. First occurrence of a gigantic pliosaurid plesiosaur in the Late Jurassic (Kimmeridgian) of Mexico. *Bulletin de la Société géologique de France*, 174 (3): 271-278.

Burckhardt, C. 1906. La faune Jurassique de Mazapil avec un appendice sur les fossiles du Crétacique inférieur. *Boletin del Instituto Geológico de México*, 23: 1-216.

Burckhardt, C. 1930. Etude synthétique sur le Mésozoïque Mexicain. *Société Paléontologique Suisse, Mémoires*, 49-50: 280.

Cantú-Chapa, A. 1963. Etude biostratigraphique des ammonites du centre et de l'est du Mexique. *Société géologique de France, Mémoire,* n.s. 99: 5-100.

Cantú-Chapa, A. 1968. Sobre una asociación "*Proniceras* - *Durangites* - "*Hildoglochiceras*", del Noreste de México. *Instituto Mexicano del Petróleo, Sección geológica, Monografia,* 2: 19-26.

Cantú-Chapa, A. 1971. La Serie Huasteca (Jurásico Medio -Superior) del Centro-Este de México. *Revista del Instituto Mexicano del Petróleo*, 3 (2): 17-40.

Castillo, A. D. & Aguilera, J. G. 1895. Fauna fósil de la Sierrade Catorce, San Luis Potosi. *Boletin del Instituto de Geología* 1: 1-56, 24 plates.

Cope, E.D. 1869. Synopsis of the extinct Batrachia and Reptilia of North America. *Transactions of the American Philosophical Society*, 14: 1-252.

Cuvier, G. 1824. Sur les ossements fossiles de crocodiles; pp. 143-160. *In Recherche sur les ossemens fossiles*, 2e édition, vol. 5 (2). Dufour & D'Occagne, Paris.

Efimov, V. M. 1998. An ichthyosaur, *Otschevia pseudoscythica* gen. et sp. nov. from the Upper Jurassic strata of the Ulyanovsk Region (Volga Region). *Paleontological Journal*, 32 (2): 187-191.

Fernández, M. S. 1997. A new ichthyosaur from the Tithonian (Late Jurassic) of the Neuquen Basin, northwestern Patagonia, Argentina. *Journal of Paleontology*, 71 (3): 479-484.

Fernández, M. S. & Fuente, M. S. de la 1993. Las tortugas casiquelidias de las calizas litográficas del area Los Catutos, Neuquén, Argentina. *Ameghiniana*, 30 (3): 283-295.

Fernández, M. S. 1998. Nuevo material de *Caypullisaurus bonapartei* Fernández (Reptilia: Ichthyosauridae) del Jurasico de la Cuenca Neuquina, Argentina. *Ameghiniana*, 35 (1): 21-24.

Fernández, M. S. 2003. Ophthalmosauria (Ichthyosauria) forefin from the Aalenian-Bajocian boundary of Mendoza Province, Argentina. *Journal of Vertebrate Paleontology*, 23 (3): 691-694.

Fitzinger, L. 1843. *Systema Reptilium*. Braumüller & Seidel, Wien.

Fraas, E. 1901. Die Meerkrokodile (Thalattosuchia n.g.) eine Sauriergruppe der Juraformation. *Jahreshefte des*

Vereins für vaterländische Naturkunde Württemberg, 57: 409-418.

Frey, E. 1988. Anatomie des Körperstammes von *Alligator mississipiensis* Daudin. *Stuttgarter Beiträge für Naturkunde, Serie A*, 424: 1-106.

Frey, E., Buchy, M.-C., Stinnesbeck, W. & López-Oliva, J. G. 2002. *Geosaurus vignaudi* n.sp. (Crocodylia, Thalattosuchia), first evidence of metriorhynchid crocodilians in the late Jurassic (Tithonian) of central-east Mexico (State of Puebla). *Canadian Journal of Earth Sciences*, 39 (10): 1467-1483.

Gasparini, Z. & Fernández, M. S. 1997. Tithonian marine reptiles of the Eastern Pacific; pp. 435-450. *In* Callaway, J. M. & Nicholls, E. L. (eds.) *Ancient Marine Reptiles.* Academic Press, San Diego.

Gasparini, Z., Fuente, M. S. de la & Fernandez, M. S. 1995. Sea reptiles from the lithographic limestones of the Neuquen Basin, Argentina. *II International Symposium on Lithographic Limestones, 9-16 july 1995, Abstracts*, 81-84.

Gasparini, Z., Goñi, R. & Molina, O. 1982. Un plesiosaurio (Reptilia) tithoniano de Cerro Lotena, Neuquen, Argentina. *V Congreso Latinoamericano de Geologia, Argentina*, 5: 33-47.

Gasparini, Z., Spalletti, L. & Fuente, M. S. de la 1997. Tithonian marine reptiles of the Western Neuquen Basin, Argentina. Facies and palaeoenvironments. *Geobios*, 30 (5): 701-712.

Gasparini, Z., Vignaud, P. & Chong, G. 2000. The Jurassic Thalattosuchia (Crocodyliformes) of Chile: a paleobiogeographic approach. *Bulletin de la Société géologique de France*, 171 (6): 657-664.

Geoffroy Saint-Hilaire, E. 1825. Recherche sur l'organisation des gavials, sur leurs affinités naturelles desquelles résulte la nécessité d'une autre distribution générique: *Gavialis*, *Teleosaurus*, *Steneosaurus*. *Mémoire du Muséum National d'Histoire Naturelle, Paris*, 12: 97-155.

Geoffroy Saint-Hilaire, E. 1831. Recherche sur de grands sauriens trouvés à l'état fossile aux confins maritimes de la Basse-Normandie, attribués d'abord au Crocodile, puis déterminés sous les noms de *Teleosaurus* et *Steneosaurus*; pp. 1-138. Firmin Didot (ed.), *Mémoire de l'Académie des Sciences*. Paris.

Goldhammer, R. K. 1999. Mesozoic sequence stratigraphy and paleogeographic evolution of north east Mexico; pp. 1-31. *In* Bartolini, C., Wilson, J. L. & Lawton, T. F. (eds.) *Sedimentary and tectonic history of north central Mexico*. *Geological Society of America, Special Papers,* 340.

Goldhammer, R. K. & Johnson, C. A. 2001. Middle Jurassic – Upper Cretaceous Paleogeographic Evolution and Sequence-stratigraphic Framework of the Northwest Gulf of Mexico Rim., pp. 45-82. *In* Bartolini, C, Buffler, R. T. & Cantú-Chapa, A. (eds.) *The Western Gulf of Mexico Basin – Tectonics, Sedimentary Basins, and Petroleum Systems*. American Association of Petroleum Geologists, Memoir 75.

Götte, M. 1990. Halotektonische Deformationsprozesse in Sulfatgesteinen der Minas-Viejas-Formation (Ober-Jura) in der Sierra Madre Oriental, Nordost-Mexiko. Unpublished Ph.D. thesis, University of Darmstadt.

Hähnel, W. 1988. Hallazgo de restos de dinosaurio en Aramberri, N.L., Mexico. *Actas Faculta Ciencias Tierra UANL Linares*, 3: 245-250.

Hay, B. U. & Wold, CH. N. 1992. The fit of North America, Africa and South America about the site of the future Gulf of Mexico and Caribbean. *VII Congreso Latinoamericano de Geología, Salamanca 1992*. Actas tomo 4: 122-126.

Hua, S. 1997. Adaptations des crocodiliens mésosuchiens au milieu marin. Unpublished Ph.D. thesis, Université Paris VI.

Hua, S., Vignaud, P. & Efimov, V. 1998. First record of Metriorhynchidae (Crocodylomorpha, Mesosuchia) in the Upper Jurassic of Russia. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 1998 (8): 475-484.

Huene, F. v. 1922. Die Ichthyosaurier des Lias und ihre Zusammenhänge. *4. Jahresversammlung der paläontologischen Gesellschaft*, Bornträger, Berlin.

Huene, F. v. 1938. Ein Pliosauride aus Abessinien. *Zentralblatt für Mineralogie, Geologie, Paläontologie, B*, 1938 (10): 370-376.

Imlay, R. W. 1939. Upper Jurassic ammonites from Mexico. *Geological Society of America Bulletin*, 50: 1-78.

Imlay, R. W. 1984. Jurassic ammonite successions in North America and biogeographic implications; pp. 1-12. *In* Westermann, G. E. G. (ed.) *Jurassic-Cretaceous Biochronology and Paleogeography of North America. Geological Association of Canada, Special Papers,* 27.

Kälin, J. 1955. Crocodilia; pp. 695-784. *In* Piveteau J. (ed.) *Traité de Paléontologie,* 5. Masson, Paris.

Kirton, A. M. 1983. A review of British Upper Jurassic ichthyosaurs. Unpublished Ph.D. dissertation, University of Newcastle-upon-Tyne.

Martill, D. M., Taylor, M. A., Duff, K. L., Riding, J. B. & Bown, P. R. 1994. The trophic structure of the biota of the Peterborough Member, Oxford Clay Formation (Jurassic), UK. *Journal of the Geological Society of London*, 151: 173-194.

McGowan, C. 1997. The taxonomic status of the Late Jurassic ichthyosaur *Grendelius mordax*: a preliminary report. *Journal of Vertebrate Paleontology*, 17: 428-430.

McHenry, C., Martill, D. M., Noè, L. F. & Cruickshank, A. R. I. 1996. Just when you thought it was safe to go back in the water - the biggest pliosaur yet. *Palaeontological Association Meeting Abstracts 1996 (Birmingham)*.

Meyer, H. v. 1830. Achte Versammlung der Naturforscher und Ärzte zu Heidelberg im September 1829. *Isis v.*

Oken B. Mineralogische Abteilung, 15 (2) 4/5/6: 517-519.

Meyer, H. v. 1837. Mittheilungen, an Professor Bronn gerichtet. *Neues Jahrbuch für Geognosie, Geologie und Petrefakten*, 4: 413-418.

Michalzik, D. 1988. Trias bis tiefste Unter-Kreide der nordöstlichen Sierra Madre Oriental, Mexiko. Inaugural-Dissertation TH-Darmstadt.

Motani, R. 1999. Phylogeny of the Ichthyopterygia. *Journal of Vertebrate Paleontology*, 19 (3): 473-496.

Noè, L. F. 2001. A taxonomic and functional study of the Callovian (Middle Jurassic) Pliosauroidea (Reptilia, Sauropterygia). Unpublished Ph.D. thesis, University of Derby.

Noè, L. F., Smith, D. T. J. & Walton, D. I. 2004. A new species of Kimmeridgian pliosaur (Reptilia; Sauropterygia) and its bearing on the nomenclature of *Liopleurodon macromerus*. *Proceedings of the Geologists' Association*, 115: 13-24.

Olóriz, F., Villaseñor, A. B., González-Arreola, C. & Westermann, G. E. G. 1999. Ammonite biostratigraphy and correlations in the Upper Jurassic-Lowermost Cretaceous La Caja Formation of North-Central Mexico (Sierra de Catorce, San Luis Potosí). *Advancing Research on Living and Fossil Cephalopods*: 463-492.

Owen, R. 1860. On the orders of fossil and recent Reptilia, and their distributions in time. *Report of the British Association for the Advancement of Science,* 29: 153-166.

Persson, P. O. 1963. A revision of the classification of the Plesiosauria, with a synopsis of the stratigraphical and geographical distribution of the group. *Lunds Universitets Arsskrift, N.F. Avd. 2*, 59: 1-59.

Pindell, J. L. 1985. Alleghinian reconstruction and subsequent evolution of the Gulf of Mexico, Bahamas and Proto-Caribbean. *Tectonics*, 4 (1): 1-39.

Quenstedt, F. A. 1856. *Sonst und Jetzt, Populäre Vorträge über Geologie von F.A. Quenstedt*, 8: 1-288, 1 pl. Laupp, Tübingen..

Salvador, A. 1991. Triassic-Jurassic; pp. 131-180. *In* Salvador, A. (ed.) *The Gulf of Mexico basin*. Geological Society of America, Boulder, Colorado.

Salvador, A., Westermann, G. E. G., Olóriz, F., Gordon, M. B. & Gursky, H. J. 1993. Meso-America; pp. 93-121. *In* Westermann, G.E.G. (ed.) *The Jurassic of the Circum-Pacific. World and Regional Geology 3*, Cambridge University Press, Cambridge.

Schumann, D. 1988. Observaciones paleoecológicas en secuencias del Kimmeridgiano / Tithoniano (Formación La Casita) de Nuevo León, Noreste de México. *Actas de la Facultad de Ciencias de la Tierra, U.A.N.L.*, 3: 43-59.

Seeley, H. G. 1874a. Note on some of the generic modifications of the plesiosaurian pectoral arch. *Quarterly Journal of the Geological Society of London,* 30: 436-449.

Seeley, H. G. 1874b. On the pectoral arch and fore-limb of *Ophthalmosaurus*, a new ichthyosaurian genus from the Oxford Clay. *Quarterly Journal of the Geological Society of London,* 30: 699-707.

Smith, A. G., Smith, D. G. & Funnel, B. M. 1994. *Atlas of Mesozoic and Cenozoic coastlines*. Cambridge University Press, Cambridge.

Tarlo, L. B. 1959. *Stretosaurus* gen. nov., a giant pliosaur from the Kimeridge Clay. *Palaeontology*, 2 (1): 39-55.

Tarlo, L. B. 1960. A review of Upper Jurassic Pliosaurs. *Bulletin of the British Museum of Natural History, Geology*, 4 (5): 145-189.

Verma, H. M. & Westermann, G. E. G. 1973. The Tithonian (Jurassic) ammonite fauna and stratigraphy of Sierra Catorce, San Luis Potosi, Mexico. *Bulletin of American Paleontology*, 63 (277): 107-320.

Vignaud, P. 1993. Thalattosuchians from the Callovian of Poitou (Vienne, France). *Revue de Paléobiologie*, vol. spec. 7: 251-261.

Vignaud, P. 1995. Les Thalattosuchia, crocodiles marins du Mésozoïque: systématique phylogénétique, paléoécologie, biochronologie et implications paléogéographiques. Unpublished Ph.D. thesis, Université de Poitiers.

Vignaud, P. 1998. Une nouvelle espèce de *Steneosaurus* (Thalattosuchia, Teleosauridae) dans le Callovien du Poitou (France) et la systématique des *Steneosaurus* longirostres du Jurassique moyen d'Europe Occidentale. *Paleovertebrata*, 27 (1-2): 19-44.

Vignaud, P. & Gasparini, Z. 1996. *Dakosaurus andiniensis* n.sp. (Crocodylia, Thalattosuchia), first record of *Dakosaurus* in the Upper Jurassic of Argentina. *Comptes Rendus de l'Académie des Sciences de Paris*, 322, série IIa: 245-250.

Villaseñor, A. B., Olóriz, F. & González-Arreola, C. 2000. Recent Advances in Upper Jurassic (Kimmeridgian – Tithonian) Ammonite Biostratigraphy of North-Central Mexico based on Recently Collected Ammonite Assemblages. *GeoResearch Forum,* 6: 249-262.

Welles, S. P. 1943. Elasmosaurid plesiosaurs with a description of new material from California and Colorado. *Memoirs, University of California*, 13 (3): 125-215.

Whetstone, K. N. & Whybrow, P. 1983. A cursorial crocodilian from the Triassic of Lesotho (Basutoland), South Africa. *Occasional Papers of the University of Kansas*, 106: 1-37.

Wilson, J. W. 1990. Basement structural controls on Mesozoic carbonate facies in northeastern Mexico - A review; pp. 235-255. *In* Tucker, M., Wilson, J. W., Crevello, P. D., Sarg, J. F. & Read, J. F. (eds.) *Carbonate platforms, facies, sequences and evolution; International Association of Sedimentologists Special Publication* 9.