Mesozoic marine reptiles from north-east Mexico: description, systematics, assemblages and palaeobiogeography

Mesozoische marine Reptilien aus Nordostmexiko: Beschreibung, Systematik, Vergesellschaftung und Paläobiogeografie

Dissertation

von

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Die Prüfung wurde bestanden mit der Note 1 (sehr gut)

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Sterhand pey

Priv. Doz. Dr. Eberhard Frey

Hiermit erkläre ich, dass ich die vorgelegte Dissertation selbst verfasst und mich keiner anderen als der von mir ausdrücklich bezeichneten Quellen und Hilfen bedient habe. Alle verwendeten Zitate sind gekennzeichnet und im Literaturverzeichnis angegeben.

Saltillo, den 5. April 2007

Marie-Céline Buchy

Mhiel-

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Abstract

Abstract

The result of six years of examination of marine reptiles from north-east Mexico is presented here. The area yielded specimens from both the Late Jurassic and Late Cretaceous. For a region where few, undescribed forms were known, the process yielded several new taxa, and a variety of forms, most of which await preparation, composing rich, hitherto non documented assemblages.

At present the assemblage of Late Jurassic Mexican Gulf marine reptiles comprises pliosaurs, thalattosuchians, ichthyosaurs and few plesiosaur remains; no turtle remain was discovered yet. All proceed from the La Caja / La Casita / La Pimienta Formations (Kimmeridgian to Tithonian). Except for the ubiquitous ichthyosaur *Ophthalmosaurus icenicus*, many specimens, even uncomplete, differ from coeval forms and appear to confirm the partial isolation of the area that was previously deduced from invertebrates and microfossils.

During the Cretaceous, the Mexican Gulf connects to both the Western Interior Seaway and the Atlantic Ocean. Late Cretaceous marine reptiles from north-east Mexico come from the Late Turonian to early Coniacian Austin Group at Múzquiz, Coahuila, a promising locality from where few specimens are available for study at present; the Campanian-Maastrichtian Méndez Formation in Nuevo León yielded few mosasaurid occurrences; most specimens at present proceed from the Early Turonian Agua Nueva Formation at Vallecillo, Nuevo León. From Vallecillo is known the only pliosaur remain from the Mexican Late Cretaceous, a partial tooth attributed to *Polyptychodon*, and several basal mosasauroids. These were discovered recently and no taxonomical frame is available at present, but preservation is usually excellent, including soft parts, and it is expected their study will greatly increase our knowledge of the group.

Kurzfassung

Kurzfassung

Die vorliegende Dissertation fasst sechs Jahre Untersuchungen an den mesozoischen Meeresreptilien Nordostmexikos zusammen. Die Gegend lieferte Stücke aus von der Oberjura- bis in die Oberkreide hinein. Für eine Region, in welcher nur wenige unbeschriebene Formen bekannt waren, förderte die Arbeit diverse neue Taxa und eine Vielzahl verschiedener Formen zu Tage, von denen viele noch präpariert werden müssen und die bislang nicht bekannte Vergesellschaftungen repräsentieren.

Nach bisherigem Stand der Kenntins umfasst die Vergesellschaftung von Meeresreptilien aus dem spätjurassische mexikaischen Golf Pliosaurier, Thalattosuchier, Ichthyosaurier und eineige wenige Reste von Plesiosauriern; bislang sind keine marine Schildkrötenreste bekannt. Alle Stücke stammen aus der La Caja-, La Casita- oder der La Pimienta-Formation (Kimmeridgium bis Tithonium). Ausser dem kosmopolitischen Ichthyosaurier *Ophthalmosaurus icenicus* untescheiden sich viele Stücke, auch die unvollständigen, von zeitgleichen Formen anderswo und scheinen eine mindestens teilweise Isolation der Region zu belegen, was aufgrund der Invertebraten und Mikrofossilen bereits vermutet wurde.

Während der Kreidezeit verband der mexikanische Golf den Western Interior Seaway mit dem Atlantik. Spätkretazische Meeresreptilien aus Nordostmexiko reichen zeitlich vomm späten Turonium bis ins frühe Coniacium der Austin-Gruppe bei Múzquiz, Coahuila, einer vielversprechenden Fundregion, von welcher nur wenige Stücke bisher für Untersuchungen zur Verfügung stehen. Die Méndez-Formation (Campanium bis Maastrichtium) in Nuevo León lieferte einige Hinweise auf Mosasaurier; die meisten Stücke jedoch stammen aus der frühturonischen Aqua Nueva-Formation bei Vallecillo, Nuevo León. In den Steinbrüchen bei Vallecillo wurde auch der erste Pliosaurierrest aus der Oberkreide Mexikos gefunden, ein Zahnfragment, welches *Polyptychodon* zugeordnet wird, sowie einige basale Mosasauroiden. Diese wurden erst kürzlich geborgen, weshalb noch keine taxonomische Bewertung vorliegt, aber die Erhaltung ist üblicherweise ausgezeichnet, einschließlich der Weichteile. Es ist zu erwarten, dass das Studium dieser Stücke, die Kenntnis der Gruppe wesentlich verbessern wird.

Resumen

Resumen

Se presentan los resultados de seis años de trabajo sobre los reptiles marinos del Noreste de México. El área proporcionó especímenes del Jurásico superior y del Cretácico superior. En una región donde se conocían pocas formas, aún no descritas, esta investigación reveló varios taxones nuevos y múltiples formas - la mayoría aún por restaurar - constituyendo conjuntos faunísticos muy diversificados, que no habían sido registrados hasta la fecha.

Actualmente, la asociación de reptiles marinos del Jurásico superior del Golfo de México incluye pliosaurios, talatosuquios, ictiosaurios y algunos restos de plesiosaurios; hasta la fecha, no se ha encontrado ningún resto de tortuga marina. Todo el material procede de las Formaciones La Caja / La Casita / La Pimienta (del Kimmeridgiano al Tithoniano). Salvo el caso del ictiosaurio cosmopólito *Ophthalmosaurus icenicus*, muchos especímenes, aún incompletos, difieren de otras formas coetáneas, lo cual parece confirmar el aislamiento parcial de la región previamente deducido de los invertebrados y microfósiles.

Durante el Cretácico, el Golfo de México conecta el Mar Interior Occidental con el Océano Atlántico. Reptiles marinos del Cretácico superior del noreste de México provienen del Turoniano tardío - Coniaciano temprano del Grupo Austin observable en Múzquiz (Coahuila), una localidad prometedora, de la cual pocos especímenes son disponibles por el momento. La Formación Méndez (Nuevo León), de edad Campaniano-Maastrichtiano ha proporcionado pocos restos de mosasauridos; actualmente, la mayoría de los especímenes proceden del Turoniano temprano de la Formación Agua Nueva, en Vallecillo (Nuevo León). De esta misma localidad de Vallecillo, se conoce la única evidencia de pliosaurio para el Cretácico superior de México - un diente incompleto atribuido a *Polyptychodon* - así como varios mosasauroidos basales, los cuales han sido descubierto recientemente. Ningún marco taxonómico está actualmente disponible para precisar su posición sistemática; sin embargo, su preservación es generalmente excelente e incluye partes blandas. Se puede esperar que el estudio de estos mosasauroidos incrementará considerablemente nuestros conocimientos acerca de este grupo.

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Abbreviations

Abbreviations

Institutions

IGPT : Geological Institute in Tübingen, Germany; MUDE: Museo del Desierto, Saltillo (Coahuila, Mexico); MHM: Museo Historico de Múzquiz, Múzquiz (Coahuila, Mexico); SMNK: Staatliches Museum für Naturkunde (Karlsruhe, Germany); UANL-FCT: Universidad Autónoma de Nuevo León, Facultad de Ciencias de la Tierra, Linares (Nuevo León, Mexico); UNAM: Universidad Nacional Autónoma de México, México, D.F.

Accession numbers

CPC: Colección Paleontológica de Coahuila, MUDE.

Anatomical abbreviations

a: angular; as: astragalus; atax: atlas/axis; ce: centrale; cor: coracoid; cv: cervical vertebra; d: dentary; dic: distal carpal; dit: distal tarsal; dt: dentary tooth; en: external nare; eo: exoccipitalopisthotic; epf: epipterygoid facet; f: frontal; h: humerus; ha: haemal arch; i: intermedium; j:jugal; l: lachrymal; mc: metacarpal; ms: mandibular symphysis; mt: metatarsal; mx: maxillary; mxt: maxillary tooth; n: nasal; na: neural arch; o: orbit; paf: parietal foramen; pal: palatine; par: parietal; ph: phalanx; pmx: premaxillary; pmxs: premaxillomaxillary suture; pmxt: premaxillary tooth; po: postorbital; pof: postfrontal; poz: postzygapophysis; pp: paroccipital process; prf: prefrontal; pro: prootic; prz: prezygapophysis; pt: pterygoid; Q1: first caudal vertebra; qj: quadratojugal; qrpt: quadrate ramus of the pterygoid; qrsq: quadrate ramus of the squamosal; R: radius; r: rib; rc: rostral cavity; re: radiale; s1: first sacral vertebra; s2: second sacral vertebra; sa: surangular; sc: scapula; sf: supraoccipital facet; spl: splenial; sq: squamosal; st: supratemporal; T: tibia; tp: transverse process; tr: tooth root; ut: upper tooth; v: vomer.

I-V: digits I to V.

Introduction

Introduction

Six years ago, very little was known about Mexican diapsid marine reptiles: Wieland (1910) named the taxon *Plesiosaurus* (*Polyptychodon*) *mexicanus* from the Lower Cretaceous of south Mexico upon a portion of rostrum. This holotype was recently located in the collections of the UNAM (Perrilliat Montoya, pers. com., 2007); it was briefly mentioned and considered non diagnostic by Welles (1962). The mosasaur *Amphekepubis johnsoni* (University of Missouri 509VP) was described by Mehl (1930) from the Upper Cretaceous of the Monterrey region (figs 1, 2); the holotype is now considered a pathological member of the genus *Mosasaurus* (Camp, 1942; Lingham-Soliar, 1995). An undetermined thalattosuchian was mentioned from the Callovian of Mexico by Gasparini (1992). None of the preliminarily descriptions of specimens in the frame of geological studies had made its way into marine reptiles students' literature (Michalzik, 1988; Schumann, 1988; Götte, 1990; Aranda-Manteca & Stinnesbeck, 1995; compare with e.g. Bardet, 1995; Vignaud, 1995).

The year 2000 opened a new chapter for north-east Mexican marine reptiles, when examination of the collections of the UANL-FCT by E. Frey (SMNK) and the author revealed the existence of a new thalattosuchian (Frey *et al.*, 2002; specimen UANL-FCT-R1, chapter I.2.1), and the remains of a giant pliosaur previously thought to be a dinosaur were properly identified (Hähnel, 1988; Buchy *et al.*, 2003; specimen UANL-FCT-R2, nicknamed The Monster of Aramberri, chapter I.2.3). The recovery of the rest of the skeleton of this specimen was the aim of several field campaigns financed by the DFG, that yielded remains of many other fossil reptiles, and the present catalogue of an exceedingly rich region for both Upper Jurassic and Upper Cretaceous fossil marine reptiles.

The area considered in this work encompasses the states of Nuevo León and Coahuila (figs 1, 2; except one specimen from Puebla state, Frey *et al.*, 2002), in the frame of a collaboration between the Universidad Autónoma de Nuevo León, Facultad de Ciencias de la Tierra, Linares (Nuevo León), the Museo del Desierto, Saltillo (Coahuila), the Universität Karlsruhe (TH) and the Staatliches Museum für Naturkunde Karlsruhe.

In what is now north-east Mexico the Laramide orogeny folded the Mesozoic sediments during the latest Cretaceous - early Paleogene. The resulting Sierra Madre Oriental divides north-east Mexico along a north-west to south-east axis into a continental desert westward and a coastal plain eastward (fig. 1). Outcropping Upper Jurassic and Upper Cretaceous sediments (and marine reptiles) are usually found as a result of mining activities in the Sierra Madre.

2



Figure 1: Schematic map of geographical regions of north-east Mexico (redrawn from Urrutia Fucugauchi *et al.*, 2003).

Mesozoic sediments of north-east Mexico document a gradual transgression linked with the opening of the Gulf of Mexico (e.g. Michalzick, 1988; Götte, 1990; Ifrim, 2006; fig. 3), starting during the Oxfordian with the evaporites of the Minas Viejas Formation. The overlying limestones of the Zuloaga Formation, deposited in shallow waters of a carbonate ramp, did not yet yield marine reptiles. Upsection, La Caja and contemporaneous La Casita (and equivalent La Pimienta) Formations, that yielded all Upper Jurassic marine reptiles described here, indicate deepening and increased terrigenous influences. Overlying Cretaceous units document pelagic, open marine environments.



Figure 2: Geographical map of north-east Mexico. SEIMP: Sierra El Montelongo Pedregoso.



Figure 3: Lithostratigraphical column of the Mesozoic in north-east Mexico (redrawn from Michalzick, 1988 and Götte, 1990).

Facing the local richness of to-be-prepared, new specimens, priorities were set, according to available time, money and space, which is of course far from ideal, but yielded a (hopefully) good preliminary overview of the various taxa. This volume represents the current status of this process, promising of what should be expected when further explorations and preparations are conducted. It is necessarily uncomplete, mainly focussing upon the Kimmeridgian/Tithonian La Casita/La Caja Formations and material from the Upper Cretaceous in official institutions (material in private collections was ignored, mostly because time was too short to check the presumed localities). Descriptions and aligned palaeobiogeographical conclusions were published as work was progressing (Frey et al., 2002; Buchy et al., 2003, 2004, 2005b, c, 2006b-e, 2007, in press; Buchy & Smith, 2005; Smith & Buchy, submitted). Work being still in progress, also upon local geology, detailed stratigraphical correlations are not available yet for most of the mentioned specimens, and therefore neither are detailed stratigraphical comparisons with possibly coeval occurrences. Though, anatomical comparisons were drawn when the available elements made it possible. In such a preliminary frame, it is also not the place here to draw definitive phylogenetic conclusions upon the affinities of the Mexican forms (most being too incomplete). For all groups dealt with here, cladistic analyses are few and/or yielding results revitalsing former blurred taxonomies (in the case of Plesiosauria), hotly debated relationships (for squamates) or only mention the group on the basis of outdated, second-hand data (typically, studies dealing with Thalattosuchia). Possibly, this has to do with a long-shadowed history of marine reptiles (Taylor, 1997), a poor understanding of the transition from terrestrial to marine life outside general trends, together with and as a consequence of poor potential for fossilisation of intermediate environments (Storrs, 1999). This also most likely has to do with the current, quasi exclusive cladistic approach to phylogeny. Groups dealt with here (Plesiosauria, Mosasauroidea, Thalattosuchia) all exhibit a very conservative anatomy of the locomotor apparatus (once it has been modified according to an aquatic life style), but also of the cranium. A high degree of homoplasy is most likely to be expected, while characters used in current cladistic analyses are rarely considered in a functional perspective that only could reveal possible convergence in relation to biomechanics, physiology, feeding behavior, etc. in an obligatory aquatic environment (see e.g. the recent suggestion by Bell & Polcyn, 2005 and Polcyn & Bell, 2005, that a fin-like limb developped at least twice within Mosasauroidea). This makes relationships both with potential terrestrial ancestors and within the group a riddle. It can therefore even not be mentioned that the current taxonomical status within a cladistic hypothesis of relationships of the groups dealt with here is ignored, as there is no current, generally accepted taxonomical status. Traditional, ranked taxonomy is followed, in order to allow future researchers to place the described specimens within a hopefully soon renewed, better understood frame.

The term 'marine reptile' is often thought of as a shortcut for 'reptile who lives in the sea', as does 'marine mammal'. Though, in the case of fossils, the 'who lives' dimension is missing, and the concept slids towards results of an often implicit biomechanical analysis of locomotory abilities of the considered taxon, in the frame of palaeogeographical finding location. 'Who lives' therefore becomes 'who swam' - in a more or less open former sea, while in an ecological perspective, 'marine' implies the ability to deal with excess salt in order to take part occasionally or obligatorily to marine trophic webs (Hua & Buffetaut, 1997). Salt glands or clear hints at their presence are rarely preserved in fossils (Fernandez & Gasparini, 2000; Gandola *et al.*, 2006; Buchy *et al.*, in press); although it is well conceived that this choice is reductionist (excluding at least some birds and pterosaurs), the definition adopted here of a diapsid marine reptile follows palaeontology text books, and includes Plesiosauria, Thalattosuchia and Mosasauroidea.

Part I. Upper Jurassic La Casita / La Caja Fm

I.1. Palaeogeographical context

The depositional context of the La Casita and La Caja Formations in north-east Mexico was summed up by Buchy *et al.* (2003, 2006d, c). The former represents deltaic and inner shelf environments, the latter more distal settings; both span from Kimmeridgian to Berriasian. Both were deposited at a time when regional tectonics caused an irregular sea floor; inner and outer shelf facies were further affected by sea level variations and consequently, a basinal context (e.g. Michalzik, 1988; Götte, 1990; Goldhammer, 1999; Goldhammer & Johnston, 2001).

Although classical palaeogeographical reconstructions exclude a direct relation between European and Pacific provinces before the Upper Jurassic, comparison of marine assemblages does support the existence of a Carribean corridor since at least the Middle Jurassic (e.g. Gasparini & Fernández, 1997, 2005; Gasparini *et al.*, 2000; Fernández & Iturralde-Vinent, 2000; Gasparini & Iturralde-Vinent, 2001; Gasparini *et al.*, 2002). By the Late Jurassic, though, connections between Tethyan and Pacific realms are established and continuous (e.g. Smith *et al.*, 1994). However, microfossils and invertebrates indicate at least partial isolation of the Mexican Gulf until the Middle Berriasian (Salvador *et al.*, 1993; Adatte *et al.*, 1994; 1996). Southward moving of Yucatan and uplifting of the Florida Strait have been proposed as possible cause for the isolation, that appears to affect as well marine reptiles (Buchy *et al.*, 2006d).

I.2. Catalogue of specimens

An annotated list of the specimens with origin and description is given here, updated from Buchy *et al.* (2006d). For those specimens which were the subject of a separate description, it is referred to the publications dealing with them (Appendix).

I.2.1. Crocodyliformes

Crocodyliformes Benton & Clark, 1988 Thalattosuchia Fraas, 1901 I.2.1.1. Thalattosuchia indet. UANL-FCT-R11 Material: One isolated, fragmentary neural arch. **Origin:** The neural arch was discovered during the excavation of the pliosaur UANL-FCT-R2, at Aramberri, Nuevo León (fig. 2; chapter I.2.3). The age of the La Caja deposits at this site, as determined by the ammonite assemblage, is late Early to early Late Kimmeridgian (see Buchy *et al.*, 2003).

Comments: This specimen was described by Buchy et al. (2006d).



Figure 4: Palaeobiogeographical map of the Late Jurassic (modified from Smith *et al.*, 1994). Note the hypothetical barrier formed by the Florida uplift. Insert: palaeobiogeographical map of north-east Mexico during the Tithonian; Cb: Coahuila block; M: Monterrey; S: Saltillo (redrawn after Goldhammer, 1999).

UANL-FCT-R15 (Buchy et al., 2006d: 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. 2).

Comments: This specimen was described by Buchy et al. (2006d).

UANL-FCT-R25

Material: Two fragmentary thoracic vertebrae.

Origin: Late Early to early Late Kimmeridgian La Casita Formation at Galeana, Nuevo León (fig. 2).

Comments: This specimen was described by Buchy et al. (2006d).

CPC 205; 209; 212; 213; 214; 229; 239; 240

Material: All numbers correspond to isolated vertebrae or partial vertebrae, possibly with rib fragments; all are awaiting preparation.

Origin: Early Tithonian section of the La Caja Formation at the Sierra El Jabalí, near Gomez Farías, Coahuila, Mexico (fig. 2). The specimens were collected during field campaigns in March 2004 and September 2006.

Comments: As for most of the material from Gomez Farías, description must await preparation. Though, in view of the incompleteness of the specimens which will most likely reveal not further diagnostic, preparation could not be set as a priority. They emphasise the richness of the area regarding Thalattosuchia (Buchy *et al.* 2006c, e).

Metriorhynchidae Fitzinger, 1843 Metriorhynchinae Fitzinger, 1843 I.2.1.2. Metriorhynchinae indet.

UANL-FCT-R13

Material: Fragment of a rostrum comprising a fragmentary mandible at the caudal terminus of the symphysis including the dentition, the crowns of the maxillary teeth and the endocast of the internal cavity of the nasal duct of the maxillary rostrum.

Origin: Late Early to early Late Kimmeridgian La Casita Formation, as determined from the matrix. The specimen comes from either Galeana or Iturbide, Nuevo León (fig. 2).

Comments: This specimen was discussed by Buchy *et al.* (2006d), and is still awaiting preparation.

UANL-FCT-R16 (Buchy et al., 2006d: fig. 5a)

Material: Nine articulated caudal vertebrae.

Origin: Late Early to early Late Kimmeridgian La Casita Formation, at Galeana, Nuevo León (fig. 2).

Comments: This specimen was described by Buchy et al. (2006d).

UANL-FCT-R17 (Buchy et al., 2006d: fig. 5b)

Material: Four articulated caudal vertebrae, neural spine of the cranially adjacent vertebra, and cranial portion of the centrum of the caudally adjacent vertebra.

Origin: Late Early to early Late Kimmeridgian La Casita Formation at Galeana, Nuevo León (fig. 2).

Comments: This specimen was described by Buchy et al. (2006d).

CPC 225

Material: Rostral portion of a rostrum with teeth.

Origin: Early Tithonian section of the La Caja Formation at the Sierra El Jabalí, near Gomez Farías, Coahuila, Mexico (fig. 2). The specimen was collected during a field campaign in March 2004.

Comments: The specimen comprises about 250 mm of the rostrum in occlusion with teeth, preserved over several, matching fragments. It is about 25 mm wide, and the teeth have a basal cross-section of about 5-7 mm. Prior to preparation, the teeth appear slender, sub-circular in cross-section. The specimen therefore fits the anatomy of either longirostrine metriorhynchs or geosaurs (Vignaud, 1995; Frey *et al.*, 2002). The dentition of geosaurs in general, and especially of *G. saltillense* Buchy *et al.*, 2006e, from the same locality, being poorly known, and the high diversity of Metriorhynchinae there only suspected at present in view of the assemblage described here, attribution of the specimen awaits preparation and further studies.

CPC 232; 242 (fig. 5)

Material: Two isolated, partial tooth crowns.

Origin: Early Tithonian section of the La Caja Formation at the Sierra El Jabalí, near Gomez Farías, Coahuila, Mexico (fig. 2). The former was collected during a field campaign in September 2004; the latter, in February 2006.

Description: Both crowns share the same characteristics: the basal section is slightly mesiodistally elongate; the enamel is ornamented with thin, closely-spaced ridges that tend to merge towards the apex; the latter is smooth. The crowns are slightly curved mesially.

Discussion: These crowns closely resemble those attributed to some *Metriorhynchus* (Vignaud, 1995; 1997). Though, the dentition of geosaurs, especially of those inhabiting the Mexican Gulf during the Late Jurassic, is poorly known (Vignaud, 1995; Frey *et al.*, 2002; Buchy *et al.*, 2006e). The specimens are therefore provisionally referred to indeterminate Metriorhynchinae, possibly pending discovery of more complete specimens.



Figure 5: CPC 242, Metriorhynchinae indet., partial, isolated tooth crown in labial view. Scale 20 mm.

CPC 221; 230; 231 (fig. 6)

Material: The former two specimens comprise partial skulls; the latter, a partial skull and extensive portion of post-cranium.

Origin: Early Tithonian section of the La Caja Formation at the Sierra El Jabalí, near Gomez Farías, Coahuila, Mexico (fig. 2). The former was collected during a field campaign in March 2004; the latter two during several campaigns between September 2004 and February 2006. All still need preparation.

Comments: Although still mostly unprepared, for both skulls CPC 221 and 231 the extent and shape of the upper temporal fossae were visible in the field prior to extraction. Preliminary preparation of CPC 230 was recently conducted at the SMNK (fig. 6). In all three cases, the upper temporal fossae are subcircular, and although the three specimens could still represent different taxa, all differ from G. saltillense in this feature (Buchy et al., 2006e; the difference cannot be ontogenetic as the size of the specimens is equivalent). The subcircular shape of the fossae resembles the situation in adult members of the genus *Metriorhynchus* (Vignaud, 1995); however, Geosaurus araucanensis Gasparini & Dellapé, 1976 also possesses subcircular fossae, and a wide angle formed by the postorbital rami of the frontal to the intertemporal bar (Gasparini & Dellapé, 1976; Vignaud, 1995). Actually, only few of the diagnostic features of Geosaurus given by Vignaud (1995) can be observed in partial specimens and used to distinguish gracile members of the genus Metriorhynchus from members of the genus Geosaurus (Broili, 1932; Vignaud, 1995: compare e.g. pl. 25a, b and pl. 28a): nares are usually not or poorly preserved, rounded prefrontal lateral margins can be due to weathering or poor preparation, the original level of the supratemporal bar compared to the intertemporal bar can rarely be judged due to distortion, and South American thalattosuchians are poorly ornamented whatever genus is considered (Gasparini et al., 2005, 2006; Buchy et al., in press). Narial anatomy appears the clearest apomorphy of the genus Geosaurus (shared with Dakosaurus, which is then defined by its massiveness; Vignaud, 1995; Gasparini et al., 2006). Preservation of most Late Jurassic Mexican specimens at present prevents evaluation of this feature. Further exploration and the (usually) good condition of the

fossils, may set an opportunity to re-assess this poorly known genus (Broili, 1932; Vignaud, 1995).



Figure 6: CPC 230, Metriorhynchinae indet., inter- and postorbital section of skull in right dorsolateral view. Scale 50 mm.

I.2.1.3. 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 state. In central-east Mexico, the Pimienta Formation is an open marine shelf equivalent of the La Caja Formation (Frey *et al.*, 2002).

Comments: The holotype and only known specimen was described by Frey *et al.* (2002) and further discussed by Buchy *et al.* (2006c, e).

Geosaurus saltillense Buchy et al., 2006e

CPC 218

Former accession numbers: CEP1823 (Buchy et al., 2005c, 2006e).

Material: Holotype partial cranium and partial mandible, cervical vertebrae including atlas and axis.

Origin: Early Tithonian section of the La Caja Formation at the Sierra El Jabalí, near Gomez Farías, Coahuila, Mexico (fig. 2), collected during a field campaign in March 2004.

Comments: The holotype and only known specimen was described and discussed by Buchy *et al.* (2006e). Note the new accession number of the holotype.

Dakosaurus Quenstedt, 1856

I.2.1.4. Dakosaurus sp.

CPC 201

Material: Section of maxillary rostrum with poorly preserved teeth.

Origin: Middle Kimmeridgian section of the La Casita Formation at San Juan de los Dolores, close to Los Lirios, Coahuila, Mexico (fig. 2). The specimen was discovered in spring 2004 by Daniel Chio Gomez (Los Lirios). A visit to the site in autumn 2005 yielded no additional material, but confirmed the stratigraphic assignment.

Comments: The description and discussion of the affinities of the specimen are in press (Buchy *et al.*, in press).

UANL-FCT-R29 (fig. 7)

Material: Fragmentary interorbital portion of a skull.

Origin: Late Early to early Late Kimmeridgian La Casita Formation, about 1 km north-west of the hamlet of El Salitre, close to the city of Zaragoza, Nuevo León (fig. 2; see UANL-FCT-R8, chapter I.2.3). The fragmentary nodule was collected in September 2003 at the finding site of the pliosaur UANL-FCT-R8, together with fragments of the latter, undoubtedly matching the originally found, pliosaurian material (Buchy *et al.*, 2006d; chapter I.2.3). However, this fragment fits nowhere within a pliosaur cranium or post-cranium, and instead represents a large thalattosuchian (fig. 7). The site also yielded ichthyosaur vertebrae (Buchy *et al.*, 2006d). The La Casita / La Caja nodules are known for their locally rich fossil contents (Buchy *et al.*, 2003 and references therein): this site may actually reveal very rich. Preliminary gluing was conducted by F. Wittler in the SMNK and mechanical preparation completed by the author in the MUDE.

Preservation: The original completeness of the specimen cannot be determined. Most of the edges represent breaks along calcite seams. Possibly more of the animal is to be discovered at the site. At present, it comprises the rostral-most portion of the intertemporal bar (whose base only is preserved) and adjacent rostral-most portions of the supratemporal fenestrae; the median portion of the left postorbital bar is present as well, as is the caudal-most part of the prefrontal. The specimen is preserved 3-dimensionally, although a poorly preserved, flat element on the ventral side, possibly a fragment of the palatine, indicates collapse of the cranium.

Description: Most of the specimen is made up of the frontal. The intertemporal bar is about 20 mm wide at its base, slightly enlarging rostrally. The interfrontal suture is visible along the midline of the broken intertemporal bar, which does not mean it was visible on the surface (see Wenz, 1968 and Buchy *et al.*, in press, about the occurrence of interfrontal sutures). On either sides it is bordered by the depressed, sub-horizontal, non-ornamented rostral portions of the

supratemporal fenestrae. No frontoparietal suture appears on the preserved fragment. The frontal forms most of the postorbital bar as preserved: the 20 mm thick buttress that borders the supratemporal fenestra rostrolaterally. The caudal margin of the buttress is concave, its rostral margin convex. Its surface is ornamented, mainly in its rostral-most part, by shallow pitting. Laterally, the postorbital ramus of the frontal contacts the postorbital in an undulating suture, whose general direction appears perpendicular to the orientation of the postorbital bar, though is unclear. A small portion of the postorbital is preserved; it keeps the shape of the postorbital bar in its frontal portion. The medial-most, preserved portion of the prefrontal appears pushed up by dorsoventral compression. Its surface is wrinkled and no original ornamentation pattern can be deduced. The prefrontofrontal suture commences at mid-point of the dorsal margin of the orbit. It runs medially straight for about 15 mm and then gently curves rostrally. In ventral view, the prefrontal projects about 5-7 mm ventral to the frontal, which confirms the specimen underwent deformation. The prefrontofrontal suture in ventral view curves gently from rostrolaterally to caudomedially. The ventral surfaces, both of the prefrontal and the frontal are smooth. The median part of the ventral surface is obscured by a flat bone, possibly part of the palatine, whose broken and weathered margins yield no anatomical details. It is compressed against the lateral walls of the olfactory tract. The latter is formed by the frontal; it is at least 20 mm high, though its original extent cannot be determined. On the rostral-most break of the specimen (i.e. between the orbits), the olfactory tract is visible, as an inverted U-shaped, 20 mm wide, 20 mm deep sulcus within the frontal. Along the caudal break of the specimen, the thickness of the frontal is about 20 mm laterally, increasing to about 40 mm medially (not counting the height of the broken intertemporal bar).



Figure 7: UANL-FCT-R29, *Dakosaurus* sp., a/ interpretative drawing of the specimen in dorsal view. Hatched areas represent bone in section or sediment. Scale 50 mm. b/ Dorsal view of the skull of *D. andiniensis* redrawn from Gasparini *et al.* (2006), with the portion represented by UANL-FCT-R29 shaded grey.

Discussion: The specimen is massive (in term of bones in cross-section) and large, with an estimated 190-200 mm wide interorbital area (therefore larger than CPC 201 described by Buchy *et al.*, in press). Middle Jurassic members of the genus *Metriorhynchus*, such as *M. brachyrhynchus* can attain large sizes (Vignaud, 1995). The sharp angle formed by the postorbital bar to the skull midline, the supratemporal fenestra much larger rostrally than the supratemporal fossa, and the discreet ornamentation of the dorsal surface of the bones strongly recall specimens attributed to the genus *Dakosaurus* (Vignaud, 1995; Vignaud & Gasparini, 1996; Gasparini *et al.*, 2006; Buchy *et al.*, in press). UANL-FCT-R29 is therefore provisionally referred to this genus, pending possible discovery of more elements, and a revision of the genus which appears less and less well-defined with attribution of new forms (see the very unusual morphology of the Argentinian specimens described by Gasparini *et al.*, 2006).

The identification of UANL-FCT-R29 among the material collected when searching for the pliosaur UANL-FCT-R8 (chapter I.2.3) casts doubt upon the attribution of the isolated, tooth imprint-bearing fragments. *Dakosaurus* was originally described with large, trihedral, smooth-enameled teeth, possibly with serrated carinae (Fraas, 1902; Vignaud, 1995). The holotype of *D. andiniensis* Vignaud & Gasparini, 1996, has (poorly preserved) teeth sub-circular in cross-section, small compared to skull size, while newly referred specimens have large teeth and serrated carinae (located more caudally in the tooth row than in the holotype; Gasparini *et al.*, 2006). In any case, none of the tooth imprint-bearing fragments collected in September 2003 appear trihedral; they all show an ornamentation pattern of regularly-spaced ridges, which was never described for *Dakosaurus* until now. They are therefore described together with the pliosaur UANL-FCT-R8 (chapter I.2.3), although a doubt must remain, especially if *Dakosaurus* (or members of a possibly new, closely related genus) does reveal as variable as it is now suspected.

Thalattosuchia Fraas, 1901

Teleosauroidea Geoffroy Saint-Hilaire, 1831

Teleosauridae Geoffroy Saint-Hilaire, 1831

I.2.1.5. Teleosauridae indet.

UANL-FCT-R12 (Buchy et al., 2006d: 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. 2).

Comments: A preliminary description of this specimen was given by Buchy *et al.* (2006d); since then, no further preparation could be undertaken.

I.2.1.6. Discussion

Buchy *et al.* (2006d) discuss the thalattosuchian assemblage of the Kimmeridgian of north-east Mexico; since then only the expected genus *Dakosaurus* was newly identified (Buchy *et al.*, in press and specimen UANL-FCT-R29). Teleosaurids appear rare when compared to European localities (Vignaud, 1995; see a discussion upon possible life-style constrains in Buchy *et al.*, 2006d), while the fragmentary condition of most other specimens prevents further faunistic conclusions.

The Early Tithonian at Gomez Farías on the contrary recently revealed extremely rich in thalattosuchians, even if results are at present preliminary (Buchy *et al.*, 2006c, e). The assemblage lacks teleosaurids and *Dakosaurus* is missing, though at present the described diversity of geosaurs is reminiscent of what is known at the time in Europe (Vignaud, 1995; Schoch, pers. com.). The absence of the genus *Metriorhynchus*, as mentioned by Buchy *et al.* (2006d), is still intriguing, less so than for the Kimmeridgian, though, as this genus is poorly represented in the Tithonian of Europe and South America (Vignaud, 1995). Several specimens of at present uncertain attribution (CPC 221, 230, 231) could change the figure, but further preparation as well as re-evaluation of European forms are necessary.

I.2.2. Ichthyopterygia

Ichthyopterygia de Blainville, 1835 Euichthyopterygia Motani, 1999 I.2.2.1. Euichthyopterygia indet. UANL-FCT-R18 (Buchy *et al.*, 2006d: fig. 7a) Former accession number: LCRPØ / 1003 Material: Portion of caudal vertebral column consisting of 14 centra. Origin: Late Early to early Late Kimmeridgian La Casita Formation at Rio Pablillo, Nuevo León (fig. 2). Comments: This specimen was described by Buchy *et al.* (2006d).

UANL-FCT-R19 (Buchy *et al.*, 2006d: fig. 7b)Former accession number: LCRPØ / 1002Material: Five centra; serial position undetermined.

Origin: Late Early to early Late Kimmeridgian La Casita Formation at Rio Pablillo, Nuevo León (fig. 2).

Comments: This specimen was described by Buchy et al. (2006d).

UANL-FCT-R20 (Buchy et al., 2006d: fig. 7c)

Former accession number: LCSLØ / 1001

Material: Seven articulated caudal centra.

Origin: Late Early to early Late Kimmeridgian La Casita Formation at San Lucas, Nuevo León (fig. 2).

Comments: This specimen was described by Buchy et al. (2006d).

UANL-FCT-R21 (Buchy et al., 2006d: fig. 7d)

Material: Three articulated centra; serial position uncertain.

Origin: Late Early to early Late Kimmeridgian La Caja Formation at La Angostura, Nuevo León (fig. 2).

Comments: This specimen was described by Buchy et al. (2006d).

UANL-FCT-R22 (Buchy et al., 2006d: fig. 7e)

Material: Five articulated centra 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. 2).

Comments: This specimen was described by Buchy et al. (2006d).

UANL-FCT-R23 (Buchy et al., 2006d: fig. 7f)

Material: Four articulated centra and rib fragments.

Origin: Late Early to early Late Kimmeridgian La Casita Formation from 2 km south-east of San Lucas, Nuevo León (fig. 2).

Comments: This specimen was described by Buchy et al. (2006d).

CPC 210; 211; 215; 216; 217; 219; 220; 223; 224; 227; 233; 234; 235; 237

Material: Isolated vertebrae, or series of vertebrae, possibly with fragments of ribs or ?limb elements.

Origin: Early Tithonian section of the La Caja Formation at the Sierra El Jabalí, near Gomez Farías, Coahuila, Mexico (fig. 2), collected during field campaigns in March and September 2004, and February 2006.

Comments: These specimens span the entire vertebral series, without taxonomical value beyond infraorder (McGowan & Motani, 2003; Buchy *et al.*, 2006d).

Ophthalmosauridae Baur, 1887

Ophthalmosaurus Seeley, 1874b

I.2.2.2. Ophthalmosaurus icenicus Seeley, 1874b

CPC 238 (figs 8-10)

Material: Skull and partial postcranium.

Origin: Early Tithonian section of the La Caja Formation at the Sierra El Jabalí, near Gomez Farías, Coahuila, Mexico (fig. 2). The first parts of the specimen were encountered together with the pliosaur CPC 226 (chapter I.2.3) by J. Lopez Espinoza (MUDE) and a team of private collectors. The skull was then secured in a plaster jacket, while a portion of vertebral column comprising 17 centra was prepared soon after and became part of the exhibition of the recently opened MUDE. The rostrum was collected in autumn 2004 by J. Lopez Espinoza, and prepared by him along with the skull in the SMNK. A field campaign in February 2006 yielded additional associated vertebrae, according to the original collector.

Preservation and taphonomy: Seen in left lateral view, CPC 238 exhibits skull and mandible in occlusion (fig. 8), while the other side of the specimen comprises both coracoids close to anatomical connection, both scapulae, the left humerus, articulated cervical centra, including fused atlas and axis, ribs and phalanges (fig. 9a, b). As is visible in dorsal view (fig. 9c, d), in the left and medial portions of the skull, the bones appear mostly undistorted, even if slightly displaced or twisted, while the right postorbital and orbital regions slid rostrally and the adjacent part of the right mandible appears 'folded'. The rostrum was broken prior to diagenesis in two main portions (its rostral extremity was recently broken but was not discovered in the field). Additional material (an articular, ribs sections, phalanges and centra) does not yet match the main block. The unusual preservation pattern suggests that the body sunk head first in the soft sediment (Martill, 1987), followed by at least part of the body, and remained subvertical during early phases of decay. When the carcass was sufficiently decayed for the weight of the bones to overcome resistance of the sediment, but being still firmly connected by at least ligaments, gravity made the post cranium slowly sink down against the right portion of the skull and the right mandible. Possibly the head was prevented from sinking as well when the rostrum reached a harder layer or an obstacle; the rostrum may have broken then. Pressure must have applied gradually over a long period of time, explaining the plastic distortion of the caudal part of the right mandibular ramus. Finally, winnowing brought the compacted skeleton to rest subhorizontally within the coquina.

As is common for fossils from the locality (Buchy *et al.*, 2006c, e), the course of most sutures cannot be determined due to the poor contrast between matrix and bone, and possibly due to the taphonomical history of CPC 238. A recent break with subsequent extensive weathering runs sub-vertically at the level of the nares. As noted by McGowan & Motani (2003), overlapping of the cranial bones in ichthyosaurs makes it difficult to extrapolate the external course of a suture when the surface is damaged. Consequently, the respective participation of the premaxilla, maxilla, nasal, prefrontal and lachrymal to the border of the naris, as well as the contacts of these bones, cannot be determined.



Figure 8: CPC 238, *Ophthalmosaurus icenicus*, a/ specimen in left lateral view. b/ Interpretative drawing of the orbital region. Scale 50 mm.

Description: *Cranium* - The rostrum being incomplete and the skull distorted, no biometric ratio can be determined for the skull (e.g. McGowan & Motani, 2003). The orbit is very large, and, taking into account distortion of the skull, especially shifting of the postorbital, it was probably sub-circular. It accounts for most of the postnarial part of the skull in lateral view, the postorbital region being reduced. The sclerotic ring is almost as large as the orbit itself; its caudoventral portion is displaced by elements of the ?palate. By extrapolation, about 11 sclerotic plates were present. In some places, the sclerotic plates are covered by a white, translucent substance.



Figure 9: CPC 238, *Ophthalmosaurus icenicus*, a/ specimen in 'ventral' view (see text). b/ Interpretative drawing. c/ Specimen in dorsal view, d/ interpretative drawing. Scale 50 mm.

The premaxilla forms most of the rostrum as preserved. A 5 mm high groove runs along the entire preserved length of the rostrum at about mid-height of the premaxilla. The rostral extent of the nasopremaxillary suture cannot be determined as the nasal appears incomplete rostrally. The maxillopremaxillary suture, and indeed the maxilla itself, cannot be identified in the weathered area ventral to the naris.

The lachrymal is subtriangular, forming the rostral margin of the orbit. A sub-circular foramen is present in the lachrymal rostral to the orbit, probably on the lachrymojugal suture,

about 30 mm caudal to the naris. What is here interpreted as the medial, preorbital portion of the lachrymal was apparently pressed laterally and now occupies the rostral-most extremity of the orbit. Note that this element could also represent a bone of the palatal area. The lachrymoprefrontal suture commences just dorsal to this element; it undulates rostrodorsally until it reaches a calcite vein, after which it cannot be further identified.

The caudal extent of the nasal in the interorbital area, and thus its contact with the frontal, cannot be identified, the area being weathered. In the preorbital region, an internasal suture is visible; there, the medial surface of both nasals are depressed, the median dorsal surface of the rostrum therefore forming a gutter. The nasal is excluded from the rostrodorsal margin of the orbit by the prefrontal and postfrontal.

The suture between prefrontal and postfrontal appears located around the middle of the dorsal margin of the orbit. The caudal portion of the postfrontal and the other bones forming the temporal bar are damaged and/or obscured by overlying elements (neural arches, ribs). At the caudal-most extremity of the postfrontal, a sinusoid line delimits the probable facet for the supratemporal. The supratemporal itself cannot be identified. The squamosal is probably visible as a superficial, triangular bone wedged between the caudoventral margin of the postfrontal and the caudodorsal margin of the postorbital. The rest of the suspensorium is obscured by a thick vein of calcite. A subrectangular bone with a vertical, straight rostral margin and a convex caudal margin is identified as the quadratojugal. The caudal margin of the quadrate is straight, vertical.

The medial margin of the postorbital was pressed laterally by the girdle elements: what is exposed in lateral view of the postorbital is mostly its medial, postorbital flange. It now appears like a boomerang-shaped bone forming the caudal margin of the orbit and the caudal half of its ventral margin, though its original extent and shape cannot be determined. Likely as a geometrical consequence of the shifting of the postorbital, the area of contact with the jugal now protrudes within the orbit, with the caudal part of the jugal dragged by the rotation of the rostral ramus of the postorbital. Consequently, the surface of the suborbital portion of the jugal is wrinkled like corrugated iron. The caudal extent of the jugal is unclear. As preserved, it wraps the caudoventral corner of the postorbital and extends further dorsally toward the quadratojugal.

The surangular is exposed laterally further rostrally than the naris. The angular is wellexposed laterally until at least the naris and appears to extend further rostrally; its rostral-most extent, though, cannot be determined due to breakage. The caudal extent of the mandible is obscured by the jugal, a phalanx and matrix.

Within the matrix between the premaxilla and the dentary, teeth and teeth fragments are poorly preserved. In the broken area ventral to the naris, cross-sections through several teeth are visible. Further caudally, poorly preserved remnants of at least two upper teeth are laterally exposed occluding over the dentary. These are small, conical, about 5 mm in basal diameter and less than 10 mm in height. Enamel is not preserved.

Post-cranium - The atlas and axis, although their surface is poorly preserved, are fused with the suture still apparent. The third cervical centrum is not fused to the atlas-axis complex. The other preserved centra are craniocaudally compressed, a point of possible taxonomical import as discussed by Bardet *et al.* (1997).

The coracoids are preserved close to their original contact, visible in ventral aspect; they bear a single, cranial notch. Their medial margin is gently rounded. The glenoideal margin is straight, as is seemingly the scapular facet. One scapula is preserved next to the left coracoid and appears slender, but few of its margins are clearly original and visible. The second scapula is probably wedged between the left coracoid and mandible, still in anatomical contact with the left humerus. The latter is exposed in dorsal view; it bears three distal facets, the middle one the largest, the cranial one the smallest and oblique compared to the proximodistal axis. All phalanges are rounded.



Figure 10: CPC 238, *Ophthalmosaurus icenicus*, left humerus in dorsal view (with overlying phalanx). Scale 50 mm.

Discussion: CPC 238 undoubtedly represents an Ophthalmosauridae as diagnosed by McGowan & Motani (2003) in having three distal facets on the humerus and in the rostral extent of the angular in lateral view. Moreover, what is preserved of CPC 238 corresponds to descriptions and diagnoses of *Ophthalmosaurus* given by e.g. Seeley (1874b), Appleby (1956), Kirton (1983), Bardet *et al.* (1997), Maisch & Matzke (2000) and McGowan & Motani (2003). All differences may be attributed to preservation.

In any case, CPC 238 differs from other members of the Family Ophthalmosauridae in the following features: *Mollesaurus* from the Bajocian of Argentina has a conspicuously small sclerotic ring compared to orbital diameter (Fernández, 1999). *Nannopterygius* (Kimmeridgian of

England) possesses a humerus reduced in size with only two distal facets, *contra* the familial diagnosis (McGowan & Motani, 2003). *Unodosaurus* from the Tithonian of Russia possesses teeth larger and more robust than CPC 238 (see Efimov, 1999; McGowan & Motani, 2003). This genus was considered synonymous with *Ophthalmosaurus* by Maisch & Matzke (2000). The three distal facets of the humerus of *Brachypterygius* (Kimmeridgian-Tithonian of England and Russia) are subequal in size; its teeth are said robust and its orbit relatively small (McGowan & Motani, 2003). The phalanges of *Aegirosaurus* (Tithonian of Germany) are polygonal, and the middle facet of its humerus is the smallest of the three (Bardet & Fernández, 2000). *Caypullisaurus*, from the Tithonian of Argentina, has polygonal phalanges (Fernández, 1997); its humerus appears very similar to the humerus of *Ophthalmosaurus* and McGowan & Motani (2003) suggest the two genera may be synonymous. The humerus of *Platypterygius* (Lower Cretaceous) has two distal facets, its phalanges are rectangular, its teeth robust and its orbit relatively small (McGowan & Motani, 2003).

Two species pertaining to *Ophthalmosaurus* are retained by McGowan & Motani (2003): the English type species *O. icenicus* and *O. natans* as a stratigraphic and geographic species for material from the New World formerly referred to the genus *Baptanodon*. Synonymy of the latter genus with *Ophthalmosaurus* has long been debated (see McGowan & Motani, 2003) and appears corroborated by anatomical data. *O. natans* was described from Argentina (Gasparini, 1988; McGowan & Motani, 2003); during the Upper Jurassic, north-east Mexico was situated at about middistance between the Western Interior Basin and the European Archipelago (e.g. Smith *et al.*, 1994, though adding the Florida barrier possibly isolating the Mexican Gulf; fig. 4). CPC 238 differing in no significant feature from the type species *O. icenicus*, the most conservative option is to refer it to this type species, even if it is stratigraphically younger.

I.2.2.3. Discussion

As was noted by Buchy *et al.* (2006d), it is highly unlikely that the ichthyosaurian fragmentary specimens from the Kimmeridgian Mexican Gulf do not represent Ophthalmosauridae (see McGowan & Motani, 2003). This conclusion stands as well for the Tithonian specimens from Gomez Farías, which are numerous but poorly diagnostic at present. The conclusion is further supported by the identification in the same site of the ubiquitous taxon *Ophthalmosaurus icenicus*. At present, nothing can be said about the diversity (high or low) of Late Jurassic Mexican ichthyosaurs as compared to other assemblages, due to the poor taxonomical value of the known material.

I.2.3. Sauropterygia

Sauropterygia Owen, 1860 Plesiosauria de Blainville, 1835 I.2.3.1. Plesiosauria indet. CPC 222

Material: Five associated phalanges.

Origin: Early Tithonian section of the La Caja Formation at the Sierra El Jabalí, near Gomez Farías, Coahuila, Mexico (fig. 2); collected in March 2004.

Comments: The current whereabouts of the specimen are unknown, therefore no proper description can be given here. Prior to preparation, the phalanges were exhibiting the typical plesiosaurian hour-glass shape. They are similar in size to known proximal phalanges of the pliosaur CPC 226 (see further), about 50 mm in proximodistal length; their location in the site appears to exclude their belonging to that individual (except in case of human transport). The phalanges were preserved together but not in natural articulation, hinting at a disarticulated (portion of) paddle.

CPC 236 (fig. 11)

Material: Portion of limb.

Origin: Early Tithonian section of the La Caja Formation at the Sierra El Jabalí, near Gomez Farías, Coahuila, Mexico (fig. 2); collected in September 2003.

Preservation: The proximal edge of the specimen is comprised of a thick vein of calcite. The specimen comprises what is interpreted as the distal half of an epipodial, in articulation with both distally following preaxial mesopodials (see Discussion). Postaxially, articular facets for central mesopodials and proximal-most metapodial were free from sediment prior to preparation and testify that the specimen has been more complete at some recent point, prior to collection. Classically for limb bones of Plesiosauria, identification of isolated elements is close to impossible; although some hints exist that the specimen might belong to the forelimb (see Discussion), it cannot be determined whether right or left. Preparation was conducted by the author at the MUDE.

Description: Possibly about half the distal portion of the epipodial (radius or tibia) is preserved. Its preaxial margin is gently rounded. Its distal margin is concave, encompassing the articular facet for the proximal-most mesopodial (radiale or centrale; nomenclature follows Caldwell, 1997 and Sato, 2003). The postaxial margin of the epipodial slopes proximally, forming the articular facet for the proximal-most central mesopodial (intermedium or astragalus). The distally

following preaxial element is either the radiale (if a forelimb) or centrale (if a hindlimb). It is subrectangular, with a slightly convex preaxial margin, and a postaxial margin divided into a proximal facet for articulation with the centrale or astragalus, and a distal facet for the distal carpal or tarsal II+III. The distal-most element, being either distal carpal I or distal tarsal I, is smaller, with an outline similar to that of the radiale or centrale in palmar/plantar view. The surface of all elements is heavily pitted and grooved, the distal and proximal edges festooned, as noted by Brown (1981), possibly hinting at strong ligamentous connections and restricted movements in a dorsoventral plane.



Figure 11: CPC 236, Plesiosauria indet., a/ portion of limb. b/ Interpretative drawing. Scale 50 mm.

Discussion: Although limb bones of Plesiosauria are generally poorly differenciated, metacarpal and metatarsal V are still easily recognised, at least when in articulation. No element in CPC 236 can be identified as such, therefore it clearly represents a preaxial series. The postaxial margin of the median element shows no hint at the presence of the spatium interosseum, which normally is present between radius and ulna and tibia and fibula (one exception is the elasmosaur *Hydralmosaurus*, however, the postaxial margin of the radius is straight in this taxon, which is not

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the case of the two distal elements of CPC 236, Welles, 1943; Carpenter, 1999). The proximalmost element is therefore identified as an epipodium, the spatium interosseum having been located proximal to the proximal break of the specimen. From a preliminary overview of published data and personal observations, it appears that hindlimb bones are more rounded than forelimb ones in Plesiosauria (however few articulated paddles are known with certainty within their anatomical context, see e.g. Caldwell, 1997). Bones in CPC 236 are rather angular, raising the possibility that the specimen pertains to a forelimb. The specimen is of poor taxonomical value.

Plesiosauroidea Welles, 1943

Elasmosauridae Cope, 1869

I.2.3.2. Elasmosauridae indet.

UANL-FCT-R5 (Buchy et al., 2006d: fig. 8)

Former accession number: LCANØ / 1006

Material: Isolated partial dorsal vertebra, 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. 2).

Comments: This specimen was described by Buchy et al. (2006d).

CPC 202; 203; 204; 206; 207

Material: Partial isolated cervical centra.

Former accession numbers: CPC 204: CEP1801; CPC 202: CEP1803; CPC 206: CEP1804; CPC 203: CEP1809 (Buchy *et al.*, 2006c, e).

Origin: Early Tithonian section of the La Caja Formation at the Sierra El Jabalí, near Gomez Farías, Coahuila, Mexico (fig. 2); collected in September 2003 and March and September 2004.

Description: Dimensions of the centra are presented in Table 1. The centra are almost platycoelous, showing only a faint depression in the centre (CPC 204 actually shows two depressions side by side on its cranial articular face). All centra exhibit a pair of subcentral foramina (the right foramen on CPC 203 is half the diameter of the left one); only CPC 206 possesses two foramina on the left side. The neural arches were not fused, and lost prior to embedding as indicated by matrix. The facets for the neural arches are sub-triangular in lateral and dorsal aspects, the cranial apex of the triangle being truncated cranially: the pedicels of the neural arches were wider cranially than caudally. The synapophyses are located in the ventrolateral-most part of the centrum, closer to the caudal articular face than to the cranial one. Viewed end-on, the

synapophyses are broadly triangular, pointed dorsally. On CPC 202, the synapophysis is incompletely divided by a sub-vertical ridge. CPC 203 and 206 present a groove in place of a ridge.

Discussion: The subcentral foramina, the general proportions of the platycoelous centra and the insertion of the rib on the ventrolateral portion of the centrum are characteristic of elasmosaurian cervical vertebrae. The specimens are not further diagnostic.

Specimen number	Length of centrum	Height of centrum	Width of centrum	Distance between
				subcentral foramina
CPC 202	55	~60	73	23
CPC 203	55	53	62	15
CPC 204	62	67	~80	28
CPC 206	~65	67	75	33
CPC 207	50	~50	~58	/

Table 1: Dimensions of the elasmosaur vertebrae from Gomez Farías, in mm.

Pliosauroidea (Seeley, 1874a) Welles, 1943

Pliosauridae Seeley, 1874a

I.2.3.3. 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 with teeth (fig. 12); the left portion of the body and parts of both left limbs were excavated between 2001 and 2005 and are currently under preparation.



Figure 12: UANL-FCT-R2, reproduction of a slide from W. Hähnel (taken year 1986 or 1987) of the lost portion of rostrum encountered during early excavation of the specimen. No scale is available.
Origin: Late Early to early Late Kimmeridgian La Caja Formation at Aramberri, Nuevo León (fig. 2; Buchy *et al.*, 2003).

Comments: The history of this specimen, nicknamed "The Monster of Aramberri", together with a description of the material mounted in the concrete stand were given by Buchy *et al.* (2003). Excavations were undertaken at the finding site from 2001 to 2005. They are now completed and allowed the recovery of the caudal portion of the animal. Preliminary field data indicate that the pliosaur was possibly complete prior to weathering of the cranium and most of the left part of the body (fig. 13). Cranial fragments were found as isolated debris, although most are unidentifiable. All cranial fragments show open sutures; at least two of them bear bite marks, only one of them, possibly the ascending process of the pterygoid, is clearly accompanied by a callus. The bite marks are oval, with their largest dimension about 70 mm; they may have been caused by another large pliosaur. The articular heads of both femurs are articulated with the pelvic girdle; of the left femur only the head is preserved. The femoral head has a craniocaudal length of 450 mm, when compared to the 140 mm length of the femoral head of a subcomplete, 5 meter long *Liopleurodon ferox* mounted in the IGPT (uncatalogued specimen; Noé, 2001: fig. 1). This femoral head and all other fragments confirm the estimation of an animal at least 15 meters in length (Buchy *et al.*, 2003, 2006d).



Figure 13: UANL-FCT-R2, sketch of the finding situation.

Discussion: The current, unprepared status of most of the material renders anatomical comparisons impossible. Though, the most striking feature of the specimen is its very large size. 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 (Tarlo, 1959; Noè *et al.*, 2004).

Additionally, a 3 m long mandible was recently found in the Kimmeridge Bay (Noè et al., 2004; Etches, pers. com.). Next to these, prior to the discovery of UANL-FCT-R2, the largest pliosaur known was Kronosaurus, from the Cretaceous of Australia (Longman, 1924; White, 1935; Romer & Lewis, 1959; Kear, 2003). The most famous specimen of the genus, a subcomplete skeleton mounted in the late 1950s at Harvard, reaches about 13 m in length, though some accounts credit the mount with 10 faked vertebrae and down-size it to 8 to 9 m in length (Creisler, 1998). The extraction method, that relied upon massive use of explosives, rendered an incomplete specimen whose missing parts were replaced by plaster; a revolutionary mounting method additionally altered some of the original parts that were left - so that it will probably be difficult for researchers in the future to assess the actual anatomy of the specimen as well as its similarities with the holotype of Kronosaurus and taxonomic status (see an excellent compilation of references at www.oceansofkansas.com). Kronosaurus was described on a piece of rostrum (Longman, 1924), and more material was referred to the genus mostly on the basis of large size and geographic and stratigraphic occurrence (White, 1935; Romer & Lewis, 1959). Adding to the confusion, a second species was created later upon a 9 m long, sub-complete but poorly preserved skeleton from Columbia, once again, mostly because of its size and stratigraphic age (Hampe, 1992). Several specimens from Australia and Colombia are currently under study (McHenry, in prep.; Gomez, in prep.) and will most likely clarify the issue, at least partly. Until now none of these specimens reaches the size of UANL-FCT-R2.

Another large, rather enigmatic pliosaur is known in the Upper Jurassic of North America: *Megalneusaurus rex* was defined by Knight in 1895 on fragmentary material that is partly lost (Knight, 1895, 1898; Weems & Blodgett, 1996). Additional postcranial, non diagnostic remains from Alaska were referred to the taxon by Weems & Blodgett (1996) on the basis of their large size, in peculiar, a humerus about 900 mm in proximodistal length. The original material of Knight seems to have been slightly larger (Knight, 1898; Creisler, 1998). Until now only the right femur head of the Monster was prepared; its rostrocaudal length is about 450 mm, which may indicate a femur of about 1,20 m in length. Both femur and humerus are preserved on the left side of UANL-FCT-R2 and were collected in 2005, but are not prepared yet; field data still hint at a proximodistal length of at least 1,2 m for the left femur (fig. 14). It appears thus that *Megalneusaurus* is smaller than UANL-FCT-R2. It also apparently does not represent a juvenile individual. At present, it is poorly defined, mostly on the basis of geographic location, pliosaurs being rare from the Upper Jurassic of North America.



Figure 14: UANL-FCT-R2, photo of the concretion as exposed in October 2005. Scale is Annabelle, 1,55 m in height. Note that due to an inverted fault, the exposed ('upper') side is the ventral side of the animal. The concretion ends shortly distal to both femur and humerus: most likely, the limbs are not preserved distal to the epipodials.

Thus UANL-FCT-R2 represents the most complete very large pliosaur known to date, and additionally exhibits an immature osteological condition, raising the question of the size, a fully ossified member of the same taxon could have reached. It was shown that forms with unfused neural arches represent juveniles in small (some meters long) plesiosaurian taxa (Brown, 1981). Fusion of the neural arch to the vertebral body may have occurred earlier in life in pliosaurs than in crocodiles (Buchy et al., 2006d); the growth rate of crocodiles most likely cannot be used to estimate growth rate in pliosaurs. Crocodiles are small when they hatch because they have to develop within the restricted space of an egg; on the contrary it was argued that pliosaurs were ovoviviparous (Cheng et al., 2004; Buchy et al., 2005a). Thus newborns could be larger compared to adults than are hatchling crocodiles, and the growth rate during the first months or years were not necessarily similar. Another aspect is sexual maturity, which might have occurred before osteological maturity, a phenomenon that is quite common, and possibly advantageous in evolutionary terms (e.g. Gould, 1977; McKinney, 1988): the parents of UANL-FCT-R2 were not necessarily much larger than it was when it died. Other far (but possibly closer) relatives are lizards. Recent forms, however, differ from pliosaurs in many aspects, such as size, anatomy, mode of life, etc., so that they cannot represent a reliable model for pliosaurs (see Buchy et al., 2005a). Moreover, osteological maturity might never have been reached in very large pliosaurs, a partly cartilaginous skeleton being then no sign of young individual age: adult giant pliosaurs might have retained juvenile features including non-fusion of the bones (*contra* Buchy *et al.*, 2006d) as a consequence of e.g. enormous metabolic requirements or to save weight. Cartilage might have played an essential role in their biomechanics. It is usually argued that cartilage is less solid than bone, less resistant against the tensions created by muscles and movement; though, it is also better absorbing shocks and loads (e.g. Evans, 2005 and references therein). Another, indirect argument in favour of preservation in adult giant pliosaurs of a partly cartilaginous skeleton is the rarity of such remains in the fossil record, when marine environments offer better opportunities for fossilisation than continental ones and remains of sauropods as large as or larger than UANL-FCT-R2 are relatively common. Giant pliosaurs must have been rare in Late Jurassic ecosystems, as are normally large carnivores as compared to herbivores; during geological time it must still have represented series of populations comprising a sufficient number of individuals to breed. A partly cartilaginous skeleton would help explain why so few among these were fossilised or had their remains correctly identified.

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 W. Stinnesbeck and M. Götte in the Sierra El Montelongo Pedregoso, Nuevo León (fig. 2; Buchy *et al.*, 2006b).

Comments: This specimen was described by Buchy *et al.* (2006b, d). The condition of the ?parietal and its rostral prolongation is unique among Pliosauridae until now, but the poor condition of the specimen prevented naming a new taxon.

UANL-FCT-R7 (Buchy et al., 2006d: fig. 9)

Material: Four and a half caudal cervical centra, and adhering portions of the coracoids.

Origin: Late Early to early Late Kimmeridgian La Caja Formation at La Angostura, Nuevo León (fig. 2), collected by W. Hähnel in 1985.

Comments: This specimen was described by Buchy et al. (2006d).

UANL-FCT-R8 (Buchy et al., 2006d: fig. 10; figs 15-20, table 2)

Material: Fragmentary maxillary and mandibular rostra with teeth; possibly a dorsal vertebra (Buchy *et al.*, 2006d).

Origin: Late Early to early Late Kimmeridgian La Casita Formation. The material was collected by a shepherd, Regulo Cortez, in August 2002, about 1 km north-west of the hamlet of El Salitre,

close to the city of Zaragoza, Nuevo León (fig. 2). It was subsequently bought by a private collector, who partly transferred it to the UANL-FCT. At least an isolated dorsal vertebra supposedly belonging to the same individual is still in the possession of this collector (Buchy *et al.*, 2006d). A visit to the site in September 2003 yielded additional fragments, some of which did find a match with the originally found cranial material. Others where described in chapter I.2.1 as belonging to *Dakosaurus* sp. (see a discussion there). It is unclear who conducted preparation of the original material.

Preservation: The original completeness of the specimen cannot be determined. At present, it comprises the rostral extremity of the mandible with occluding portion of the palatal area; the caudally adjacent fragments build up about 450 mm of the maxillary rostrum and an occluding portion of the right caudal part of the mandibular rostrum (figs 15-18). For convenience in the following description, each fragment constituting the rostrum was given a Roman number from I to VIII, as depicted in figure 19.

The specimen being comprised of fragments separated by sub-vertical breaks, further anatomical features are available in cross-section. These are designated by the number of the fragment followed by .1 for the rostral section, .2 for the caudal section (fig. 19). Except for fragment I and dorsal-most part of fragment VII, most of the bone lateral to the teeth is weathered, and tooth roots are exposed while the crowns are poorly preserved. Several additional, isolated fragments represent tooth imprints (fig. 20a) and unidentified bone pieces (which could also be part of UANL-FCT-R29, chapter I.2.1). None of the tooth imprints bearing fragments match the preserved teeth. The rostrum underwent vertical shearing, that distorted the right side of the specimen dorsally, obscuring the extent of most individual bones. Moreover, the teeth of the left row were split down their middle along a sagittal plane, so that the lateral halves of the teeth (both dentary and occluding premaxillary crowns) slid rostrally against their medial halves.

The individual age of the animal is difficult to assess; bones appear to have slid against one another without extensive breakage, hinting at loose sutures. On the other hand, a certain elasticity of the contact between constituting elements of the rostrum may be a biomechanical requirement in order to absorb torque forces, as was briefly discussed by Buchy *et al.* (2006b).

Description: *Premaxilla* - The palatal rostral-most portion of the premaxilla is partly preserved on fragment I in occlusion with the rostral extremity of the mandibular rostrum; what is visible is therefore the floor of the rostral cavity. From the location of the preserved premaxillary teeth, it can be deduced that the maxillary rostrum must have overhung the mandibular rostrum by several centimetres at least until level with premaxillary tooth 3; the rostral extremity of the maxillary rostrum most likely had a more rounded profile in dorsal and ventral view than the mandibular rostrum. The internal surface of the premaxilla appears

smooth and continuous until its rostral-most extremity. Incompetent preparation caused what superficially may look like an anterior vomerian fenestra bordered rostrally by the premaxilla, though obvious air scribe scars and the fact that the 'fenestra' is only present on the left proves that it is artificial. The medial portion of the vomeropremaxillary suture is well exposed in dorsal view on the left side; on the right side, bone surface is flaked off though the general course of the suture can still be followed. It undulates caudolaterally from level with the caudal margin of right dentary tooth 2 to level with the rostral margin of right dentary tooth 4. Only a fragment of the dentigerous part of the premaxilla is preserved, around the mesiolingual face of left premaxillary tooth 3. It appears to be set about 3 mm more dorsally than the medial portion of the premaxilla, possibly due to distortion. In dorsal view, the alveolar surface of the premaxilla around tooth 3 is waved, forming spikes toward the tooth root. The palatal portion of the premaxillomaxillary suture is not visible. If a count of 5 premaxillary teeth can be suggested in the specimen as in most other plisosaurs (e.g. Tarlo, 1959, 1960; Taylor & Cruickshank, 1993; Noè et al., 2004), and by extrapolation of the course of the suture more caudally (see further), it must have been located in the caudal part of fragment I (fig. 18). What is preserved further caudally of the premaxillomaxillary suture is better visible on the right side, and can be reconstructed on the left side on the basis of the sections. It slopes caudodorsally between fragments I and V, then runs sub-horizontally straight on fragment V; further caudally, on fragment VI (right) and VII (left) it appears to diverge laterally, possible due to distortion. In section, the premaxilla in its intermaxillary portion is about 20 mm thick. The premaxillomaxillary suture in section runs from medioventrally to laterocaudally. Distortion along the midline obscures the anatomy of the dorsal-most part of the specimen; on section VII.1 an element oval in cross-section possibly underlies the medial-most portion of the left premaxilla, although it could merely be a broken portion of the premaxilla itself (fig. 19). Preservation prevents assessing its presence on the right side and further caudally. This represents the only possible hint at the presence of a medial bone or bone ramus underlying the premaxillae or excluding them from the midline as is the case in UANL-FCT-R3 (Buchy et al., 2006b).

Maxilla - Of the external surface of the maxilla, little is left. Where preserved, it is spread with foramina and wrinkled, whether originally or due to weathering. An oval portion of the bone is missing at the right dorsorostral portion of fragment V, possibly representing a bite mark. The ventrolateral margin of the maxilla appears slightly festooned around the teeth. In ventral view, the lateral margin of the maxilla, as deduced from the alveolar row, is sub-parallel to the midline, only slightly enlarging caudally. As deduced from the sections, the maxilla is forming rostrally the

palatal surface of the maxillary rostrum together with the vomer (see this section). Somewhere within fragment IV (or possibly rostral to fragment IV, though section IV.1 is unclear; fig. 19), between sections IV.1 and V.1, the palatine inserts between vomer and maxilla and from there to caudally restricts the latter in ventral view to the lateral-most, dentigerous portion of the ventral surface of the maxillary rostrum. In section, the palatomaxillary suture is sub-vertical.

Vomer - The dorsal surface of the vomer is smooth as well. As mentioned earlier, the intervomerine suture appears to have been loose, as the left vomer was pushed dorsally compared to the right one without extensive breakage. On section I.2, the vomer reveals trapezoidal in section, its largest face the dorsal. Therefore, while the vomer accounts for most of the dorsal surface of the floor of the rostral cavity, in ventral view it must have had a lateral extent of about 10 mm only, and the premaxilla must have composed most of the lateral portion of the ventral surface. In section, the vomeropremaxillary suture runs from medioventrally to laterocaudally at low angle (as are, further caudally, the vomeropalatine and palatopterygoid sutures). Where visible, on fragments IV, V and VII, the palatal surface appears uniform, with no clearly visible sutures; these can only be located thanks to the sections (fig 19). Unclearness of sutures in this area for a specimen whose sutures otherwise appear loose is most likely due to such bevelled contacts between the bones. On sections IV.1 to V.1, the vomer keeps its trapezoidal section, forming most of the floor of the rostral cavity. By drawing a line between the ventral exposure of the vomer on sections IV.1 and IV.2, the lateral margin of the vomer would run caudomedially. The vomer still appears present caudally as visible on sections V.2 and VII.1, trapezoidal in crosssection and forming most of the floor of the rostral cavity, though excluded from its ventral face by underlying palatine and rostral ramus of the pterygoid. The caudal-most extent of the vomer cannot be determined; it is not visible on section VII.2. For its whole length, the vomer exhibits a highly porous texture, with large, irregular intertrabecular spaces.

Palatine - On section V.1 (less clearly on section IV.2 due to calcite cover), the palatine is visible as a triangular bone forming almost half of the ventral face of the palatal area of the maxillary rostrum, restricting the participation of the maxilla to this face. The palatine keeps its triangular cross-section until section VII.1, extending dorsally to form the lateroventral corner of the rostral cavity, separating the maxilla from the vomer. On section VII.2, the palatine is trapezoidal and forms the floor of the rostral cavity; the palatomaxillary suture is still sub-vertical, while the palatopterygoid suture undulates from lateroventrally to mediodorsally. The only clear, genuine structure identifiable on the palatal surface is located toward the caudal margin of fragment V (only the left portion of the palatal surface at that level is visible). This shallow, 20 mm long, oval depression appears to be located on the palatopterygoid suture (as deduced from section V.2), about 10 mm lateral to the midline. Keeping in mind distortion the specimen

underwent, this depression is the only structure possibly identifiable as the traditionally called 'choana' (Buchy *et al.*, 2006a, b).



Figure 15: UANL-FCT-R8, Pliosauridae indet., a/ preserved portion of rostrum in left lateral view. b/ Interpretative drawing. Solid lines mark original margins of bone and teeth; dotted lines mark broken margins. Original surfaces are stippled. Teeth are numbered as discussed in the text (see also table 2). Note the contact area between fragments II and IV is reduced therefore the fragments were not glued to avoid further breakage. Scale 100 mm.



Figure 16: UANL-FCT-R8, Pliosauridae indet., a/ preserved portion of rostrum in right lateral view. b/ Interpretative drawing. Drawing conventions as in fig. 15. Scale 100 mm.



Figure 17: UANL-FCT-R8, Pliosauridae indet., a/ preserved portion of rostrum in ventral view. b/ Interpretative drawing. Drawing conventions as in fig. 15. Scale 100 mm.



Figure 18: UANL-FCT-R8, Pliosauridae indet., a/ preserved portion of rostrum in dorsal view. b/ Interpretative drawing. Drawing conventions as in fig. 15. Scale 100 mm.



Figure 19 (first part): UANL-FCT-R8, Pliosauridae indet., a/ sketch of the preserved portion of rostrum in right lateral view, showing the various fragments and their numbers as mentioned in the text. b/ Sections along the breaks discussed in the text, photos and interpretative line drawings. Each section is designated by the number of the fragment (from I to VIII) followed by . 1 for the rostral section, or .2 for the caudal one. For clarity in the photos, elements which should be visible due to perspective were erased und er Croel Photopaint. Matrix is hatched. Solid lines mark original margins of bone and teeth; dotted lines mark broken margins. Arrows point to the right of each section. Note smaller scale for Section VII.2. Scale 50 mm.



Figure 19 (continued).



Figure 19 (continued).

Pterygoid - The rostral ramus of the pterygoid is poorly visible on section V.2 due to calcite cover, but clearly visible on section VII.1, as a sub-triangular, medial element. Its contact with the palatine runs from ventromedially to caudolaterally; it underlies the vomer. Caudally, on section VII.2, it forms the medial half of the ventral surface of the maxillary rostrum. Tracing a

line between sections VII.1 and VII.2, the palatopterygoid suture is oriented caudolareally, though its actual course in ventral view cannot be determined.

Mandibular rostrum (dentary and splenial) - The mandibular symphysis reaches about the level of the rostral third of fragment VII and the rostral margin of upper tooth 11 (figs 15-17), that is, it is about 350 mm in length; the mandibular rostrum includes 9 to 10 teeth (as counted when reconstructing regularly alternating mandibular and dentary teeth, figs 15-18, table 2; see Discussion). The external face of the rostral-most portion of the mandibular rostrum (fragment I) is slightly weathered but close to original. It is spread with numerous millimetric foramina; a row of these runs 15 to 20 mm ventral to the dorsal margin of the dentary. This margin is subhorizontal, slightly festooned around the bases of the teeth. In lateral view, the ventral margin of the dentary gently slopes dorsally from the level of the fourth dentary tooth. The preserved portion is horizontal caudally. In ventral and dorsal views (although the latter is obscured by adjacent portions of the palatal area) the lateral margin of the dentary parallels the midline caudal to the same fourth dentary tooth; it runs straight rostromedially rostral to it, therefore forming a sharp, pointed mandibular rostral extremity. On the left side of the dentary an oval, 30 mm in maximal length, 10 mm in maximal width, depressed area filled with matrix possibly represents a bite mark; its centre is located about 30 mm lateral to the mandible midline, and about 40 mm rostral to the caudal break of the fragment. An area located ventral to dentary tooth 3 exhibits a wrinkled, irregular texture, possibly representing scar of an abscess.

In ventral view, the splenial possibly emerges also around the level of dentary tooth 4, but the area is obscured by glue and distorted. Due to partial preparation and calcite coverage, the extent of the splenial is not better visible on section I.2 (fig. 19): it may be reconstructed as a 10 mm high, triangular area with a 5 mm wide, ventral base. Of the caudal-most preserved portion of the mandible, on fragment VII, only the medial face is original, exposing the splenial whose width is better visible in section VII.2 (fig. 19): there, its width at mid-height of the mandibular ramus is 5 to 7 mm. Its ventral and dorsal extent cannot be determined.

Dentition - None of the teeth is completely preserved. As far as can be deduced from the various preserved fragments, the crowns are sub-circular in basal section and may become labiolingually compressed toward the apex. They exhibit very expressed mesial and distal carinae (fig. 20). The crowns appear stout, some bulbous at the base (whether originally or due to distortion); the mesial curvature being little expressed compared e.g. to UANL-FCT-R3 (Buchy *et al.*, 2006b). Incompleteness of all crowns, though, prevents definitive conclusion. The only preserved apex, of left premaxillary tooth 2 (fig. 20c), is blunt, possibly due to crushing; in any case it was not pointed. The carinae almost reach the smooth apex. Unusually, the preserved imprints of enamel from the lingual face of the crowns are smooth or only faintly ornamented

with discreete ridges; the fragments bearing imprints of the labial face of non-preserved crowns on the contrary are ornamented with clear, 2 mm-spaced ridges (fig. 20a).

Teeth preserved in occlusion appear to alternate regularly, except that no premaxillary tooth is preserved on either side between dentary teeth 3 and 4. Otherwise, clearly alternating teeth are preserved until fragment II on the left and fragment IV on the right (upper tooth 6 and following dentary tooth; figs 15-18). If a diastema was existing, it must have been located either between dentary teeth 3 and 4, or at least 2 tooth positions caudal to the premaxillomaxillary suture, or the premaxilla must have housed either only 3 teeth or more than the usual 5 teeth (all alternatives appearing unlikely according to the course of the premaxillomaxillary suture in lateral view, see above). The first right dentary tooth is located so close to the symphysis that its alveolus appears confluent with it. Its right counterpart cannot be seen due to matrix cover, though the first right premaxillary tooth occludes over the rostral-most extremity of the right dentary, leaving no space for a symmetrical dentary tooth (figs 16, 17). As the middle portion of the mandibular rostrum is missing, it cannot be determined which of the presumed 9-10 symphysial teeth are the largest. As preserved, they appear to increase abruptly in size between dentary teeth 2 and 3, the largest being located in positions 6 to 9 (table 2).

Discussion: UANL-FCT-R8 differs from UANL-FCT-R3 in tooth morphology, the absence of a ventral inflection of the mandibular rostrum rostral to the point where the splenial disappears in ventral view, of a rostral prolongation of the ?parietal between the premaxillae, of a vomerine cavity; and in the sub-triangular cross-section of the maxillary rostrum (fig. 19; Buchy *et al.*, 2006b). These differences would warrant distinction at generic level of the two Mexican specimens (Noè *et al.*, 2004), though erection of new taxa can only be done in a proper context of well-defined related and/or coeval forms, which is currently not the case for Late Jurassic pliosaurs (UANL-FCT-R3 possibly represents a peculiar case, in being the first pliosaur described as possessing a rostral prolongation of the ?parietal, Buchy *et al.*, 2006b). Late Jurassic English pliosaurs were last reviewed by Tarlo (1960), and few selective studies since brought spot light upon some taxa (Bardet *et al.*, 1993, 1994; Taylor & Cruickshank, 1993; Noè *et al.*, 2004).

In their description of a new species of Kimmeridge Clay pliosaur preliminarily assigned to the genus *Pliosaurus*, Noè *et al.* (2004) consider of taxonomical import the 'length of the mandibular symphysis' (i.e. the number of teeth born by the mandibular rostrum), and the number of dentary tooth positions (the length of the tooth row); they reject the number of caniniforms within the mandibular rostrum and the position of the largest caniniform. It is to be noted that the mandibular rostrum is the most massive part of a pliosaur skull, therefore the most likely portion to be preserved - and the easiest element to identify. It appears natural to seek diagnostic features in what is the most abundantly available for study, though, as for most features considered diagnostic in Plesiosauria, the absence of close, Recent relatives prevents a sufficiently supported application of the principle of actualism (see e.g. a discussion about tooth count in Buchy *et al.*, 2005a). Similarly, the length of the tooth row as such has little biological meaning. It should at least be considered e.g. relative to skull length (from the rostral extremity to either the glenoid or the occipital condyle - depending on the mechanical model considered), or relative to skull width. In all instances, a simplistic, strict relationship between length of the rostrum and diet (e.g. Massare, 1987) does not resist a close examination of anatomy and feeding habits of Recent forms (Buchy, submitted).



Figure 20: UANL-FCT-R8, Pliosauridae indet., a/ imprint of two teeth preserved on an isolated, non-matching fragment. b/ First right premaxillary tooth in rostrolateral view. c/ First and second left premaxillary teeth in lateral view. Scale 20 mm.

Right dentary tooth #	Basal diameter (mm)	Right upper tooth #	Basal diameter (mm)
1	12	1	17
2	17	2	/
3	26	/	/
4	27	/	/
5	/	5	27
6	/	6	29
/	/	7	30
/	/	8	/
9	/	9	/
10	25	10	28
11	/	11	25
12	25	12	/
Left upper tooth #		Left dentary tooth #	
1	15	/	/
2	18	2	/
3	/	3	/
/	/	4	/
5	20	5	27
6	/	6	/
7	30		
8	28		
9	30		
10	/	1	
11	30		
12	/]	

Table 2: UANL-FCT-R8, Pliosauridae indet., diameter of the preserved teeth, in mm.

Of the two features rejected by Noè *et al.* (2004), both deal with 'caniniform' teeth. The usage of this term is very characteristic of what the same authors lament upon: poor description of dental anatomy of pliosaurs - indeed of sauropterygians in general. 'Caniniforms' cannot exist in the absence of 'incisiforms' and/or 'molariforms'. These terms are qualitative, they refer to the presence of different tooth morphotypes, i.e. when the dentition is heterodont (e.g. Peyer, 1968; Buchy, 1998). What is meant by these authors (and many others) is a difference in size - quantitative - as is clear in the discussion dealing with the size of the alveoli compared to the size of the (non preserved) tooth crowns: dentition of Late Jurassic pliosaurs is anisodont, 'caniniformes' are merely enlarged teeth in most instances, and when not, general confusion in the use of terms makes it impossible to understand.

The number of enlarged teeth in the mandibular rostrum is rejected by Noè *et al.* (2004) as a diagnostic feature because they are considered constrained by the size of corresponding premaxillary/maxillary teeth. It is unclear why the number of enlarged premaxillary/maxillary teeth should not be diagnostic; possibly as noted above, because often only the mandibular rostrum is preserved. As for the taxonomical import of the position of the largest of the enlarged teeth of the mandibular rostrum, the problem is probably biologically very complex - and very simple: for the living animal, the only parameter that counted was to have a functional tooth row, despite permanent replacement (Buchy, 1998). Therefore, evaluation of this feature and its taxonomical meaning will require proper understanding of - among others - tooth replacement pattern, biomechanics of the jaw apparatus, bone/tooth physiology and turn over. In response to permanent replacement, a very high plasticity in the location of the functional part of the dentition is to be expected - though the relative size of the teeth and position of largest teeth could still reveal genetically constrained and therefore taxonomically significant.

In summary, for matter of comparison with the presently discussed specimen, the number of symphysial teeth has to be given primordial import, both because it is currently the most considered feature, and what is preserved. The length of the tooth row is available in few taxa only, and therefore of dubious usefulness (Noè *et al.*, 2004). As for the size of the teeth (symphysial or not), it is still believed here that the position of the largest enlarged teeth should be considered, at least in the frame of a comparison of the anatomy of the rostrum in general, as it is unknown whether the size of the teeth constrains the size of the rostrum or *vice-versa*; hopefully, re-assessment of old specimens and discovery of new ones will clarify the debate.

With an estimate of 9-10 symphysial teeth, UANL-FCT-R8 represents a 'longisymphysial' form, excluding close affinities to forms characterised by a short or spatulate mandibular rostrum, like e.g. Liopleurodon, Kronosaurus, Simolestes and Maresaurus, (Gasparini, 1997; Noè, 2001; Noè et al., 2004; pers. obs). Late Jurassic 'longisymphysial' pliosaurs though are very poorly known, including the historical genus *Pliosaurus* and forms currently wanting taxonomical reassessment (Tarlo, 1959, 1960; Taylor & Cruickshank, 1993; Noè, 2001; Noè et al., 2004). As noted by Taylor & Cruickshank (1993), the two Kimmeridgian species of Pliosaurus recognised by Tarlo (1960) differ by poorly diagnostic features; Noè et al. (2004) emphasise the fragmentary nature of both holotypes and the lack of recent, comprehensive studies cleaning up 150 years of poorly justified assignment of specimens. Noè (2001) suggests to restrict the genus to forms with a long mandibular rostrum (bearing 10 to 12 teeth) and trihedral teeth, leaving forms with subsymmetrical teeth in a taxonomical fog. At present, Noè et al. (2004) list as Late Jurassic pliosaurs preliminarily assigned to the genus Pliosaurus (also wanting a thorough comprehensive review, suspected to belong to at least two different genera, and the tooth anatomy of some being unknown): P. brachydeirus with 10-11 symphysial teeth, P. brachyspondylus with 9-10 (Bardet et al., 1993, 1994), P. portentificus with 8, and specimens formerly assigned to Liopleurodon macromerus reverted to Pliosaurus macromerus, with 5-6. However, Tarlo's (1960) diagnosis of the genus remains, emphasising trihedral teeth and long symphysis.

UANL-FCT-R8 does not fit the current diagnosis of *Pliosaurus*: it differs from specimens currently assigned to the genus in the premaxilla overhanging the rostrally pointed mandibular rostrum, the tooth crown morphology (at least rostrally), the straight ventral (caudal to dentary tooth 4) and dorsal margins of the dentary. Pending re-description of European forms, its

taxonomical status is for now unresolved, as are, like for UANL-FCT-R3, its affinities with European contemporaneous forms.

UANL-FCT-R8, a Kimmeridgian form with teeth sub-circular in cross-section confirms the doubts expressed by Bardet et al. (1994) and Noè (2001) upon Tarlo's (1960) assumption as to the stratigraphical import of pliosaurian tooth cross-section. If Tarlo's (1960) conclusions reveal valid and are to be viewed in an evolutionary perspective (a trend from simple, conical teeth toward trihedral teeth between Middle and Upper Jurassic), the Mexican form may reveal a relic in the protected Late Jurassic Mexican Gulf.

CPC 226 (figs 21-23)

Material: Possibly sub-complete skeleton, including weathered skull and mandible.

Former accession number: CEP1843 (Buchy et al., 2006c)

Origin: Early Tithonian section of the La Caja Formation at the Sierra El Jabalí, near Gomez Farías, Coahuila, Mexico (fig. 2); parts of the skull and cervical vertebrae were first collected by J. Lopez Espinoza in 1999, more parts of the specimen (a humerus, cervical vertebrae, rib fragments) were rescued during subsequent field campaigns in March and September 2004, and February 2006. More postcranial material is awaiting collection in the field. Preparation of the postorbital portion of the skull and several cervical vertebrae was conducted by J. Lopez Espinoza and the author. Preparation of what appears to be the rostrum and other postcranial remains collected recently could not be completed yet.

Preservation: At present, the embedding situation of the skeleton cannot be evaluated as most of the collected material is awaiting preparation, while possibly the caudal half of the specimen is to be excavated. Moreover, collection by several persons over many years yielded incomplete data. The material available for study now comprises the medial portion of the postorbital region of the skull with underlying elements of brain case, all heavily weathered and/or incompletely prepared; several cervical vertebrae; phalanxes. Like for all vertebrate remains from the locality, the contrast is poor between matrix and bone (Buchy *et al.*, 2006c), resulting in many uncertainties upon the actual anatomy of the specimen. This is especially the case for the skull, where individual bones were pressed against one another and, also because of partial preparation, whose outlines are difficult to trace. Neural arches - at least of the known vertebrae - were unfused, hinting at what is traditionally called a 'juvenile' individual (see UANL-FCT-R2).

Description: *Skull* - The preserved portion of skull is broken in two parts, approximately level with the middle of the upper temporal fenestrae; the contact between the two parts is faint and for convenience they were not glued together (figs 21, 22). The rostal portion of skull is heavily weathered so that almost no original dorsal surface is preserved; sutures are therefore visible at an

unknown level within the skull thickness, which renders comparisons with described taxa impossible.



Figure 21: CPC 226, Pliosauridae indet., a/ both preserved parts of skull in dorsal view (see text). b/ Interpretative line drawing. Scale 100 mm.

Frontal - A suture runs caudolaterally and individualises a sub-quadrangular portion of bone at the left rostral-most corner of the specimen. From its location, this bone may be the frontal, but no anatomical detail is preserved.

Prefrontal - Similarly, a clear suture separates the right laterorostral-most portion of the specimen. It should separate the prefrontal rostrolaterally from the postfrontal.

Postfrontal - On both sides the postfrontal is poorly preserved; its suture with the parietal runs caudally, slightly laterally and then slightly medially, from the rostral extremity of the specimen until approximately level with the rostral fourth of the parietal foramen. The caudal

margin of the postfrontal on both sides may be close to original, according to the breakage pattern of the lateral margins of the intertemporal bar.

Parietal - About 20 mm lateral to the midline on either side on the rostral-most portion of the specimen, runs a possible suture for 10 mm on the right side, slightly longer on the left. If this structure actually represents a suture, it may be marking a ventral process of the frontal or premaxilla underlying the parietal there, and visible due to weathering. Noè (2001) indicates that the parietal underlies the frontal in *Liopleurodon*, while Buchy *et al.* (2006b) describe a ventral process of possibly the parietal underlying the premaxillae in the pliosaur UANL-FCT-R3 (see above); the nature of this element in CPC 226, if not an artefact, is therefore enigmatic.

The parietal foramen is long oval. Its margins are gently rounded. Lateral and rostral to it, the surface of the parietal slopes ventrally so that the foramen is set higher than the level of the interobital surface of the skull. Nothing more of the original surface of the intertemporal part of the parietal is preserved. The lateral margins of the intertemporal bar were pressed dorsally, and are preserved as broken, overlapping fragments; their original ventral extent cannot be determined. Level with the caudal extremity of the parietal foramen, an oval, lateroventrally oriented depression in the lateral margin of the intertemporal bar may represent the epipterygoid facet. The caudal-most dorsal portion of the parietal is better preserved, except for the temporal bar itself that most likely was weathered prior to collection. The lateral margin of the parietal curves gently caudolaterally to form the mediocaudal corner of the upper temporal fossa; due to distortion over underlying brain case elements, the margin of the upper temporal fossa there appears asymetrical between right and left side. It is probably closer to original on the left side, as there, are fewer underlying elements. The rostral-most portion of the contact with the squamosal is not visible due to overlying unidentified bones. It runs caudally, slightly medially until the broken caudal extremity of the specimen. Along that break, the parietosquamosal suture is Sshaped, a flange of the squamosal overlaping the parietal dorsally, while a flange of the parietal underlaps the squamosal ventrally. The ventral face is difficult to interpret; the parietosquamosal suture appears to run along the same path as its dorsal part. The visible portion of the ventral surface of the parietal located where the bone forms the caudomedial corner of the upper temporal fossa bears large, irregular grooves, possibly the facet for the supraoccipital.

Squamosal - The dorsal surface of the squamosal slopes gently caudally until its caudal extremity. Its caudal margin, where preserved, is gently rounded. In ventral view, poorly preserved bone might represent its quadrate ramus and obscures the ventral surface of its parietal ramus. The rostral margin of the parietal ramus forms a flange (that may have been a buttress prior to weathering) bordering the upper temporal fossa.



Figure 22: CPC 226, caudal portion of skull (see fig. 21) a/ in ventral view. b/ Interpretative line drawing. Scale 100 mm.

Elements of the brain case - Interpretation of the various bones preserved in the area is additionally hindered by the generally poor knowledge of pliosaur brain case, possibly due to poor ossification (e.g. Noè, 2001; O'Keefe, 2001). All conclusions reached here are therefore provisional, pending further preparation and study of comparable material. Two fan-shaped elements preserved in the right upper temporal fossa rostral to the rostral-most point of contact between parietal and squamosal (fig. 21) are similar in outline to the prootic of Muraenosaurus described by Maisch (1998: fig. 11). However, no surface details are visible. Various fragments of flat, thin bones, with few identifiable original margins, probably represent parts of the pterygoids and other bones of the palate. Moreover, the quadrate ramus of the pterygoid is possibly partly present, ventral to the right caudal-most portion of the parietal (fig. 22; see also White, 1935: pl. 9). It is high oval in cross-section, the visible suface slightly concave along its long axis. The right exoccipital-opisthotic is visible in caudomedial view, and although distorted, comparable to what is described in *Muraenosaurus* by Maisch (1998: fig. 9a; see also Storrs & Taylor, 1996). It differs from the same element in *Liopleurodon* described by Noè (2001: fig. 43), possibly due to incomplete preservation of the latter. In CPC 226, the paroccipital process is sub-triangular in cross-section where broken about 20 mm away from the main body of the bone. This is high triangular in outline, its dorsal portion broken and/or obscured by sediment. Its surface is spread with numerous foraminae, four of which are larger. The first is located on the rostral margin of the bone, about 10 mm dorsal to its ventral margin; the second is slightly higher, 10 mm further caudally; the third is the largest, almost 5 mm in diameter and located 20 mm dorsal to the second; the fourth is at the level of the first, about 15 mm caudal to the second. They could represent exits for the cranial nerves respectively IX to XII, following the interpretations of Maisch (1998) and Carpenter (1997: fig. 5). Clearly, taxonomically close specimens with comparable preserved material would help assess the accuracy of this interpretation.

Cervical vertebrae - The cervical vertebrae available for study are oval in articular aspect, mediolaterally elongate (fig. 23). They confirm the pliosaurian nature of the specimen in being craniocaudally short. A notochordal pit is visible, located in the center of a raised area in the middle of the articular faces.



Figure 23: CPC 226, Pliosauridae indet., cervical vertebra in a/ articular, b/ dorsal and c/ ventral views. Scale 100 mm.

Discussion: The specimen being mostly unprepared, little can be said upon its affinities. Most of the skull was weathered, leaving as original only the parietosquamosal suture and possibly the exoccipital-opisthotic, which are unfortunately poorly known in most pliosaurs (e.g. Noè, 2001). From the size of the known cervical vertebrae, it most likely represents a medium-sized animal, possibly 8 to 10 m in length, and uncompletely ossified (see UANL-FCT-R2).

CPC 228

Material: Partial isolated cervical centrum.

Former accession number: CEP1850 (Buchy et al., 2006c)

Origin: Early Tithonian section of the La Caja Formation at the Sierra El Jabalí, near Gomez Farías, Coahuila, Mexico (fig. 2); collected in March 2004.

Preservation: The specimen is a 'slice' of the centrum, comprising ventrally the medial-most portion (as testified by both subcentral foramina) and dorsally a portion of the neural arch facet. The specimen was prepared by S. Stinnesbeck at the SMNK and the author at the MUDE.

Description: The height of the centrum was about 120 mm, its length about 60 mm. Its width cannot be evaluated, nor whether it was sub-circular or transversely enlarged (as e.g. CPC 226). The articular faces appear slightly depressed in their middle.

Comments: The size and anatomy of what is preserved of the centrum fits the pliosaur CPC 226. Though, the finding places within the site of both fossils indicates that they probably belong to different individuals (except in case of human transport), if possibly to the same taxon.

I.2.3.4. Discussion

Buchy *et al.* (2006d) identified three, possibly four different pliosaur taxa from the Kimmeridgian Mexican Gulf. This count is confirmed by the above description of UANL-FCT-R8. The Mexican assemblage described here comprises a very large form, whose skeleton shows clear signs of osteological immaturity, whether due to young individual age or of taxonomical import (UANL-FCT-R2). A medium-sized group (possibly about 10 m in length) is represented by UANL-FCT-R7 and R8, the former also showing immature bone condition, while the individual age of the latter cannot be determined - and neither the taxonomic similarity of the specimens. UANL-FCT-R3 is a smaller form, anatomically distinct from UANL-FCT-R8. The Kimmeridgian Mexican Gulf was populated by at least three taxa of pliosaurs (see a discussion in Buchy *et al.*, 2006d), which is similar to the pliosaurian assemblage of the English Kimmeridge Clay (Noè *et al.*, 2004), although none of the Mexican forms can be clearly referred to a previously known taxon.

As for the Tithonian, with a single, potentially diagnostic pliosaur wanting preparation, not much can be said, except that it appears to represent a medium-sized taxon, based on the size of the cervical vertebrae.

At present, Mexican pliosaurs are of unclear affinities, 'longisymphysial', of large size and massive (in terms of thickness of the bones in cross-section; however, few studies describe cross-sections as most were re-glued prior to study, see Buchy *et al.*, 2006a).

Elasmosaurs are rare in both the Kimmeridgian and the Tithonian of Mexico, and known specimens are of no current taxonomic value beyond family level (but see Buchy, 2005: poor understanding of the group makes taxonomical status of even sub-complete specimens uncertain; Elasmosauridae appears to be one of the last groups for which 'gattungsmackery' [Owen, 1869: 8] is still at work, see e.g. Sato, 2003; Druckenmiller & Russell, 2006). The raison d'être of the exceedingly long neck of elasmosaurs has long been an enigma, possibly due to the lack of proper biomechanical analysis to the benefit of sole examination of tooth morphology (e.g. Massare, 1987): long, sharp, closely-spaced teeth were long considered a fish-piercing device, by comparison with Recent piscivorous crocodiles, resulting in the beautiful, biomechanically unlikely reconstructions of animals with a snake-like neck snapping at fish or even pterosaurs.

Recently, several authors more or less independently came to re-examine the question, and slowly emerges the picture of sediment sieving elasmosaurs, and a diet mostly relying upon sea floor invertebrates in the shallow, soft substrate areas available following transgressive phases (Buchy, 1998, 2005, 2006; McHenry *et al.*, 2005; Noè, 2006). Clearly, under this life-style hypothesis, the Late Jurassic Mexican Gulf, at least where the La Casita/La Caja Formations yielded marine reptiles for now, did not constitute favourable environments. It is to be noted that elasmosaurs appear more abundant in the Upper Cretaceous (?Campanian-Maastrichtian) of the region of Saltillo (fig. 2), represented by several clusters of vertebrae; the material (of at present poor taxonomical value) is in private hands and of currently unprecise origin, and therefore not dealt with here, study pending examination of the localities and clarification of the status of the specimens.

I.3. Discussion

The Kimmeridgian assemblage of marine reptiles in the Mexican Gulf was discussed by Buchy *et al.* (2006d), and little can be added for now. Of the two specimens which were not known then, both referred to *Dakosaurus* sp. (specimens CPC 201 and UANL-FCT-R29), one comes from the south of Nuevo León (Zaragoza; fig. 2), the second from a northern site (San Juan de los Dolores; fig. 2), therefore possibly invalidating the suggested trend of thalattosuchians to become rare in the south. As was concluded by Buchy *et al.* (2006), more specimens are to be added to the sample to deduce ecological partitions.

The same holds for the Tithonian at Gomez Farías. The assemblage is dominated (numerically) by thalattosuchians and ichthyosaurs. Pliosaurs are rare though one is probably subcomplete; such large predators must have been rare anyway in the fauna. The preservation status of elasmosaurs most likely indicates distant living areas. A point of interest is that, after several field campaigns and exploration of a very rich site (Buchy *et al.*, 2006c) by private collectors as well as members of institutions, no specimen referrable to Testudines was found yet. It was suggested by Buchy *et al.* (2006d) that turtles had not made it from Europe to the Mexican Gulf by the Kimmeridgian. Marine turtles are present in the Tithonian Neuquén Basin of Argentina (Fernández & Fuente, 1993; Gasparini & Fernández, 1997, 2005). Their absence in the Tithonian Mexican Gulf appears the main peculiarity of the assemblage.

As was emphasized by description of new taxa (Frey *et al.*, 2002; Buchy *et al.*, 2006e), but also by other specimens (Buchy *et al.*, 2003, 2005c, 2006b, d, in press), marine reptiles from the Late Jurassic Mexican Gulf do not show clear affinities to European and Pacific forms and appear to confirm the isolation of the area as deduced from invertebrate assemblages (Buchy *et al.*, 2006d)

and references therein). The statement has to be somewhat moderated, though, due to the incompleteness or need of preparation of most of the Mexican specimens, but also to the poor knowledge of European forms (especially pliosaurs and thalattosuchians) and consequently, of their palaeobiogeographical history. The rostral prolongation of the ?parietal in UANL-FCT-R3 appears to indicate affinities with Cretaceous Australian forms (Buchy *et al.*, 2006b), though, a similar anatomy may be present as well in some English Upper Jurassic specimens (Noè, pers. com., 2006). Pending description of these, and also of Australian specimens, it is unknown whether the same bone is involved and the feature can be considered as an apomorphy, or if the structure is a mere biomechanical requirement achieved along different paths. At present, the identification of *Ophthalmosaurus icenicus* in the assemblage is interpreted as marking more ubiquitous habits of ichthyosaurs as compared to other marine reptiles, though discovery of more complete Mexican specimens might change the figure.

Marine reptiles described here do substantially increase our knowledge of the groups apart from palaeobiogeographical considerations: the 3-dimensional preservation of several specimens was the opportunity to reassess the nature of choanae in plesiosaurs (Buchy *et al.*, 2006a; confirmed by UANL-FCT-R8), and location of salt glands in thalattosuchians (Buchy *et al.*, in press).

Part II. Upper Cretaceous

II.1. Early Turonian Agua Nueva Formation at Vallecillo, Nuevo León

II.1.1. Palaeogeographical context

The laminated limestones of the Agua Nueva Formation at Vallecillo (fig. 2) and their fossil contents were recently the subject of two PhDs (Blanco-Piñon, 2003; Ifrim, 2006). A summary of both regarding marine reptiles and their palaeogeographical context was given by Buchy *et al.* (2004, 2005b). It is of some import for the discussion of the assemblage to re-emphasise that the Vallecillo limestone represent an open marine Plattenkalk deposit (Ifrim, 2006; fig. 24).



Figure 24: Palaeobiogeographical map of the Turonian (modified from Smith *et al.*, 1994). Insert: palaeobiogeographical map of north-east Mexico during the Turonian; M: Monterrey; S: Saltillo (redrawn after Stinnesbeck *et al.*, 2005).

II.1.2. Pliosauridae cf. Polyptychodon

UANL-FCT-R26 (fig. 25)

Material: Isolated partial tooth.

Origin: Early Turonian Agua Nueva Formation at Vallecillo, Nuevo León (fig. 2), collected in March 2002 by C. Ifrim (Ifrim *et al.*, 2004, 2005a, b; Ifrim, 2006, in press; pers. com.).

Preservation: The apex is broken approximately at two-thirds of the crown height; only the apical-most portion of the root is preserved. Enamel is absent and dentine was probably replaced by calcite, as is common for fossils from this locality (Blanco-Piñon *et al.*, 2001; Blanco-Piñon, 2003; Ifrim, 2006).

Description: The basal diameter of the crown is approximately 20 mm. It is slightly curved mesially and labiolingually compressed, though carinae appear absent. Both lingual and labial surfaces show regularly spaced ridges. A vertically oval wear facet is present distally at the base of the crown.



Figure 25: UANL-FCT-R26, cf. *Polyptychodon*, isolated partial tooth. Scale 20 mm. Photo C. Ifrim.

Discussion: Absence of shouldering between crown and root excludes mosasaurian affinities. The pattern of regularly spaced ridges around the crown, the subcircular cross-section at the base of the crown, the slight mesial curvature of the crown, as well as the palaeogeographical and stratigraphical occurrences are strongly reminiscent of the pliosaurian genus *Polyptychodon* Owen, 1841 from the Cenomanian of England, also known from the Eagle Ford Shales of Texas (Cenomanian-Turonian; Welles & Slaughter, 1963).

Squamata Oppel, 1811 Anguimorpha Fürbringer, 1900 Mosasauroidea Gervais, 1853

II.1.3. 'Aigialosaurs' indet.

The systematics and taxonomy of what was formerly considered as ancestral forms to mosasaurs (e.g. Gorjanović-Kramberger, 1892; Dollo, 1892, 1903; Nopcsa, 1903, 1923; see a review in Dutchak, 2005; Smith & Buchy, submitted) are currently undergoing a maelstrom of cladistic analyses, that yielded yet no generally accepted, comprehensive, stable results concerning relationships, and therefore taxonomy (Dutchak, 2005; Smith & Buchy, submitted). Possibly due to certain similarities to Recent forms, Cretaceous marine squamates appear a favourite subject for cladistic analyses probing what softwares may add to traditional views of the transition from terrestrial to marine life, although few independant data sets have been analysed, as pointed out by Dutchak (2005). Bell's (1993; 1997) matrix is the most commonly used, while its published version allegedly contains several miscodings (N. Bonde, oral communication, 1st Mosasaur Meeting, Maastricht, 2004).

Allegedly seeking to clarify the matter and examine specimens within a frame 'unburdened by phylogenetic context' Bell & Polcyn (2005: 178) and Polcyn & Bell (2005) introduce the terms 'plesiopedal' versus 'hydropedal'. As discussed by Smith & Buchy (submitted), the use of the new terms by their authors is at best self-contradictory, and in any case of little more use than an informal 'aigialosaurs'. And, as implied by Dutchak (2005), stable nomenclature is still wanting following the introduction of the new terminology. While the terms aigialosaur, coniasaur and dolichosaur are still in 'loose' use (Evans *et al.*, 2006: 1143, 1155), these groups are also now designated by convoluted expressions, like 'early', 'basal' or 'primitive' mosasauroid (e.g. Bell & Polcyn, 2005), or 'long-bodied lizard' (Evans *et al.*, 2006). Moreover, an intriguing, fresh water form was recently discovered in the Santonian of Hungary (Makádi, 2005), which was not included in these analyses. It is expected that mosasauroid systematics will be explored for a while, and that possibly cladistic analyses will not have the last word. As this volume is more of a catalogue of north-east Mexican fossils, the systematic debate is eschewed in favor of examination of the specimens themselves, in the hope that new data will finally help solve the issue.

UANL-FCT-R27 (Buchy *et al.* 2004: fig. 2; 2005b: fig. 3a, b; Buchy & Smith, 2005; Ifrim, 2006: fig. 7.17c; Smith & Buchy, submitted; figs 26, 27).



Figure 26: UANL-FCT-R27, aigialosaur indet., line drawing of the specimen, parts -1 (left) and -4 (right; see text; modified from Smith & Buchy, in press). Note an undetermined fish is preserved in the abdominal area, possibly representing gastric contents. Scale 50 mm.



Material: At present, this specimen (fig. 26) comprises a main slab (UANL-FCT-R27-1) preserving a long segment of tail, subcomplete left hind limb, right femur, left pelvic girdle and part of the lumbar region. Two small slabs (UANL-FCT-R27-2, -3) are partial counterparts of the main slab, mostly comprising fragments of vertebrae. A further slab (UANL-FCT-R27-4) and its counterpart (UANL-FCT-R27-5) comprise the trunk (lacking vertebrae) and the two subcomplete manus. The portion comprising the counterpart of the left pelvic region and hind pes and right femur bears number UANL-FCT-R27-6, while the adjacent portion comprising the counterpart of the cranial-most portion of the tail bears number UANL-FCT-R27-7. The specimen shows exquisite preservation of integumentary structures, as well as a possible gastric contents and pebble-like elements within the abdomen.

As emphasised by the sequence of numbering, the history of discovery (or rather rediscovery) of the specimen is complex. The fragments were collected by the quarry owner for the UANL-FCT and transferred first to the UANL-FCT; some then made their way to Germany for study. Thus, the author and colleagues were first aware of UANL-FCT-R27-1 to -3, and gave preliminary descriptions of these remains (Buchy *et al.*, 2004, 2005b; Buchy & Smith, 2005). Together with these fragments was a slab containing a partial manus (Buchy *et al.*, 2004, 2005b; Buchy & Smith, 2005; fig. 28), thought to belong to the same individual. Smith & Buchy (submitted) expressed a doubt upon the attribution of this manus, and noted it was given accession number UANL-FCT-R28. Subsequently, more fragments of UANL-FCT-R27 turned up, rediscovered (together with UANL-FCT-R30) among the Vallecillo collections at the UANL-FCT by C. Ifrim and S. Giersch (pers. com., 2006). As the part and counterpart, UANL-FCT-R27-4 and -5, contain both manus, the isolated, partial manus UANL-FCT-R28 obviously does not belong to UANL-FCT-R27 (Buchy & Smith, in prep.).

Origin: Early Turonian Agua Nueva Formation at Vallecillo, Nuevo León (fig. 2), collected by the quarry owner for the UANL-FCT.

Comments: A detailed description of parts -1 to -3 of the specimen by Smith & Buchy is in the review process. A brief account of its anatomy and relationships was given by Buchy *et al.* (2004; 2005b), reference to which it is here made in order to respect rules of priority. A description of parts -4 to -7 is in preparation. Here is illustrated the manus (fig. 27), and measurements of its elements are given in table 3, for comparison with UANL-FCT-R28 (see further). Smith & Buchy (submitted) indicate that the specimen represents a new taxon, distinguished from other 'aigialosaurs' by, among others, features of its hind limb. Assessment of its affinities, however, is hindered by its incompleteness, as well as poor understanding of the relationships within the

group as was noted in introduction. Buchy *et al.* (2005) and Smith & Buchy (submitted) note that it shares features with Mosasauroidea but lacks derived features of Mosasauridae.



Figure 27: UANL-FCT-R27-4 (see text), aigialosaur indet., partial left manus. a/ Photograph and b/ interpretative drawing (no original surface is preserved). Scale in mm. Photo K. T. Smith.

Element	Length	Element	Length	
metacarpal I	8.5	phalanx IV.1	5.5	
phalanx I.1	6.2	phalanx IV.2	5.1	
metacarpal II	9.6	phalanx IV.3	/	
phalanx II.1	/	metacarpal V	7.7	
metacarpal III	10.5	phalanx V.1	6.6	
phalanx III.1	/	phalanx V.2	6.7	
metacarpal IV	10.5	phalanx V.3	/	

Table 3: Measurements on the left manus of UANL-FCT-R27, in mm. All measurements made, when possible, at the midpoints of articulation of the bone.

UANL-FCT-R28 (Buchy et al., 2005b: fig. 3c; fig. 28, tables 4, 5)

Material: Partial manus.

Origin: The origin of this specimen is unclear. It was formerly thought to belong to UANL-FCT-R27, and illustrated as so (Buchy *et al.*, 2005b: fig. 3c; see above). The matrix and repository conditions indicate an Early Turonian Agua Nueva Formation at Vallecillo, Nuevo León (fig. 2).

Preservation: Metacarpals I–IV are poorly and only partially preserved, while metacarpal V is missing altogether. Some of the surface bone was most likely lost to the counterpart.

Description: Measurements of the various elements of the manus can be found in table 4. On either side of metacarpal I, unidentified bone fragments indicate some disarticulation of the digits in relation to the carpus. Metacarpal I appears sub-complete, and is short. The length of all other metacarpals is unknown. Digits III and IV are subequal in length. The phalangeal formula was probably 2-3-4-5-3.



Figure 28: UANL-FCT-R28, aigialosaur indet., partial manus. a/ Photograph and b/ interpretative drawing. Places where stippling is absent are places where the bone surface has been stripped away. Scale 5 mm. Photo K. T. Smith.

Discussion: UANL-FCT-R28 is larger than the manus of UANL-FCT-R27; the various elements also appear more slender, although this might be due to the orientation of the bone and splitting pattern. The only preserved elements of UANL-FCT-R28 whose length can be determined and are also known in UANL-FCT-R27 are phalanges I.1, IV.1, IV.2 and V.2. Calculated ratios (table 5) indicate different proportions for these elements in UANL-FCT-R27 and -R28, although the significance of the differences is unknown, and could be ontogenetic, related to sexual dimorphism and/or individual variation.

Part II.1.	Upper	Cretaceous	Early	Turonian	Agua	Nueva	Formation
			~		<u> </u>		

Element	Length	Element	Length
phalanx I.1	11.2	phalanx IV.1	9.7
phalanx I.2	5.3	phalanx IV.2	7.5
phalanx II.1	10.2	phalanx IV.3	6.4
phalanx II.2	10.0	phalanx IV.4	7.1
phalanx II.3	4.0	phalanx IV.5	4.1
phalanx III.1	10.8	phalanx V.1	/
phalanx III.2	8.2	phalanx V.2	7.2
phalanx III.3	8.5	phalanx V.3	4.5
phalanx III.4	4.6		

Table 4: Measurements on the manus UANL-FCT-R28, in mm. All measurements made, when possible, at the midpoints of articulation of the bone.

Ratio	UANL-FCT-R27	UANL-FCT-R28
I.1/V.2	0.92	1.55
I.1/IV.1	1.12	1.5
I.1/IV.2	1.2	1,5
IV.1/IV.2	1.07	1.29
IV.1/V.2	0.82	1.34
IV.2/V.2	0.76	1.04

Table 5: Ratios calculated between elements known in both manus UANL-FCT-R27 and -R28.

UANL-FCT-R30 (fig. 29)

Material: Ten articulated vertebrae including first caudal and sacrals, and fragments of 2 additional, cranially adjacent centra, poorly preserved on a slab; articulated ribs and portions of 3 additional ribs pertaining to cranially adjacent, non preserved vertebrae; possibly portions of pelvic girdle.

Origin: Although the matrix clearly indicates that the specimen comes from the Vallecillo limestones, the finding data are unknown. The specimen was re-discovered by S. Giersch among the Vallecillo 'fish collection' of the UANL-FCT in September 2006.

Preservation: The specimen is preserved on a limestone slab broken into 6 fragments. The bone is weathered so that only the outline of the vertebrae is original. The specimen is currently coated with glue that further obscures its anatomy; some areas (synapophyses, possibly pre- and postzygapophyses) are still covered with matrix. The centra are therefore actually identified by the ribs they bear. It is impossible for now to determine whether the specimen is visible in ventral or dorsal view; in what follows, 'left' and 'right' refer to the current visible aspect of the specimen (fig. 29).

Description: All centra measure approximately 20 mm in length, with a minimum, median diameter of about 12 mm.

The last preserved vertebra on the slab is the first caudal, its transverse process laterally directed; the following two vertebrae are sacrals, as witnessed by the sacral ribs. These are better visible on the right side, whereas they are either broken or still partly embedded in matrix on the left. The caudal-most sacral rib points laterally. The first sacral rib is directed caudolaterally; its

caudal margin is thickened and forms a buttress. A patch of bone-like substance underlies the caudal-most sacral rib and could represent part of the girdle.



Figure 29: UANL-FCT-R30, aigialosaur indet., partial vertebral column. a/ Photograph and b/ interpretative drawing. Scale 50 mm.

What appears as a pair of long oval elements, oriented craniolaterally on either side of the vertebral column, could also represent parts of the girdle, possibly the ilia, then close to their original contact with the sacral ribs.

Along the caudal break of the specimen, to the right of the vertebral column, a fragment of bone, 20 mm in proximodistal length, is present lateral to the sacral region; it may represent part of the girdle or hind limb.

The cranially following vertebra bears no rib, and no bulging of the surface of the slab indicates that ribs could be still embedded in matrix.
The four cranially adjacent centra bear short ribs on the right side (about 30 mm in proximodistal length). These ribs are straight for most of their length, apparently only curved in their proximal portion; they are laterally, slightly caudally oriented. On the left side, only the caudal-most of these short ribs is preserved close to articulation: the other 3 are either embedded or absent. In this region, a fragment of rib parallels the vertebral column; at least two more ribs are still embedded in the area, being visible along breaks. Possibly, rupture of the abdominal cavity during decay disarticulated the ribs in this area.

The cranially following vertebra in the series bears slightly longer ribs, about 50 mm in proximodistal length. Possibly the cranially following vertebra also bears ribs intermediate in length. The right rib is broken along the edge of the slab, while the left one disappears below the rib of a cranially adjacent vertebra, but still appears shorter.

The cranially following vertebrae are dorsals with long, smoothly curved ribs that rotated when the rib cage collapsed.

Lumbar and dorsal synapophyses are located in the cranial third of the centra. The only well visible synapophysis is on the left of vertebra 'sacrals minus 6'; it is about 10 mm in proximodistal length and about 5 mm in width, pointing caudolaterally. Where visible, rib and synapophysis are separated by a seam of sediment, indicating non-fusion of the ribs.

Discussion: Although originally mistaken for a fish, the vertebral anatomy as well as heteromorphous ribs leave no doubt about the mosasauroid affinities of the specimen (see e.g. Smith & Buchy, submitted). Its poor condition prevents detailed comparisons, though further preparation might clarify some issues. It appears to present one vertebra without rib followed by four vertebrae bearing short ribs and further cranially one, possibly two vertebrae with ribs intermediate in length. This pattern is similar to that of UANL-FCT-R27 (Smith & Buchy submitted). For now, it is to be noted that its size exceeds dimension of most known aigialosaurs, only comparable to the 'Trieste aigialosaur' (Carroll & deBraga, 1992).

CPC 254 (fig. 30)

Material: Nine procoelous, articulated caudal vertebrae, forming a segment of tail that was disarticulated prior to embedding (as witnessed by the exposed cranial-most cotyle); the condyle of the terminal-most preserved vertebra is broken along the edge of the slab. Two additional disarticulated centra, located respectively 50 mm craniolateral and 90 mm cranial to the first articulated vertebra. Imprints of two long bones, possibly metatarsals.

Origin: Early Turonian Agua Nueva Formation at Vallecillo, Nuevo León (fig. 2), collected in September 2006 by C. Ifrim and S. Giersch for the MUDE.

Preservation: As is normal for the locality, the specimen is preserved on a slab. The bones are visible in subcoronal section, the missing portions presumably having been lost to the counterpart. Within the tail, the bone substance itself appears better preserved than in e.g. UANL-FCT-R27, with visible trabeculae. The two isolated centra are badly weathered, partly visible as imprints, and yield no anatomical detail. Parallel to the right transverse process of the 6th vertebra preserved in articulation, the articular head of a long bone is preserved, while the rest of it is visible laterally as a clear imprint. About 20 mm left to the same level of the portion of tail, and parallel to it, a shallow imprint probably represent another long bone, as far as can be judged, of similar morphology. Partial haemal arches are preserved slightly displaced, visible to the right of articulated vertebra 5, to the left of more caudal vertebrae. As deduced from the overlapping pattern of neural spines, pre- and postzygapophyses and transverse processes, the specimen is visible in dorsal view, except for the cranial-most vertebra, which is slightly displaced from the series and visible in left dorsolateral view.

Description: The two isolated vertebrae have a length of about 11 mm, similar to the cranial-most vertebrae preserved in articulation. The centra very slightly diminish in length terminally, the penultimate measuring about 10 mm in length. Little can be said on the anatomy of the centra due to poor preservation. The transverse processes insert near mid-length on the centra. The original width of the transverse processes cannot be determined, as what is visible is actually their ventral-most portion, the rest having been lost to the counterpart. The five terminal-most right transverse processes appear sub-completely preserved, ranging in length from about 11 mm cranially to 8 mm terminally. All exhibit a sinusoidal distal margin, convex cranially and concave terminally. This could be attributed to a lesser thickness of the process terminally, and consequently differential matrix covering and breakage pattern. Neural arches appear to have collapsed caudally and to the right, now overlying the right postzygapophyses. Pre- and postzygapophyses are partly preserved, depending on the level of the coronal break, and along the preserved fragment of tail appear well-expressed, although no further detail can be deduced. The haemal arches were not fused to the centra; their articular head could have been oval instead of rounded.

The two long bones measure about 18 mm in length. The shaft is the narrowest at about mid length. The right one shows a distinct epiphysis ?proximally. Assuming these elements pertain to the hind limb(s), and although few anatomical details are preserved, they likely are central metatarsals, by comparison with UANL-FCT-R27, their length representing about 1.5 times a vertebral length (Smith & Buchy, submitted).



Figure 30: CPC 254, aigialosaur indet., portion of tail. a/ General view of the slab; 1, 2: two isolated, poorly preserved vertebrae; scale 50 mm. b/ Detail of the series of articulated caudal vertebrae; c/ interpretative line drawing; scale 20 mm.

Discussion: CPC 254 is of poor taxonomical value, at least within the current taxonomical frame for 'aigialosaurs'. CPC 254 is slightly smaller than UANL-FCT-R27. No feature contradicts its belonging to the new taxon represented by UANL-FCT-R27 (Smith & Buchy, submitted), but neither does any significant feature support it. Smith & Buchy (submitted) indicate that transverse processes in UANL-FCT-R27 extend until at least caudal vertebra 15, gradually decreasing in proximodistal length, but incompletely preserved; all caudals except the first one bear haemal arches. All nine articulated vertebrae of CPC 254 possess a transverse process, whereas haemal arches are visible only on the terminal six. However, no vertebra (including the two isolated centra) can be surely identified as a sacral or first caudal (on the basis of either shortened centra, or sacral rib or wide transverse process as possesses UANL-FCT-R27). CPC 254 is therefore interpreted as a cranial portion of tail, between caudals 2-15, and on the ground of transverse processes length, closer to the sacrum than to the point where they disappear.

Preservation hints at a disarticulated carcass, with at least the cranial-most portion of tail kept in articulation. The cloaca (located level with the first caudal, lacking a haemal arch, Evans *et al.*, 2006) being usually the area where decay is initiated (see Salisbury *et al.*, 2003), that the tail was disarticulated just caudal to it appears coherent. Articulated vertebrae of CPC 254 might therefore, on taphonomical argument, represent caudals 2-10.

II.1.4 Discussion

It is first to be noted that more specimens referable to mosasauroids were recently discovered in Vallecillo and are presently kept in the MUDE. Some likely represent aigialosaurs, while several vertebrae of clear mosasaurian anatomy (and much larger than known aigialosaurs) are indicative of hitherto undocumented taxa. However, these specimen are in crucial need of preparation and it is not felt a preliminary description of the visible portions of the remains would make sense here.

The extreme paucity of marine reptiles from the Vallecillo deposits (limited to UANL-FCT-R26 and three turtles awaiting description, e.g. Ifrim, 2006), in view of the richness and diversity of fishes (Blanco *et al.*, 2001; Blanco-Piñon *et al.*, 2002; Blanco-Piñon, 2003; Ifrim *et al.*, 2005b; Ifrim, 2006), was intriguing until the discovery of UANL-FCT-R27. Re-discovery of UANL-FCT-R30, re-evaluation of UANL-FCT-R28 and discovery of the new specimens above-mentioned further complete the assemblage of marine squamates. Vallecillo limestones can now be qualified as very rich for these, more so than any other locality that yielded coeval taxa; the assemblage is unique in its richness, and no faunistic comparison can be made with other 'aigialosaur' yielding sites, most occurrences being unique (see a review in Jacobs *et al.*, 2005).

Diversity at Vallecillo cannot be evaluated either, as most specimens cannot be assigned yet with certainty to the species level. As far as can be judged, all may represent members (of different ontogenetic stages or gender) of the new taxon described by Smith & Buchy (submitted) on the basis of UANL-FCT-R27.

Pliosaurs (*sensu* Buchy *et al.*, 2006a) are generally rare and exhibit a low diversity during the Turonian (e.g. Bardet, 1995). Coeval deposits that yielded marine reptiles exhibit on the contrary a high diversity of Plesiosauroidea, especially elasmosaurs and polycotylids, with or without associated marine squamates (e.g. Williston, 1903; Carpenter, 1996; Bardet, 1995; Bardet *et al.*, 2003a, b; Buchy *et al.*, 2005a). However, most of these deposits represent shallow marine environments (Jacobs *et al.*, 2005), while the Vallecillo limestone were deposited in an open marine environment (Ifrim, 2006). The absence of elasmosaurs and polycotylids until now might actually be a further argument in favour of a shallow coastal life-style of at least the former (chapter I.2.3). The latter were re-assessed as Plesiosauroidea a decade ago, after having long been referred to Pliosauroidea (Carpenter, 1996). Their affinities with elasmosaurs appear now generally accepted (e.g. O'Keefe, 2001; Bardet *et al.*, 2003a; Buchy *et al.*, 2005a). However, in the shadow of their long-necked cousins, their life style has elicited little attention until now. The possible significance of their apparent absence in the Vallecillo deposits therefore is yet uncertain.

Part II.2. Late Turonian to early Coniacian Austin Group at Múzquiz, Coahuila

II.2.1. Palaeogeographical context

Excavations of the late Turonian to early Coniacian fossiliferous limestone of the area north and northwest of Múzquiz (fig. 2) are currently ongoing, as are sedimentological, palaeontological and taphonomical studies (Rindfleisch, 2004; Stinnesbeck *et al.*, 2005). What is currently deduced from preliminary studies in relation to marine reptiles was summed up by Buchy *et al.* (2004, 2005b). The fossil-yielding lithographic limestone were deposited in an open marine context, at the junction of the opening Atlantic Ocean and the Western Interior Seaway (Stinnesbeck *et al.*, 2005; fig. 24).

II.2.2. Squamata indet.

MHM PAS 337 (Buchy *et al.*, 2005b: fig. 4)Material: Isolated fragmentary vertebra obtained from a local collector.Comments: This specimen was described by Buchy *et al.* (2004; 2005b).

MHM PAS 338A and B

Material: Two articulated partial vertebrae.Comments: This specimen was described by Buchy *et al.* (2004; 2005b).

II.2.3. Mosasauridae indet.

MHM PAS 336 (Buchy et al., 2005b: fig. 5)

Material: The specimen comprises 16 articulated vertebrae preserved on the edge of a slab; they are visible in right lateral and partly ventral views.

Comments: This specimen was described by Buchy et al. (2004; 2005b).

II.2.4. Discussion

The locality clearly appears very promising for marine reptiles, when adding specimens currently in private hands and hearsay from quarrymen. Preservation is usually exquisite, possibly due to anoxia and stagnation at the sea floor, in an open marine shelf environment (Stinnesbeck *et al.*, 2005). El Rosario, like Vallecillo, was located at the entrance of the Western Interior Seaway (fig.

24); stratigraphic correlation with coeval well-documented, mosasauroid-yielding North American localities will be a further point of interest of the to-be-found marine reptiles of the Mexican sites.

Part II.3. Campanian-Maastrichtian Méndez Fm.

II.3.1. Geological setting

The marls, shales and sandstones of the Méndez Formation (Campanian-Maastrichtian) are widely distributed in the Gulf Coast plain of Mexico, east and southeast of Monterrey; they were deposited in an open marine shelf environment in water depths from approximately 100 m near Los Ramones (40 km northeast of Monterrey) to more than 400 m in the La Sierrita region (40 km north of Linares; Keller *et al.*, 1997; Stinnesbeck *et al.*, 2001; Ifrim *et al.*, 2004, 2005a; figs 2, 31).



Figure 31: Palaeobiogeographical map of the Maastrichtian (modified from Smith *et al.*, 1994). Insert: palaeobiogeographical map of north-east Mexico during the Maastrichtian; M: Monterrey; S: Saltillo (after Goldhammer & Johnson, 2001).

II.3.2. Mosasauridae indet.

UANL-FCT-R6

Former accession number: MZ0/0001

Material: A fragmentary jaw with three tooth bases, probably a portion of right mandible.

Origin: The specimen comes from the vicinity of Hualahuises, N.L. (fig. 2), and no co-preserved fossils permit a stratigraphic assignment more precise than Méndez Formation.

Comments: The specimen was described by Aranda-Manteca & Stinnesbeck (1995) and further discussed by Buchy *et al.* (2004, 2005b).

UANL-FCT-R4 (Buchy et al., 2005b: figs 6, 7; Buchy et al., 2007)

Material: UANL-FCT-R4 comprises the skull roof (the frontal, most of the parietal, the medial portions of both prefrontals and both postorbitofrontals, as well as the caudal portion of the internarial bar) preserved in articulation, extending rostrally to the caudalmost extremities of the external nares. The dentigerous portions of both maxillae are almost completely preserved and articulate with the rostral extremity of the premaxilla. Portions of the jugal and pterygoid are also preserved, as are the ventral half of the right quadrate and the caudal two-thirds of both anterior lower jaws.

Origin: The specimen comes from east of Linares (fig. 2). Although the exact origin of the specimen could not yet be determined, Buchy *et al.* (2005, 2007) indicate that local geology and adhering foraminifer-yielding marks assign the specimen to the Early Maastrichtian.

Comments: The specimen was described and its affinities discussed by Buchy *et al.* (2007). As noted by these authors, the specimen exhibits the pattern of exit for cranial nerve V on the premaxillary that has been described in tylosaurs, though lacks the premaxillary rostrum characteristic of these. The morphology of its quadrate, though, excludes direct affinities with tylosaurs within the current taxonomical frame for mosasaurs, in the very close proximity of the infra- and suprastapedial processes.

UANL-FCT-R24 (Buchy et al., 2004: fig. 8; 2005b: fig. 8)

Material: 18 caudal vertebrae from the vicinity of Icamole, N.L. (fig. 2). All were found in the same area, but excavation at the site did not yield more material (Lopez Oliva, pers. com.). The sediment at the locality clearly belongs to the Méndez Formation, but a more precise stratigraphic determination has not yet been possible.

Comments: This specimen was discussed by Buchy et al. (2005b).

II.3.3. Discussion

The paucity of mosasaurs from the Campanian-Maastrichtian of north-east Mexico in regard to apparently favorable palaeoenvironments and the richness of both the European Archipelago and

nowadays USA is puzzling. At first sight, this would appear a bias in collection and/or identification, although the Méndez Formation is reputedly exceedingly poor in macrofossils (Ifrim *et al.*, 2004, 2005a). In any case, further work, both in collections (especially private ones) and in the field is necessary.

Conclusions and perspectives

The region that previously was a 'white spot' for marine reptiles, despite theoretically favorable palaeoenvironmental conditions, yielded a rich and varied assemblage of Late Jurassic and Late Cretaceous forms. While 6 years ago little was known, due to that richness, studies now have to wait until preparation is completed.

Work by the author and co-workers revealed a variety of new taxa, but also, that most Late Jurassic forms do differ from coeval forms from both the European Archipelago and Pacific margin. A basinal palaeogeographical context during the Late Jurassic may explain endemism of thalattosuchians and pliosaurs. That ichthyosaurs were possibly searching for such protected environement for parturition may explain the presence in the Mexican Gulf of the ubiquitous *Ophthalmosaurus icenicus*. The absence of turtles during the Tithonian cannot be explained at present. While the Kimmeridgian yielded mostly isolated occurrences, the Tithonian at Gomez Farías was qualified a concentration Lagerstätte for marine vertebrates (Buchy *et al.*, 2006c). Exploration of this site is one of the main objective of the author in the future, especially collection, preparation and study of the pliosaur CPC 226.

Another Lagerstätte (Blanco *et al.*, 2001), the Vallecillo deposits yielded the best (in term of preservation, including integument and gut contents) and richest assemblage of 'aigialosaurs' to date. Study of these just started, but already indicates at least one new taxon (Smith & Buchy, submitted); more material awaiting preparation (including cranial material) will yield the most complete information upon these animals ever. The offshore Vallecillo limestone appear to contradict the poor swimming abilities and shallow coastal life-style suggested for 'aigialosaurs', while the absence at present of elasmosaurs tends to confirm that these were shallow dwellers.

More Late Cretaceous specimens hint at an unsuspected richness of the area; though, these most likely being occurrences, more discoveries will come with chance (and contact with local collectors).

Clearly, most of the material discussed here was discovered by private collectors, and came to official institutions very late, when much information had already been lost. Ideally in the future, exploration by members of institutions, turning occurrences into proper digging sites will yield proper data for anatomical comparisons as well as stratigraphical settings, taphonomy and associated elements.

Elucidation of the affinities, in particular of Late Jurassic Mexican pliosaurs and thalattosuchians, can only be done when the European material is properly restudied; being preserved in 3-dimensions, Mexican pliosaurs revealed a rostrum anatomy that crushed European forms had not disclosed previously. The latter now should be reexamined under a new

perspective, while the biomechanics of the structures should be assessed. Relationships with Australian Cretaceous forms of (possibly superficially) similar anatomy could then be studied. Moreover, the holotype of the only plesiosaur described from the Mexican Gulf prior to this work, *Plesiosaurus (Polyptychodon) mexicanus* Wieland, 1910 from the Lower Cretaceous of south Mexico was recently rediscovered. This specimen must be reassessed in oder to understand the evolution of the Mexican Gulf pliosaurs.

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