

First occurrence of a gigantic pliosaurid plesiosaur in the late Jurassic (Kimmeridgian) of Mexico

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Key words. – Kimmeridgian, Pliosauridae, Mexico, Palaeobiogeography.

Abstract. – Reinvestigation of a partial vertebral column from the Kimmeridgian La Caja Formation of Mexico, housed in the University of Linares (Mexico), and previously attributed to a dinosaur, proves to be from a very large pliosaurid plesiosaur. This specimen represents the first plesiosaur described from the Jurassic of Mexico. Its length has been estimated at 15 metres and, as a juvenile, is considered to be one of the largest Jurassic marine reptiles. The remains of this animal are here described. The morphology of the vertebral column is not diagnostic beyond family level. Large pliosaur vertebrae of a similar size are known from the Upper Jurassic of Europe, and are often referred to the genera *Liopleurodon* or *Simolestes* but these identifications are based only upon the size of the centra and have no taxonomic justification. A portion of rostrum with teeth was discovered together with the vertebral column but is unfortunately now lost. The Mexican pliosaur fills geographical and chronological gaps between western Tethys and South American pliosaurs, and is an additional support to the hypothesis of a Hispanic corridor linking at least temporarily the NW European marine province with the western South American marine (Pacific) realm during the late Jurassic.

Première occurrence d'un plésiosaure pliosauride géant dans le Jurassique supérieur (Kimméridgien) du Mexique

Mots clés. – Kimméridgien, Pliosauridae, Mexique, Paléobiogéographie.

Résumé. – Le réexamen d'une colonne vertébrale partielle provenant de la Formation La Caja (Kimméridgien) du Mexique, conservée à l'Université de Linares (Mexique), et attribuée à un dinosaure, prouve qu'elle appartient à un très grand plésiosaure. Il s'agit du premier plésiosaure décrit dans le Jurassique du Mexique. Sa longueur estimée à 15 mètres, pour un individu juvénile, en fait l'un des plus grands reptiles marins du Jurassique. Les restes de cet animal sont ici décrits. La morphologie de la colonne vertébrale n'est pas diagnostique au-delà du niveau familial. De grandes vertèbres de taille similaire sont connues dans le Jurassique supérieur d'Europe, et souvent attribuées aux genres *Liopleurodon* ou *Simolestes*, mais ces identifications basées uniquement sur la taille des centra n'ont aucune justification taxonomique. Une portion de rostre portant des dents a été découverte avec la colonne vertébrale, mais est aujourd'hui perdue. Le plésiosaure mexicain comble les lacunes géographique et chronologique entre les formes ouest-téthysiennes et sud-américaines, et est un élément supplémentaire en faveur de l'hypothèse d'un corridor hispanique joignant, au moins temporairement, les provinces marines nord-ouest européenne et sud-américaine (Pacifique) au Jurassique supérieur.

INTRODUCTION

History of the find

During a field trip in autumn 1985 a geology student discovered a large bone-bearing calcareous concretion near Aramberri, Nuevo León, Mexico (fig. 1). During extraction, a second bone-bearing concretion was discovered. Both were brought to the Facultad de Ciencias de la Tierra of the Universidad Autónoma de Nuevo León (UANL-FCT) in Linares, Mexico.

Preparation of the first concretion revealed a partial 3D-preserved vertebral column, which was later mounted upright in a stand of concrete and displayed in the department (fig. 2). Its accession number is UANL-FCT-R2. The

second concretion contained part of a rostrum with teeth. On the base of the size of the vertebrae and the shape of the teeth, the specimen was identified as a carnivorous dinosaur by Hähnel [1988]. Unfortunately, the second concretion containing cranial material is now lost. Recent reinvestigation of the vertebrae, however, shows clearly that they are from a pliosaurid plesiosaur.

Geology

In northeastern Mexico the late Jurassic represents a time of gradual transgression. Marine deposition began during the Oxfordian with evaporites of the Minas Viejas Formation (fig. 3), probably as the result of widespread rifting caused by the opening of the Gulf of Mexico [e.g., Michalzik,

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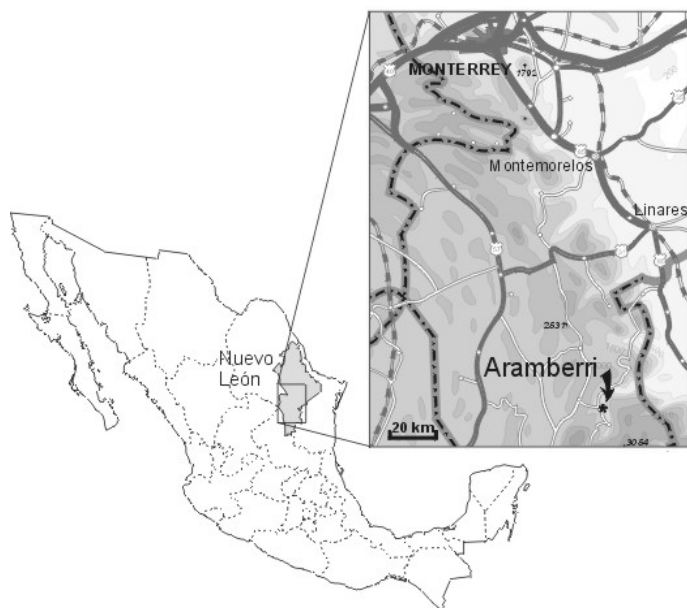


FIG. 1. – Map of Mexico and detail of South Nuevo León.
 FIG. 1. – Carte du Mexique et détail du sud du Nuevo León.

1988; Salvador, 1991]. Limestones of the Zuloaga Formation overlie the evaporites and were deposited in shallow water environments on a carbonate ramp. The La Caja Formation is characterized by shales, siltstones and phosphorites. This unit is of late early Kimmeridgian to early Berriasian age and overlies the Zuloaga Fm with a gradual contact. Lithologies and fossil content indicate deepening to outer shelf environments and increased terrigenous influence, probably from the Coahuila Peninsula north and west of Saltillo, Coahuila [Michalzik, 1988; Adatte *et al.*, 1994; Michalzik and Schumann, 1994; Goldhammer, 1999]. The Upper Jurassic sequence is overlain by Cretaceous strata of between 1 000 m and more than 2 000 m thick. In the Sierra Madre Oriental foldbelt outcrops of Upper Jurassic sediments outcrop only in the cores of anticlines and diapiric domes.

The La Caja Fm and its equivalents La Casita and Pimienta Formations are well known in northeastern and eastern Mexico for their abundant and diverse invertebrate remains. Faunas are preserved 3-dimensionally in calcareous concretions a few centimeters to more than 2 m in diameter. Diverse assemblages of ammonites have been described [Castillo and Aguilera, 1895; Burckhardt, 1906; 1930; Imlay, 1939; 1984; Cantú-Chapa, 1963; 1968; 1971; Verma and Westermann, 1973; Adatte *et al.*, 1994; Olóriz *et al.*, 1999; Villaseñor *et al.*, 2000], but belemnites, bivalves (e.g., *Aulacomyella*, *Inoceramus*), brachiopods, and serpulids are also present, as well as radiolarians and calpionellids. In addition, marine vertebrates are known to occur in the La Caja Formation. (e.g., fishes, ichthyosaurs, crocodiles, pliosaurs). However, for northeastern Mexico this vertebrate fauna has only been briefly mentioned by Michalzik [1988], Schumann [1988] and Aranda-Manteca and Stinnesbeck [1993], but has not been documented or formally described before very recently [Frey *et al.*, 2002].

The giant pliosaur described herein was discovered at approximately 1 km north-west of Aramberri, a village in

the Sierra Madre Oriental in the southern part of the state of Nuevo León (fig. 1). The site is situated on a donkey track, at an altitude of approximately 1 200 m. Strata here are inverted and form the overturned flank of a small anticline. The base of the section is formed by thick-bedded oolitic limestones of the Zuloaga Formation which form a small cliff immediately south of the main outcrop. The contact between the Zuloaga and La Caja Formations is conformable but sharp and characterized by an approximately 0.5 m-thick interval of thin-bedded (0.1 m-thick layers) micritic limestones and interbedded yellow marls and marly siltstones. Upsection, siltstones and shales gradually increase in abundance and thin dark grey clay layers rich in phosphatic grains appear for the first time. The thickest phosphoritic layer reaches 0.2 m in thickness and has been locally mined, leaving depressions and holes more than a meter deep below the limestone cliffs. Calcareous concretions of elliptical shape and up to 0.3 m horizontal diameter occur isolated in the shales or are in layers. These concretions contain ammonites (e.g., idoceratids, aulacostephanoceratids) and wood fragments. Upwards in the section, phosphoritic beds and concretions gradually decrease in abundance and disappear. A monotonous sequence of yellow to buff siltstones and shales is present and reaches a visible thickness of approximately 10 m. The sequence shows vertical faulting at approximately 14 m above the base of the La Caja Formation.

Numerous authors have assigned an early Kimmeridgian to early Berriasian age to the La Casita Formation based on ammonites and calpionellids [Imlay, 1943; López-Oliva, 1991; Adatte *et al.*, 1994; Adatte, Stinnesbeck, Remane and Hubberten, 1996; Villaseñor *et al.*, 2000]. Ammonites are generally abundant near the base of the unit and assemblages include *Glochiceras*, *Haploceras*, *Idoceras*, *Aspidoceras* and *Procraspedites*, among others. This assemblage indicates late early to early late Kimmeridgian ages [e.g., Olóriz *et al.*, 1999; Villaseñor *et al.*, 2000]. At Aramberri, idoceratids, aulacostephanids, *Subneumeyeria* and *Glochiceras* occur in beds immediately under- and overlying the discovery site of the pliosaur, at approximately 5 m above the base of the La Caja Formation, as well as on the specimen kept in the UANL-FCT. This assemblage confirms the “middle” Kimmeridgian age assigned to the Aramberri pliosaur.

Lithologies below and above the pliosaur-bearing layer include organic-rich shales and siltstones, phosphorites and calcareous concretions. Fine lamination on a millimetric scale is frequently present in the shales and is also evident in many concretions. This suggests low energy, anoxic-dysoxic environments with a muddy soft substrate. Low levels of oxygen are further indicated by the absence of benthic fauna. Body fossils discovered at the site in Aramberri include numerous ammonites, rare belemnites, fish debris and wood. Radiolarians and calcispheres were recognized during thin section studies of the calcareous concretions and thin limestone layers. No bivalve other than *Aulacomyella* or *Inoceramus*, no brachiopod, or other benthic organisms and no trace of bioturbation have been identified, not even in layers immediately overlying the Zuloaga oolitic limestones. This suggests the substrate was not suitable for colonization by endobenthic dwellers, whereas epibenthic faunas were apparently kept off by the soft and muddy substrate. Even ammonite shells at Aramberri which could have served as hard substrates are not encrusted by bi-

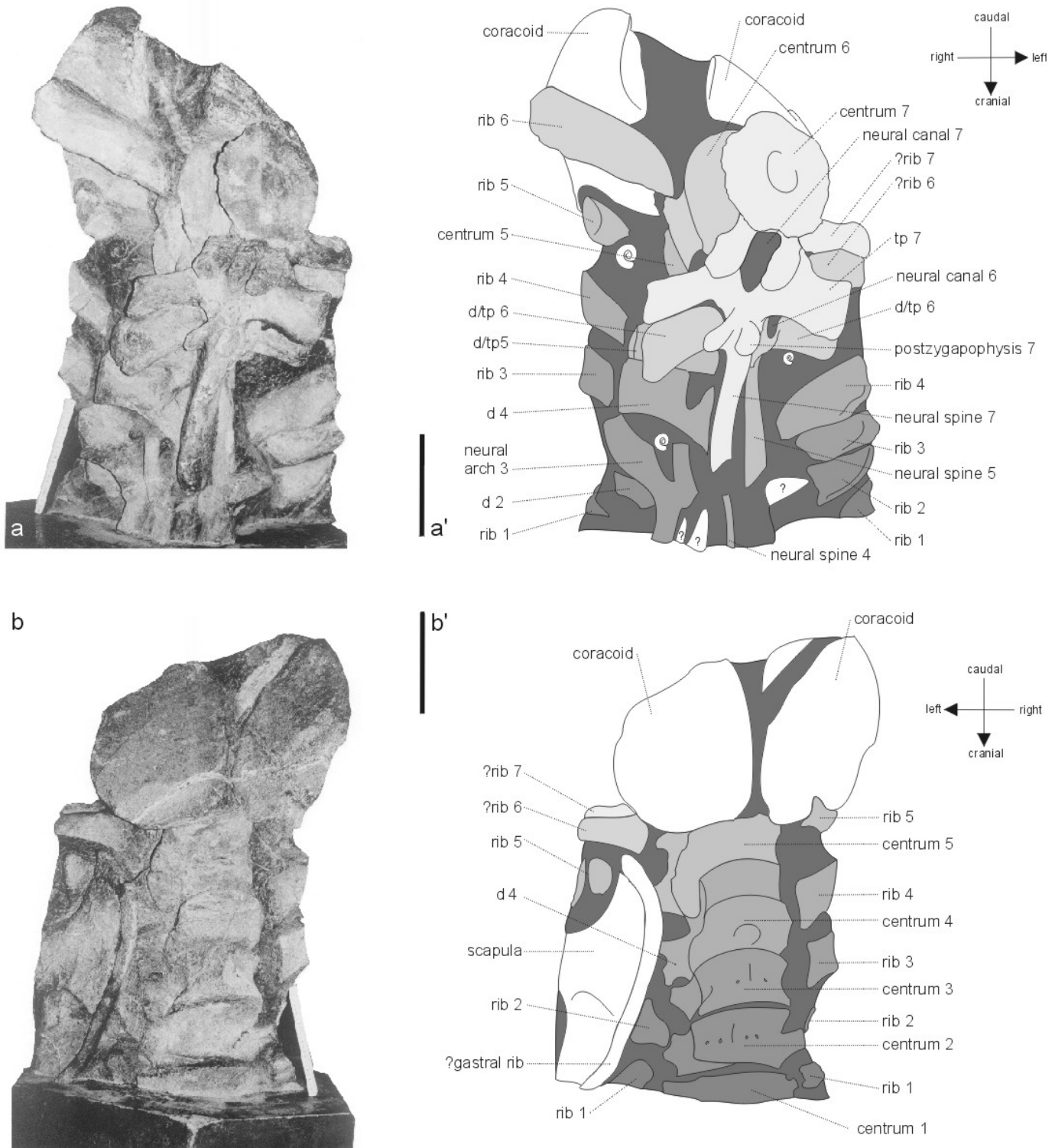


FIG. 2. – a) Dorsal view of UANL-FCT-R2 mounted “head-down” in a concrete stand in Linares; a’) interpretative line drawing; b) ventral view of the specimen; b’) interpretative line drawing. tp : transverse process ; d : diapophysis. Scale bar 200 mm.
 FIG. 2. – a) *Vue dorsale de UANL-FCT-R2 monté “tête en bas” dans un socle de béton à Linares ; a’) dessin interprétatif ; b) vue ventrale du spécimen ; b’) dessin interprétatif. tp : processus transverse ; d : diapophyse. Échelle 200 mm.*

valves (e.g., oysters, inoceramids), in marked contrast with other localities in the La Caja basin in northeastern Mexico.

Abundant pyrite and high organic carbon content also suggests low oxygen and reducing conditions on the sea floor. Pyrite is preserved in fresh shale outcrops and concretions and occurs as cubes of millimetric size, either finely

dispersed in the sediment or enriched in layers accentuating the lamination. In surface outcrops pyrite is usually oxidized and hydrated to goethite; these weathered layers are characterized by yellow to buff surfaces.

Phosphoritic layers up to 0.2 m thick occur repeatedly in the basal 4 m of the La Caja Formation of the Aramberri

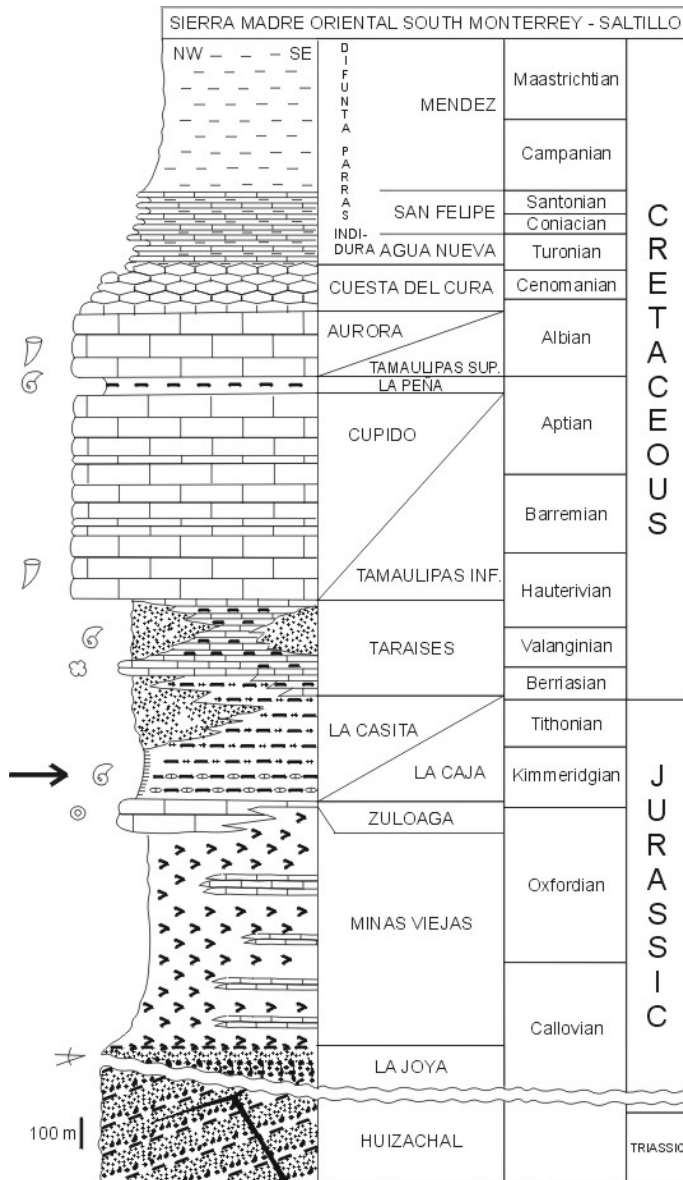


FIG. 3. – Geological profile of the Mesozoic in Northeast Mexico. Arrow marks the occurrence of the Aramberri pliosaur.
 FIG. 3. – Profil géologique du Mésozoïque au nord-est du Mexique. La flèche indique le pliosaure d'Aramberri.

pliosaur locality. The fixation of phosphorous from sea-water requires slightly reducing environment and is favoured by the presence of unoxidized organic matter and an outer shelf setting between 150 and 300 m deep [Michalzik and Schumann, 1994; Dill and Kantor, 1997]. These conditions agree well with the faunal and sedimentological data. Occasionally, storms or currents must have interrupted the quiet water conditions and phosphate particles must have been concentrated by mechanical action, either *in situ* or in re-worked form.

Open marine outer shelf conditions are also suggested by ammonites and radiolarians. On the other hand, the abundance of driftwood and layers of plant debris in the shales suggest that islands existed in the Kimmeridgian area close to Aramberri. A paleoisland is known to have been emerged at a distance of less than 50 km south of

Aramberri, close to Miquihuana, Tamaulipas [Salvador, 1991].

SYSTEMATIC PALAEOONTOLOGY

- Sauropterygia Owen, 1860
- Plesiosauria Blainville de, 1835
- Pliosauroida (Seeley, 1874) Welles, 1943
- Pliosauridae Seeley, 1874
- Pliosauridae indet.

DESCRIPTION

Orientation and preservation

The specimen mounted upright in a concrete stand at UANL-FCT consists of a series of seven pectoral vertebrae, almost articulated, the bottom-most one being half embedded in the stand (fig. 2).

The top-most vertebra lies subparallel to the vertical long axis of the specimen as it is mounted, and is seen in caudal view as indicated by the postzygapophyses, preserved as elongate elements with a rounded tip, slightly bent laterally.

The specimen is mounted “head-down” in the concrete stand. Therefore the top-most vertebra is actually the caudal-most vertebra of the preserved portion of vertebral column. According to the natural orientation of the specimen, this top-most vertebra will be designated as n^o7. Vertebrae 6 to 1 then follow downwards i.e. cranial, according to their anatomical relationships to this 7th vertebra. Arabic numerals are used here because the exact position of the vertebrae in the vertebral column *in vivo* is unknown. The description herein given refers to the natural orientation of the animal as shown in figure 2, and not to the “head-down” condition of the mounted specimen.

The 7th neural arch is visible in dorsal view. It lacks only the dorsal extremity of its neural spine. It is dissociated from the centrum, and leans cranially.

Cranial to the 7th vertebra, parallel and slightly shifted cranially and towards the right, is the 6th vertebra. Its neural arch is incomplete, apparently recently broken dorsal to the neural canal, maybe during extraction or preparation.

The succeeding five vertebral centra are slightly displaced towards the right side of the specimen when its natural orientation is considered. They are leaning cranially in relation to the ventrodorsal axis, like a collapsed series of dominoes. The associated neural arches are still partly embedded in matrix and obscured by overlapping bones. The 4th and 3rd neural arches cannot be identified. Three bone fragments might represent broken parts of these neural arches. The remaining neural arches parallel the craniocaudal axis, and appear to be completely preserved although they are still partly embedded in the matrix.

On each side of the partial vertebral column lies a series of elongate distally broken bones, parallel to one another. The proximal end of each of these elements is situated level with the middle of a centrum. The long axis of these bones is directed from craniomedially to caudolaterally, forming an angle of 50° to 70° with the craniocaudal axis of the body. From their position and morphology, these elements are identified as proximal extremities of the ribs. By com-

parison with the cranialward shift of the centra, the ribs now presumably lie on their cranial surface, the caudal surface being exposed when the specimen is seen in dorsal view (fig. 2a, a').

On the ventral side of the specimen, three large bony plates are preserved. They are incomplete, with broken and/or abraded margins. Two of the plates are paired and situated caudal to the third one. They obscure in ventral view the 6th and 7th vertebrae. The third plate is lying on the left side of the cranial-most part of the specimen. Its medial border is covered by an elongate bow-shaped bone rounded in cross-section. Although they look associated in ventral view, these two elements are clearly distinct in lateral view, being separated by matrix. The long bone is identified as a possible gastral rib, and the bony plates as parts of the pectoral girdle (see discussion).

Description

Vertebrae : centra – The cranial and caudal articular surfaces of the centra are slightly convex, with well-marked margins forming dorsolateral frills [“lips” of Tarlo, 1960] on the lateral faces. A circular boss of 30 mm in diameter is visible in the centre of the cranial articular surface of the 4th centrum and on the caudal articular surface of the 7th. The latter surface is rounded pentagonal in outline, dorsally concave at the level of the neural canal, and slightly convex ventrally. Its width is 200 mm, its height 220 mm.

The centra are pulley-shaped in lateral and ventral views, the lateral surfaces of the 6th and 7th being more concave than their ventral ones. The length of the centra ranges from 90 to 105 mm, increasing cranially.

The ventral edges of the 1st to 4th centra are rounded; there is a trace of a faint ventral keel on the 2nd and 3rd. Two foramina are visible on either side of this keel on the 3rd centrum, while two pairs of foramina are visible on the 2nd centrum (fig. 2b, b', 4).

Along the preserved portion of the vertebral column, the rib articulations on the centra migrate dorsally from the lateral face of the centra to the neural arch.

The right diapophyses of vertebrae 1 to 4 are dorsoventrally elongate, and rise from the cranial half of the centra. Their position along the dorsoventral axis of the centra appears central on the 2nd and 3rd centra, slightly higher on the 4th. The outline of the articular facet for the rib is oval to rounded quadrangular.

The left diapophyses are obscured by matrix and other bones, and are thus identified by comparison with elements of the right side. The left diapophysis of the 5th centrum is more dorsally located than that of the preceding centra. The 5th left diapophysis is located more centrally on the centrum in respect to the longitudinal axis than the diapophyses of the preceding vertebrae. The corresponding element on the right side of the 6th centrum overlaps the area of contact between the centrum and the neural arch.

There are no diapophyses on the 7th centrum, and transverse processes are entirely borne by the neural arches, level with the neural canal, and ventral to the postzygapophyses.

Vertebrae : neural arches – The neural arches 3 to 7 are of similar dimension, with a height of approximately 350 mm.

As noticed above, the neural arches 3 and 4 are reverse Y-shaped bones without transverse processes, while on the 6th and probably the 5th a diapophysis/transverse process is borne half by the centrum, half by the neural arch. On the 7th, a pair of transverse processes is completely borne by the neural arch. These transverse processes are quadrangular in cranial view, oval in section with a height of 80 to 100 mm and a length of 120 mm.

From what is visible all the neural spines are of similar shape and size. They appear in lateral view as quadrangular blades. They are 200 mm high and 50 to 80 mm long. The caudal margin is 5 mm thick, while all the cranial margins are obscured by matrix.

The exposed neural canals are oval, 80 to 100 mm high, 20 to 30 mm wide, with lateral walls 20 to 30 mm thick.

Ribs – Only the proximal straight horizontal portion of the ribs is preserved. Their articular heads are all embedded in matrix. The preserved portions of the three cranial-most left and of the caudal-most right ribs are 200 mm long, while the other preserved fragments are shorter, ranging from 100 to 10 mm. They all show a similar dorsoventral extension of approximately 100 mm.

The left ribs associated with vertebrae 1 to 3 exhibit a recurved dorsal margin, forming a crest, which, according to the collapsing pattern of the centra, was caudally directed *in vivo*. The right 6th rib lacks this crest, despite its preserved part being longer than the preserved parts of the left ribs 1 to 3.

Dentigerous bone and teeth – The rostrum portion excavated together with UANL-FCT-R2 is now lost. It was illustrated by a photograph and briefly described in the original publication by Hähnel [1988 : fig. 4]. It is a 600 mm-long bone, 300 mm-high caudally and 250 mm-high rostrally, bearing at least 3 broken teeth. According to the original photograph, another tooth might be present, belonging to the opposite jaw, as it appears in occlusion between the first and second preserved teeth. On this base, it is impossible to determine whether this fragment represented a portion of dentary, premaxilla or maxilla. The teeth are described as bicarinated. As visible on the photograph, the tooth diameter at the base of the crowns is about 55 mm. They appear quite massive, yet no further precision can be given.

DISCUSSION

Identification

The foramina situated on the ventral side of the pulley-shaped centra are characteristic of the Plesiosauria [Tarlo, 1960; Brown, 1981]. Furthermore, the migration of the rib articulations from the lateral side of the centrum to the neural arch is typical of plesiosaurian (*s.l.*) pectoral vertebrae, i.e. the vertebrae being transitional between the cervical vertebrae and the thoracic ones [Brown, 1981]. This confirms the plesiosaurian nature of the specimen.

The proportions of the centra, their length being approximately half their height, are indicative of pliosaurs, especially

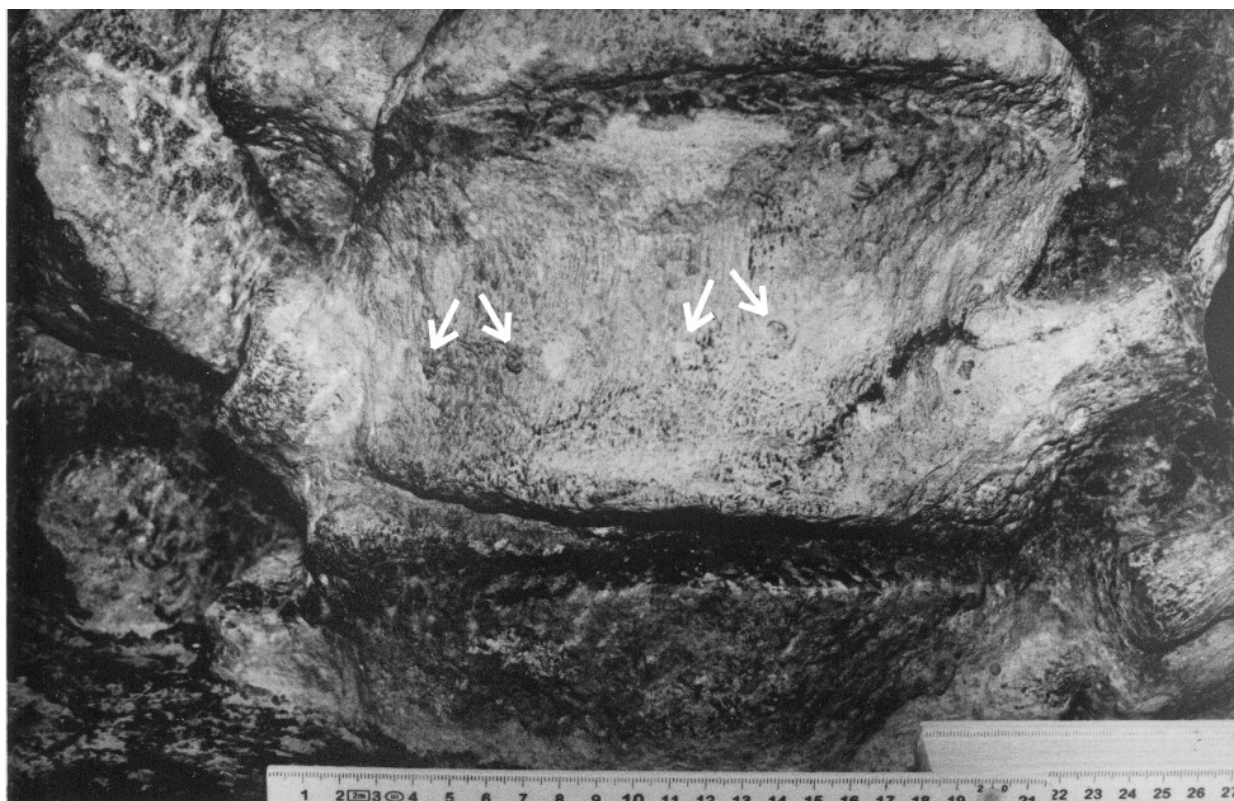


FIG. 4. – Detail of the ventral side of the 2nd vertebra, showing the ventral foramina characteristic for Plesiosauria (arrows).

FIG. 4. – Détail de la face ventrale de la 2^e vertèbre, montrant les foramens ventraux caractéristiques des Plesiosauria (flèches).

for vertebrae situated in the pectoral region [Brown, 1981]. The vertebral morphology of UANL-FCT-R2 is otherwise not diagnostic among Plesiosauria. In particular, a central boss or swelling was described for example in the pliosaurian genera *Pliosaurus* and *Liopleurodon* [Tarlo, 1959; 1960; see Noè, 2001 for a discussion], and in the elasmosaur *Mauisaurus* [Welles and Gregg, 1971; Wiffen and Moisley, 1986]. A pit in the centre of this boss is present on some of these vertebrae, possibly reminiscent of the notochordal canal [Wiffen and Moisley, 1986]. More likely, this pit could be the scar of an attachment of a synovial bursa, and would then witness a synovial joint, as described for recent crocodylians by Salisbury and Frey [2000]. However, this pit may be present or not on the vertebrae of one single individual, and is therefore of no taxonomical significance [Wiffen and Moisley, 1986].

The unfused condition of the 7th neural arch to the corresponding centrum cannot be confirmed for any of the other neural arches. Specimens showing unfused neural arches are usually referred to as juveniles [Brown, 1981].

From the bony plates themselves, not much could be inferred about their anatomical nature. Yet their ventral situation in the pectoral region of a plesiosaur suggests with a good certainty that they are parts of the pectoral girdle. The paired elements certainly represent the cranial half of both coracoids, where a dorsoventral transverse enlargement is in line with the humerus articulation [Andrews, 1913], as such an enlargement of these bones is visible on top of the mounted specimen. The uneven plate can then be interpreted as the medial portion of the left scapula.

The large size of the centra is the most amazing feature of the specimen. Vertebrae of a similar diameter are known

from the Callovian and Kimmeridgian of England and the Upper Jurassic of northern France (Martill and Naish, in prep., pers. com.). They are usually referred to the genus *Liopleurodon*, which until recently was reputed the largest pliosaur of the Upper Jurassic. Yet, the unpublished work of Noè [2001] restricts the genus to the Callovian of England. Hence, if the existence of very large pliosaurs by the end of the Jurassic is proved in Europe and now in Central America, no taxonomic value can be given to the vertebrae size only, and the identification of these very large beasts remains imprecise. Still, a 5.3 meter long subcomplete *Liopleurodon ferox* (uncatalogued specimen, Institut und Museum für Geologie und Paläontologie, Tübingen, Germany) [Noè 2001 : fig. 1; E.F. and M.C.B. pers. obs.] exhibits thoracic vertebrae of about 70 mm in diameter. A cautious extrapolation would then indicate a 15 meter long juvenile animal. The Mexican pliosaur ranges then among the largest of all pliosaurs known from all times, together with the Cretaceous *Kronosaurus* from Australia [Longman, 1924; Hampe, 1992; E.F. pers. obs.].

Palaeobiogeography

The record of sauropterygians from Central America is until now very scarce. *Plesiosaurus* (?*Polyptychodon*) [sic] *mexicanus* WIELAND, 1910 is based on a portion of a pliosaur rostrum from the Lower Cretaceous of South Mexico, being non diagnostic according to Welles [1962].

Several fragmentary remains of plesiosaurs are described from the Jurassic of Cuba [Iturralde-Vinent and Norell, 1996]. The specimen UANL-FCT-R2 is the first Jurassic Mexican pliosaur, together with a new form currently

under investigation [Buchy *et al.*, in prep.], and therefore of palaeobiogeographic significance.

From the Jurassic of South America, only *Maresaurus coccai* GASPARINI, 1997 was described from the Bajocian of Argentina. A fragmentary rostrum from the Tithonian of Argentina has been attributed doubtfully to *Liopleurodon macromerus* by Gasparini *et al.* [1982]. Other fragments from the Tithonian of the same area are reported by Gasparini and Fernandez [1997] and Gasparini *et al.* [1997] as belonging to *Pliosaurus* sp. and an indeterminate Pliosauridae.

Gasparini and Fernandez [1997] emphasize that some marine reptiles that were abundant during the Callovian to Kimmeridgian in western Tethys become rare there during the Tithonian, while they persist in South America. At least concerning pliosaurs, the generic similarities identified between the two assemblages necessitate a revision [Noè, 2001]. The hypothesis of faunal exchange from western Tethys towards South America through a Hispanic corridor before the Tithonian, as suggested e.g. by Gasparini and Fernandez [1997] and Gasparini *et al.* [2000], is confirmed by subsequent finds of marine reptiles from the Oxfordian

of Cuba [Fernandez and Iturralde-Vinent, 2000; De la Fuente and Iturralde-Vinent, 2001; Gasparini and Iturralde-Vinent, 2001; Gasparini *et al.*, 2002], as well as by the Kimmeridgian Mexican pliosaur described here. UANL-FCT-R2 is situated intermediate both in time and palaeogeography between western Tethys and South American forms described so far. Further discoveries from this area will hopefully fill the gap between European and South American forms and help understanding the palaeobiogeography of Upper Jurassic pliosaurs, prior to the opening of the North American Western Interior Seaway in the Cretaceous, from where several pliosaurs of uncertain affinities are known [Carpenter, 1996; Druckenmiller, 2002].

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