

TITHONIAN MARINE REPTILES OF THE WESTERN NEUQUÉN BASIN, ARGENTINA. FACIES AND PALAEOENVIRONMENTS

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GASPARINI Z., SPALLETTI L. & DE LA FUENTE M. 1997. Tithonian marine reptiles of the Western Neuquén Basin, Argentina. Facies and palaeoenvironments. [Reptiles marins tithoniens de l'Ouest du Bassin du Neuquén, Argentine. Faciès et paléoenvironnements]. *GEOBIOS*, **30**, 5: 701-712. Villeurbanne, le 31.10.1997.

Manuscrit déposé le 04.01.1996; accepté définitivement le 20.05.1996.

ABSTRACT - Remains of marine reptiles have been found in the Vaca Muerta Formation, at Trincajuera Creek (Neuquén province, Argentina) in uppermost Tithonian levels. A new specimen of the turtle [*Neusticemys neuquina* (FERNANDEZ & DE LA FUENTE, 1988)] and a pliosaurid, are described. The Vaca Muerta organic-rich shales and marls represent the basinal sedimentary record of the Tithonian transgression in the Neuquén Basin. They are associated with nodular limestones rhythmically spaced, isolated coquinas and three sandstone facies. Cycles of two orders are defined through shale/marly-shale alternations. The marine reptiles "assemblage" is composed of pelagic forms. The high content of organic matter, the phosphate concentrations, the absence of benthic organisms and the lack of bioturbation suggest anoxic conditions of the sea floor. This euxinic environment was favored by the organic matter productivity and preservation. Productivity is related to upwelling from an oceanic oxygen-minimum zone. Preservation was conditioned by stagnation, controlled by the development of a thermo-pycnocline and very low sedimentation rates. A period of highstand, dry climatic conditions and low surrounding relief may have been favorable for the proposed model. Tithonian ichthyosaurs, pliososaurs and crocodiles of the Neuquén Basin share several genera with those of the Middle and Late Jurassic European Tethys. The turtles instead, are undoubtedly endemic of western South America.

KEYWORDS: TURTLES, PLIOSAURIDS, TITHONIAN, ARGENTINA, FACIES, PALAEOENVIRONMENTS.

RÉSUMÉ - Des restes de reptiles marins ont été trouvés dans la Formation Vaca Muerta à Trincajuera (Province du Neuquén, Argentine) dans des niveaux du Tithonien supérieur. Un nouveau spécimen de tortue [*Neusticemys neuquina* (FERNANDEZ & DE LA FUENTE, 1988)] et un pliosauridé sont décrits. Des lutites et des marnes riches en matière organique ont été déposées lors de la transgression tithonienne dans le Bassin du Neuquén. Il leur est associé des calcaires noduleux cycliques, des lumachelles isolées et trois faciès de grès. Des cycles à deux ordres sont définis par l'alternance des lutites/lutites marneuses. L' "association" de reptiles marins est composée de formes pélagiques. La teneur élevée en matière organique, la concentration de phosphates, l'absence d'organismes benthiques et celle de bioturbation suggèrent des conditions d'anoxie sur les fonds marins. L'environnement euxinique fut favorisé par la productivité de matière organique et par la préservation. La productivité est liée à l'upwelling d'une zone à minimum d'oxygène. La préservation a été facilitée par des conditions stagnantes contrôlées par le développement d'un thermo-pycnocline et des taux de sédimentation très faibles. Des périodes de haut niveau et de climat sec avec des reliefs bas dans les régions marginales du bassin peuvent avoir été favorables au modèle proposé. Les ichthyosaures, plésiosaures et crocodiles tithoniens du Bassin du Neuquén partagent quelques genres avec ceux du Jurassique moyen et supérieur de la Téthys européenne mais les tortues sont endémiques de l'Ouest de l'Amérique du Sud.

MOT-CLÉS: TORTUES, PLIOSAURIDÉS, TITHONIEN, ARGENTINE, FACIÈS, PALAEOENVIRONNEMENTS.

INTRODUCTION

In 1992, Sergio and Rafael Cocca, from the Museo Olsacher of Zapala, Neuquén province, found remains of marine reptiles in the west of this province. Several fieldtrips (1993-1995) were organi-

sed with paleontologists and geologists from the Universidad Nacional de La Plata. Remains of marine turtles [*Neusticemys neuquina* (FERNANDEZ & DE LA FUENTE, 1988)], pliosaurids, crocodiles (*Geosaurus* sp.) and mainly ichthyosaurs, were recovered.

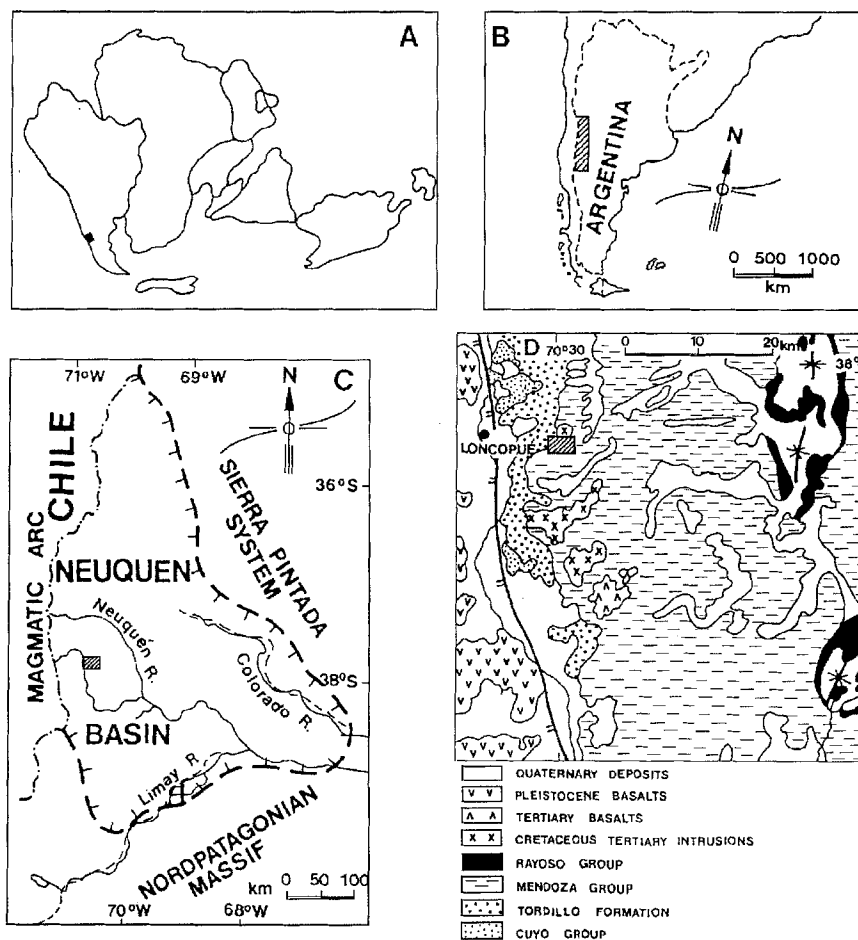


FIGURE 1 - Location map of the Trincajuera area and sketch geological map (from Digregorio & Uliana 1978). *Carte de localisation géographique de la région de Trincajuera et carte géologique (d'après Digregorio & Uliana 1978).*

The reptiles were found on the northern margin of Trincajuera Creek ($38^{\circ} 06' 45''$ S and $70^{\circ} 29' 45''$ W), some 12 km east of Loncopué village (Fig. 1), in the western sector of the Fold and Thrust Agrio Belt (Braccini 1970, Ramos 1978). The fossil-bearing unit, known as the Vaca Muerta Formation, is composed of dark shales and marls. The ammonite *Substeuoceras koeneni* found associated with the vertebrates suggests an uppermost Tithonian age (H. Leanza, pers. comm.).

The aim of this paper is to describe the first marine reptiles from the study area, and to provide a palaeoenvironmental model based on facies analysis. The Tithonian taxa from the Neuquén Basin are compared with those of the European Tethys, and endemism in the Oriental Pacific is reported.

GEOLOGICAL SETTING AND GENERAL FEATURES OF THE BLACK SHALES

From the Early Jurassic (Late Sinemurian) to the Albian, the Neuquén Basin went through a sag

evolutionary stage and behaved as a marginal marine basin (Mitchum & Uliana 1985). The basin infill, composed of clastic, carbonate and evaporitic deposits, was controlled mainly by eustatic and climatic changes (Gulisano et al. 1984; Legarreta & Gulisano 1989). Since Groeber (1946), two sedimentary cycles have been recognized: "Jurásico" and "Andico" (Fig. 2). The Andico cycle extends from the Tithonian to the Albian, and comprises the Mendoza and the Rayoso groups.

In most of the Neuquén Basin, the Vaca Muerta Formation is the basal unit of the Mendoza Group, concordantly overlaying the clastic and mostly continental deposits of the Tordillo Formation (Fig. 2). The contact marks the beginning of the marine Tithonian transgression (Leanza 1981). This author suggested that the base of the Vaca Muerta Formation is isochronous throughout the basin and corresponds to the Early Tithonian (*Virgatospinectes mendozanus* Zone), but its top is roughly diachronous, and includes younger stages from south (Middle Tithonian) to north (Valanginian) (Leanza & Hugo 1977).

Period	Stage	Lithostratigraphic units		Groeber Cycles
Cretaceous	Albian	Rayoso Group	Rayoso Fn.	Andico
	Aptian		Huitrin Fn.	
	Barremian	Mendoza Group	Agrio Fn.	
	Hauterivian		Mulichinco Fn.	
	U. Valanginian		Quintuco Fn.	
L. Valanginian	Vaca Muerta Fn.			
Berriasian				
Tithonian				
Jurassic	Kimmeridgian		Tordillo Fn.	Jurásico
	Oxfordian		Auquico Fn.	
			La Manga Fn.	
		Lotena Fn.		
	Callovian	Cuyo Group	Tábanos Fn.	
	Bathonian		Challacó Fn.	
	Bajocian		Lajas Fn.	
	Aalenian		Los Molles Fn.	
Toarcian				
Pliensbachian				

FIGURE 2 - Stratigraphic column of the Jurassic - Lower Cretaceous in the south-central Neuquén Basin. *Colonne stratigraphique du Jurassique - Crétacé inférieur du Bassin de Neuquén sud-central.*

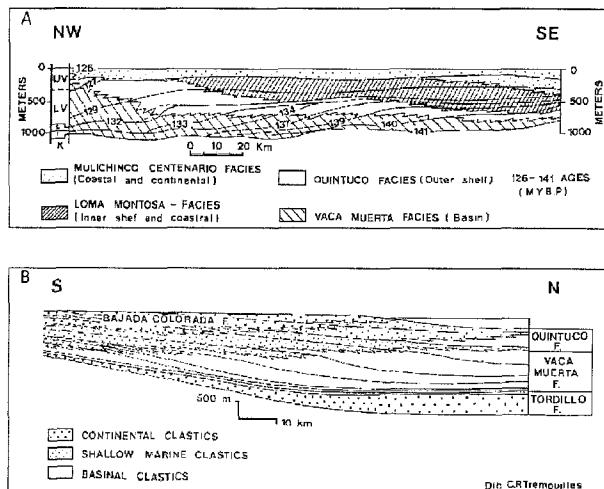


FIGURE 3 - Regional cross-sections of Tithonian - Valanginian sequences in southern Neuquén Basin. A, SE-NW section according to Mitchum & Uliana (1985); K: Kimmeridgian, T: Tithonian, B: Berriasian, LV: Lower Valanginian, UV: Upper Valanginian. B, S-N section according to Legarreta & Gulisano (1989). *Section transversale régionale de la séquence tithonienne - valanginienne au Sud du Bassin du Neuquén. A, coupe SE-NW d'après Mitchum & Uliana (1985); K: Kimmeridgien, T: Tithonien, B: Berriasien, LV: Valanginien inférieur, UV: Valanginien supérieur. B, coupe S-N d'après Legarreta & Gulisano (1989).*

In the studied area, the Jurassic - Lower Cretaceous succession is composed of the Tordillo, Vaca Muerta and Mulichinco Formations, intruded by Tertiary andesitic subvolcanic bodies (Fig. 1). Leanza (1973) measured 761 m of outcropping thickness for the Vaca Muerta Formation in the neighboring Cajón de Almanza locality, and the top is not exposed. This author described this formation as composed mainly of dark shales with thick sections of light brown fissile marls and

intercalations of black and grey limestones, dark calcareous concretions and aragonite veins. He mentioned thin sandy levels, which were not included in his systematic description of the profile. On account of its ammonite content, Leanza (1973) suggested that this section extends from the Early Tithonian to the Early Berriasian, though Leanza & Hugo (1977) restrained it to the Early-Late Tithonian.

Recent observations allow the above synthesis to be confirmed. However, the Vaca Muerta Formation has strong inner structural complications, faults and tight folds, which prevent a precise measurement of its thickness. Besides, studies on the fossil vertebrate-bearing sections, at its middle-lower part, revealed the presence of thin sandy levels subordinated to important sections composed almost only of black shales.

THE JURASSIC - CRETACEOUS SEQUENCE STRATIGRAPHY

The Mendoza Group constitutes a Supersequence, subdivided into five Mesosequences (Legarreta & Gulisano 1989). The oldest, Lower Mendoza Mesosequence, includes the fine-grained rocks of the Vaca Muerta Formation. The Lower Mendoza Mesosequence shows a general shallowing up trend: in its lower part transgressive dark shales prevail; overlain by shallower carbonates with subordinated siliciclastics (Fig. 3). Mitchum & Uliana (1985) and Legarreta & Gulisano (1989) mentioned that the top of the mesosequence is characterized by continental deposits even in central areas of the basin, which were attributed to a sudden relative fall in sea-level.

Nine depositional sequences can be recognized within the Lower Mendoza Mesosequence (Gulisano et al. 1984; Mitchum & Uliana 1985; Legarreta & Gulisano 1989). The lower three show a transgressive or retrogradational arrangement of parasequence sets (Gulisano et al. 1984, Legarreta & Uliana 1991). The upper sequences instead, have a sigmoidal pattern and a shallowing up vertical trend. This progradational arrangement is evident in either S-N and SE-NW sections (Fig. 3). Legarreta & Uliana (1991) suggested that though sigmoidal geometries may reflect progradation, the shift from shallow marine zones to deeper ones was very transitional, with very low relief. Consequently, the depositional profile lacked either talus slope or slope break. These features can be better developed in a period of relative sea-level fall, when accommodation is less than sediment supply.

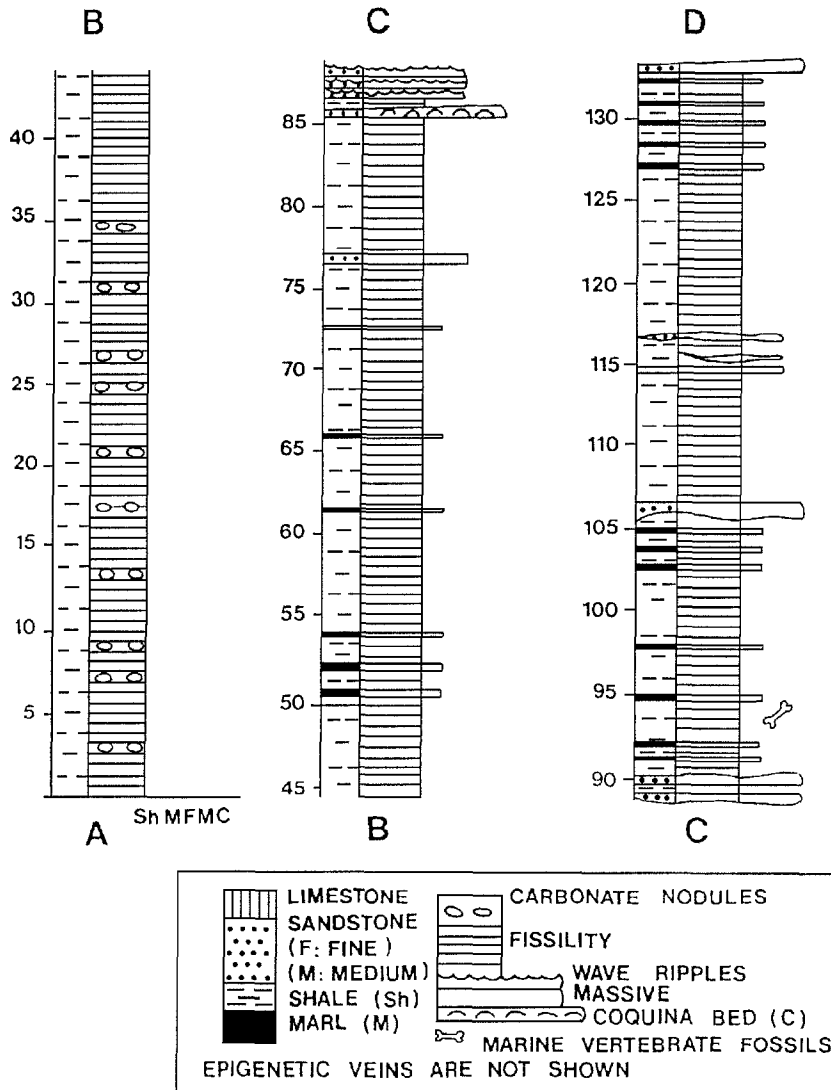


FIGURE 4 - Schematic column of the Vaca Muerta Formation at Cajón de Almanza area. Vertical scale in meters. *Colonne schématique de la Formation Vaca Muerta au Cajón de Almanza.*

FACIES ANALYSIS

A detailed profile (1:100) at Cajón de Almanza (Fig. 4) and studies on the northern margin of Trincajuera Creek, allowed the recognition of a set of facies in the Vaca Muerta Formation, and their vertical relationships.

Following previously established criteria (Spalletti 1995), Table I shows the facies types with their sedimentary features and designation codes. This new information points out the predominance of fine-grained sediments, black shales and dark marls (especially the former ones), formed by suspensive fall-out processes in geochemically anoxic to suboxic environments, in which vertical circulation was inhibited.

Nodular limestones and coquinas are associated with the fine-grained rocks. Nodule concentra-

tions are rhythmically spaced, and were mostly precipitated on skeletal cores (small to large fragments). In addition, extremely isolated thin lenticular bodies of bioclastic limestones (tempestites, according to Aigner 1982 and Allen 1984), occur. It is noteworthy that coquinas were previously mentioned by Leanza et al. (1977) and Leanza (1981).

Very thin sandstone bodies are relatively frequent, from 2 to 10 cm thick, occasionally reaching 80 cm thick. Their base is sharp, and many times erosive, on shales. Among sandstones, prevail massive layers or those with well developed normal gradation. They are interpreted as low density or dilute gravitational flow deposits related to storm surges (Walker 1984). Sandstones with symmetrical and asymmetrical combined flow ripples, as well as some thick isolated beds

Facies Code	Lithology	Structures	Depositional Mechanism
Ff	Shale	Fissility	Fall-out deposits
Mf, Mh	Marl	Fissility, lamination	Fall-out deposits
Cq	Coquina	Massive, disorganized	Storm beds (tempestites)
Ln	Micritic waxkestone	Nodular	Low energy bioclastic carbonates
Sm	Sandstone	Massive, normal grading	Low-density gravitational currents
Sr, Fr	Sandstone Siltstone	Asymmetric/symmetric combined flow ripples	Low-regime translational and orbital waves
S	Sandstone	Hummocky	High-regime orbital waves

TABLE 1 - Sedimentary facies of the Vaca Muerta Formation. *Faciès sedimentaires de la Formation Vaca Muerta.*

with hummocky structures (HCS) reflect the presence of a wide range of oscillatory (wave) flows (Myrow & Southard 1991).

Cyclic sedimentation is evident in the Vaca Muerta Formation. The most conspicuous cycles (which are also observed in profiles published by Leanza 1973) are those composed of alternations of shales and marly-shales, in which two orders of magnitude were established. The thickest ones comprise sections of 45 to 54 m, and the thinnest ones average 20 m each. Though less evident, high order cycles in the scale of 4-4.5 m are defined by the rhythmic concentration of nodular carbonates.

Some local palaeocurrent data could be obtained from wave ripples, with crest trains arranged E-W and northwards palaeoflow wave-approach (350°). Reptile orientation can be shown to coincide with these palaeoflows. Two specimens of *Geosaurus* sp., one of them with skull, was northwestwards (350°) oriented, while a longirostral ichthyosaur skull, not yet studied, appears with 250° azimuth. Comparing these data with those of wave ripples, it can be inferred that relationships between the orientation of the wave trains and the deposition of the marine reptile remains may be coincident. The preferred orientation of the organisms may indicate the presence of still weak currents (flows) even in areas dominated by fall-out of fine particles.

MARINE REPTILES

Ichthyosaurs are the prevailing marine reptiles of the studied area. Two specimens of *Geosaurus* sp. have been found (one of them with skull and mandible in perfect preservation conditions), in addition to pliosaurids and turtles. Those best preserved specimens are described below.

SYSTEMATICS

CHELONII Brongniart, 1800

CRYPTODIRA Cope, 1864

Genus *Neusticemys* FERNÁNDEZ & DE LA FUENTE, 1993

Neusticemys neuquina (FERNÁNDEZ & DE LA FUENTE, 1988)
Figs 5D,E; 6D,E

Material - MOZ 6094P. mandible, right humerus, right femur, fragmentary remains of girdle bones and dorsal carapace (preserved in two halves). The main part is enclosed in a nodule together with the mandible, the humerus, the femur and fragments of the pelvic girdle bones. Its counterpart is the dorsal carapace cast (Figs 5E, 6E).

Description

Mandible

It is exposed ventrally. Both mandibular rami are completely fused. The symphysis is rather short and its length (27 mm) is approximately 30 percent of the whole mandible length (73 mm). The mandibular rami are rather narrow, and though the mandible crushing surface cannot be observed, the comparison with those of the specimen MOZ P (not yet listed) from Los Catutos, referred to as *Neusticemys neuquina* (de la Fuente, in study), suggests a narrow crushing surface for the Trincajuera specimen. Unfortunately, fossilization damaged the mandible bone edges.

Dorsal carapace

It is approximately 470 mm long and only its visceral side can be observed. Its shape is similar to that of *Neusticemys neuquina* (MLP 92-IV-10-1) from the Middle Tithonian of Los Catutos. The anterior margin is elongate, and the anterolateral margins, formed by the first two pairs of peripheral plates, are rectilinear. The lateral and posterolateral margins cannot be precisely determined due either to the lack of peripheral plates or to their bad preservation condition. However, their impressions, the

disposition of the free ends of the ribs, and the lateral and posterolateral margins are curved as in the specimen figured of Los Catutos area (Fernández & de la Fuente 1993: Pl.III).

The odd plate series begins with a nuchal plate, wider than long. Its length is 60 percent of its width. The morphology of the anterior margin visceral surface is like the one observed in the paratype MOZ 1106P of *Neusticemys neuquina*. In both specimens the visceral margins of the nuchal plate have a slightly convex flange, extended up to the edges of the visceral surface of the first and second pair of peripheral plates. Likewise, no postnuchal foramina can be seen between the nuchal plate, the first pair of pleural plates and the first neural one. These foramina are only present in *Toxochelys* (see Zangerl 1953), the Chelonioidae basal taxon. Another conspicuous feature of the Trincajuera specimen is the scar produced by the break of the neural spine of the first dorsal vertebra which extends the fusion from the first neural plate to the distal end of the nuchal plate. The odd series of bones continues with nine neural plates aligned one after the other until the first suprapygial. The first and second neural plates are ovorectangular. The third, fourth, fifth and sixth are hexagonal with their anterolateral margins shorter than the remainders. The neural plates increase in length from the third to the fifth. Then, this condition is reversed. The seventh and eighth, irregular in shape, are slightly longer than wide and the ninth is trapezoidal. That bone regarded as the first suprapygial in MLP 92-IV-10-1 from Los Catutos, is divided in two plates in the Trincajuera specimen. The first one would correspond to the ninth neural above mentioned, with remains of the scar produced by the dorsal vertebrae in the proximal end of the visceral surface. The second one, because of its relative position with respect to the eighth pair of pleural plates, may correspond to the first suprapygial of Los Catutos specimen. This suprapygial plate is followed by two other fairly wider than large, and one pygal plate partially preserved. The first suprapygial is trapezoidal, while the second and third suprapygial are subrectangular. The odd series ends with a rectangular pygal plate. This pattern is similar to that one observed in MLP 92-IV-10-1 from Los Catutos.

At both sides of this series there are eight pairs of pleural plates. The pleural ribs are well developed and can be clearly distinguished in the visceral surface of the pleurals. The heads of those ribs are not well preserved. The anterolateral margins of the first pair of pleural plates contact with the first and second pair of peripheral plates. Most peripheral plates have been preserved on the left margin, but not on the right side. The pleuroperipheral fenestrae are well developed from the sector between the

first and the second pleural, the free ends of the ribs and the third and fourth peripherals on.

Right humerus

It is complete and well preserved by the nodule, as more than the other known humerus of *Neusticemys*, MLP 92-IV-10-1 from Los Catutos. The axis is 125 mm length and the proximal and distal ends are fairly expanded. Unlike the continental turtles (e.g. *Chelydra*) the angular relationship between the caput humeri and the humerus axis is 120. This is approximately that of the Cheloniidae (127), but lower than that of the Toxochelyidae (140) (Zangerl 1953). In spite of this angular relationship, the sigmoidal curve of the axis and the disposition of the radial processus (partially preserved) level with the caput humeri, approach the humerus of the specimen MOZ 6094P interpreted as the primitive condition observed in continental aquatic turtles. A marked ectepicondylar furrow can be seen in the posterior third of the humerus mid-dorsal surface.

Right femur

This is the first known femur of *Neusticemys*. It is in a lateral position, displaced from the corresponding pelvic girdle bones (ilium, pubis and isquion, partially preserved and covered in part by the carapace), being the distal end closer to the pelvic bones than the proximal. Unfortunately, the proximal end is badly preserved, and its main features are not clear. The axis of the femur (134 mm) is slightly longer than that of the humerus (125 mm). This condition is not observed in Chelonioidae.

Remarks - This marine turtle species was named by Fernández & de la Fuente (1988). It was first assigned to the genus *Eurysternum* from the European Tithonian, based upon three specimens from the lower levels of the Vaca Muerta Formation, outcropping at Cerro Lotena. These levels belong to the *Virgatosphinctes mendozanus* Zone, which is referred to the Early Tithonian (Leanza & Hugo 1977, Leanza 1980).

Later, Fernández & de la Fuente (1993) studied two other specimens from the middle levels of the Vaca Muerta Formation referred to the upper part of the Middle Tithonian (*Windhausenicerias internispinosus* Zone), Leanza & Zeiss (1990). When comparing the new remains with the figure of the lost holotype of *Eurysternum wagneri*, type species of the genus *Eurysternum*, they proposed the relocation of the Neuquén species within a new genus *Neusticemys*.

This taxonomic decision was finally adopted comparing *Neusticemys* with the Kimmeridgian-Tithonian turtles of Stuttgart, Munich, Eichstätt, Frankfurt am Main, Lyon and Paris Museums and with other Jurassic European turtles figured

in papers published by the end of the last century (see Fernández & de la Fuente 1993, and literature therein). The comparison of *Neusticemys* with European Kimmeridgian-Tithonian specimens was based on the tentative assignation of the Neuquén turtle to the family Plesiochelyidae.

Gaffney & Meylan (1988) and Gaffney et al. (1991) proposed the monophily of the Plesiochelyidae on the basis of craneal features. Consequently, only three genera can be included in its cladogram (*Plesiochelys*, *Portlandemys* and "*Thalassemys*"), as most taxa included within this family by Kuhn (1964) lack of craneal material. Later, Broin (1994) referred to the family Plesiochelyidae those genera included by Gaffney & Meylan (1988) and also those taxa of the chelonian faunas from the Late Kimmeridgian-Early Tithonian of Solothurn (Switzerland), Cerin and Canjuers (France) and Bayer (Germany). Up to now, there is not a clear definition of the Plesiochelyidae as a monophyletic taxon, including all the species referred to this family, which reflect the relationships among all its members.

The Trincajuera specimen, as others from Cerro Lotena and Los Catutos assigned to *Neusticemys*, shares with the Plesiochelyidae the width of the carapace, the shortening of the nuchal plate and the first pleural ones. But these are primitive characters not useful to establish relationships with European taxa (Fernández & de la Fuente 1993). However, *Neusticemys* shares derived features of the carapace with other turtle specimens which have been assigned to Plesiochelyidae, such as the holotype SMNS 10817 of *Thalassemys marina* FRAAS, unpublished specimens of the Bayerische Staatssammlung für Paleontologie und Historische Geologie of Munich (BSP-AS- 1921 and BSP-1952-1-113) and primitive Chelonioida from the Early Cretaceous of Australia, as *Notochelone costata* DE VIS (QM F 33511) (see Gaffney 1981). Among these characters are: the anteroposterior elongation of the dorsal carapace, the presence of broad pleuro-peripheral fenestrae, the loss of a firm sutural contact of the plastron with the dorsal carapace along the bridge, and the development of broad lateral fenestrae and a large fenestra on the plastron. However, these characters do not suggest relationships, as they characterize carapaces of marine turtles with pelagic habits (see Zangerl 1980).

Fernández & de la Fuente (1993) discarded the assignation of *Neusticemys* to the Chelonioida and suggested its tentative reference to the Plesiochelyidae. However, the relationships of *Neusticemys* with other marine turtles below the infraordinal hierarchy are still uncertain due to the lack of skulls, so important when establishing turtle relationships.

Finally, the finding of *Neusticemys neuquina* in the middle-upper sector of the Vaca Muerta Formation referred to the Late Tithonian by Leanza (pers. comm.) confirms the presence of the Neuquén species between the Early and Late Tithonian.

SAUROPTERYGIA Owen, 1860
PLESIOSAURIA de Blainville, 1835
PLIOSAUROIDEA (Seeley) Welles, 1943
PLIOSAURIDAE Seeley, 1874

gen et sp. indet.
Figs 5A,B,C; 6 A,B,C

Material - MOZ 6113V. Posterior fragment of rostrum and anterior part of the skull with part of the mandibular rami.

Description - The material is included in a nodule, unfortunately incomplete, as its edges show very recent fractures. Probably most of the skull was originally preserved, because the posterior edge, which coincides with the anterior part of the temporal fenestrae, was recently broken. Likewise, another fracture on the lateral right edge of the rostrum coincides with the loss of most of the snout.

The rostrum, in front of the nares, is as high as wide. Dorsally, the premaxillae are dome shaped, like most pliosaurids, and continue in the parietal without a net contact between both elements (Figs 5B, 6B). The nares are large, oval, and ventrally limited by the anterior maxilla, and posteriorly by the frontal. Probably the premaxilla limited it dorsally. The nares are dorsally placed. The only maxilla preserved is the left one. It is almost plane in front of the nare and nearly vertical in its lateral side. The premaxillae lie on the maxillae, increasing the rostrum height. They are dome shaped, with a marked fissure which put them sagittally apart. The orbits are laterodorsal, 2/3 longer than high. The inferior border of the orbit is formed by the jugal and in front, by a probable lacrimal. The presence or absence of lachrymal in pliosaurids is subject to controversy; however, Taylor & Cruickshank (1993) marked it clearly in *Pliosaurus brachyspondylus* (OWEN). One of the most distinctive features of the specimen MOZ 6113V is the prefrontal expansions, which are either rarely preserved or very much reduced in pliosaurids (Figs 5B, 6B). There is one specimen in The Natural History Museum (London) referred to *Peloneustes philarchus* SEELEY, with expanded prefrontals (BMNH-R 8574); however, the rostrum height, among other features, suggests that it may not belong to this species. The prefrontals of the specimen MOZ 6113V cover almost 2/3 the length of the orbit and have externally a rough completion as the prefrontals of metriorhynchid crocodiles and as the palpebrals of many mesoeucrocodylians. The position of the

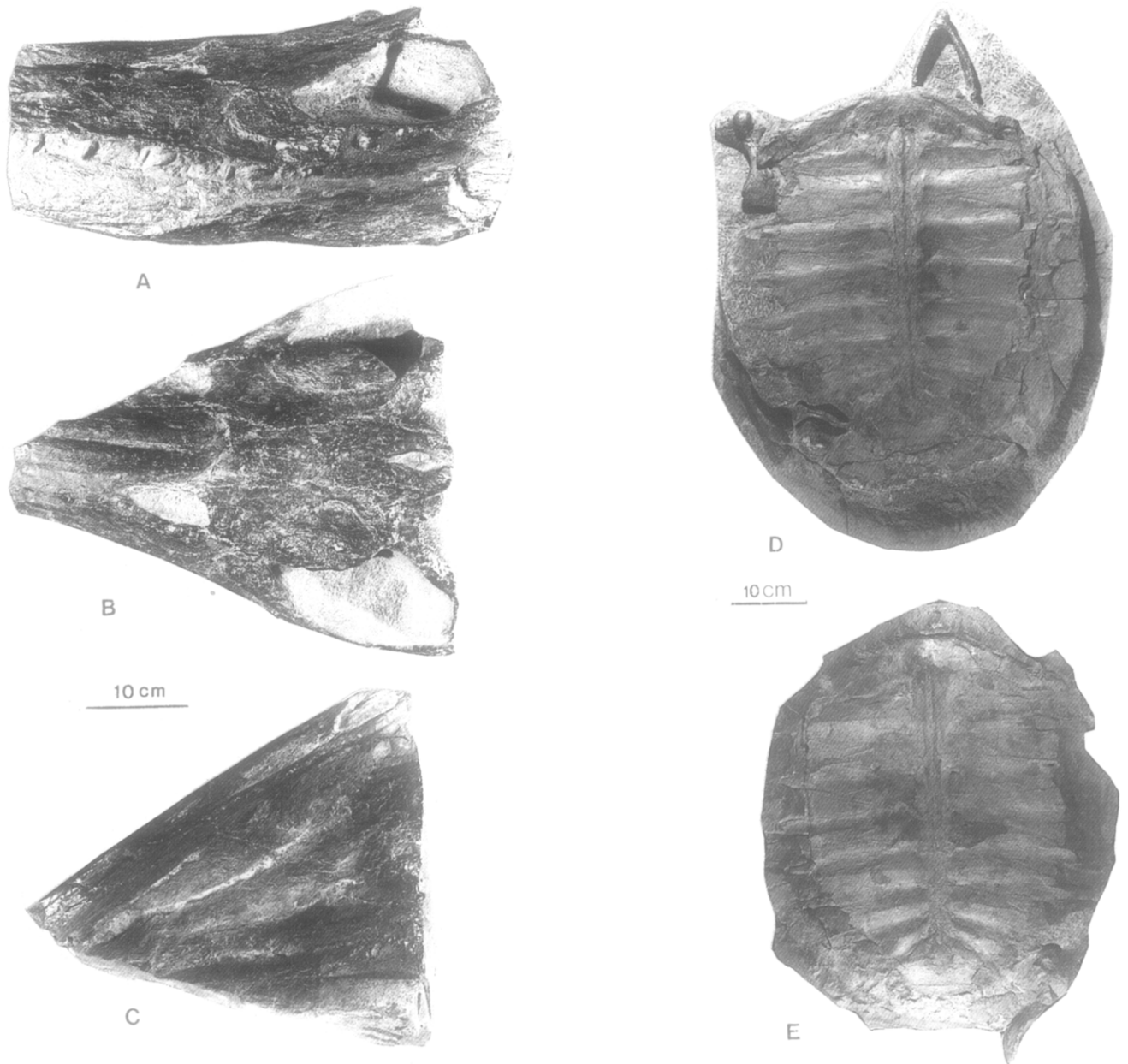


FIGURE 5 - MOZ 6113V, Pliosauridae gen. et sp. indet., skull: A (lateral view), B (dorsal view), C (ventral view). MOZ 6094P, *Neusticemys neuquina* (FERNÁNDEZ & DE LA FUENTE, 1988): D (visceral view of the carapace, appendicular skeleton and lower jaw), E (visceral view of the carapace cast and remaining bones). MOZ 6113V, Pliosauridae gen. et sp. indet., crâne: A (vue latérale), B (vue dorsale), C (vue ventrale). MOZ 6094P, *Neusticemys neuquina* (FERNÁNDEZ & DE LA FUENTE, 1988): D (vue ventrale de la carapace, fragments du squelette appendiculaire et mandibule inférieure), E (vue ventrale du moule de la carapace et reste des os).

prefrontals in the Trincajuera pliosaurid (Figs 5B, 6B) coincides with that of the crocodiles' palpebrals, which protect the eyes while it guides the view laterally-anteriorly. In the specimen MOZ 6113V, the left orbit is posteriorly surrounded by the postfrontal and postorbital. The pinneal fora-

men, on the parietal, has its anterior edge level with the anterior edge of the depressed platform preceding the temporal fenestra; the posterior edge of the pinneal coincides with the temporal fenestra itself (Figs 5B, 6B).

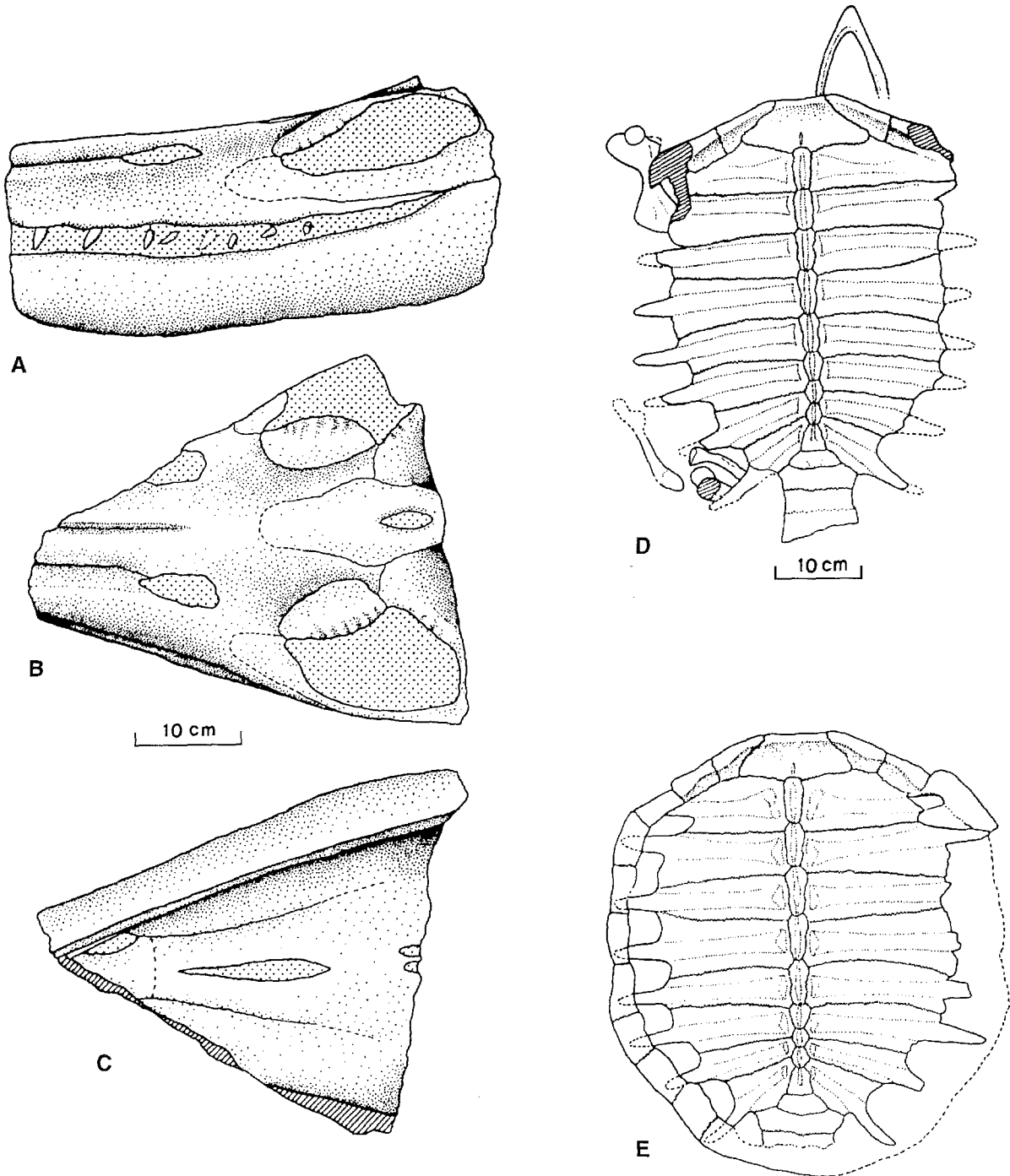


FIGURE 6 - Drawings corresponding to Figure 5. Dessins correspondant aux photographies de la Figure 5.

Some teeth were preserved in the left maxilla, though they must have rotated in their alveoli when the connective tissue disappeared, because of the curve of the crowns (some of them forwardly oriented). The teeth are rather small. In *Pliosaurus brachyspondylus* (OWEN) from the

Kimmeridge Clays, Westbury, Wiltshire, the last teeth are much weaker than the anterior ones, and have curved tips to hold the prey preventing its slipping outwards (Taylor et al. 1995). The crowns and enamel preservation is bad, and it is impossible to know whether they had striae. Two

teeth of the right mandibular fragment are transversely broken, confirming that, as in all post-Callovian pliosaurids they are triangular in cross section, though the posterior ones would be sub-circular. This shift can also be seen in *Pliosaurus brachyspondylus* (Taylor & Cruickshank, 1993).

The right maxilla is missing, and the left one is preserved fused to the mandible (Figs 5A, 6A). The left external naris is limited by the vomer, palatine and maxilla, being the pterygoid excluded. An extended anterior interpterygoid vacuity lies on the pterygoid anterior ramus. On the rear of the palate it can be observed the anterior part of the posterior interpterygoid vacuities, separated by a thin bar of the parasphenoid, which is level with the palate (Figs 5C, 6C).

Remarks - The Late Jurassic Pliosauroida come mostly from western Europe and the best defined genera are *Pliosaurus* OWEN, *Liopleurodon* SAUVAGE, *Peloneustes* and *Simolestes* ANDREWS (Tarlo 1960; Bardet 1992; Bardet et al. 1994; Taylor & Cruickshank 1993). *Liopleurodon* and *Pliosaurus* have been found in the Neuquén Basin (Gasparini & Fernández 1997; Gasparini in study). Differences between *Liopleurodon* and *Pliosaurus* are not so marked (Bardet et al. 1994), and cannot be recognized in the pliosaurid fragment found at Trincajuera.

DISCUSSION

The marine reptiles "assemblage" of the northern margin of Trincajuera Creek, found on the lower middle sector of the Vaca Muerta Formation (Late Tithonian), is composed merely of pelagic forms. Such a diversity suggests that there was enough food of nectonic forms like ammonites, belemnites, fish and even some reptiles, ending the trophic pyramid with pliosaurids, probably predators (Massare 1988).

The invertebrates associated with the reptiles are very scarce and generally reduced to casts. Most reptile skeletons instead, are articulated (*Geosaurus*, *Neusticemys*, ichthyosaurs) and none of them, even those more fragmented, bear epibiotic incrustations. Both conditions suggest that bottoms were euxinic and therefore, did not lodge invertebrates which could be skeleton scavengers. The high content of organic matter in the black shales, phosphate concentrations (Leanza 1973), the absence of benthic organisms and the lack of bioturbation structures suggest also anoxic conditions of the seafloor. That is: the redox line was above the sediment/water interphase. A similar scenario is described by Martill (1985) for the marine vertebrates in the Lower Oxford Clay of

central England. The turtle *Neusticemys neuquina* (MOZ 6094V) is an interesting case of preservation. Its plastron was not preserved as it is weakly attached to the carapace by soft tissues. But curiously, the mandible, which is commonly detached by scavengers' action, is in life position. Buccal and anal holes are the first areas attacked by scavengers in different vertebrate groups (Weigelt 1989). In a turtle, protected by the carapace, the soft tissues of the mouth would be the first torn off. Furthermore, the mandible, as a light part of the skeleton, would be first in being detached and transported, even when the carapace lays on the bottom. Consequently, the mandible in life position may prove the absence of scavengers. The proposed palaeoenvironmental model supports suspensive fall-out phenomena of very fine particles in a depositional setting with null or very low kinetic energy, and not greater palaeobathymetry than 200 m. The preferred disposition of some specimens, especially two crocodiles (*Geosaurus*), may indicate very weak flows even in areas with fine-grained particle settling. These flows could have been effective, only during the specimens' fall, resulting in their orientation, but they would have had not enough energy as to dismember the bodies.

The concurrence of two main phenomena accounts for the euxinic environment: productivity and organic matter preservation (Beier & Hayes 1989). Productivity is related to a constant supply of organic material, mainly by upwelling. Upwelling brings organic matter from deeper to shallower zones, together with oxygen. Whenever the oceanic water comes from an oxygen-minimum zone (Heckel 1977), the upwelling will supply only organic matter together with phosphates. It is noteworthy that several other Upper Jurassic - Lower Cretaceous oceanic basins such as the Weddell Sea, the South Atlantic, and the Mozambique Basin (Doyle & Whitham 1991) were characterized by very scarce dissolved oxygen content (anoxia).

The organic matter preservation can be related to an extremely low circulation of the marine waters (Stein et al. 1989), favoured by bottom waters stagnation (e.g. the present day Black Sea) and low sedimentary rates. This latter subject is enhanced by a rather high sea level and deficient terrigenous supply, related to dry climates and low surrounding relief (cf. Veiga and Orchueta 1988; Legarreta and Uliana 1991).

The information provided by fossils, suggests that during the Late Jurassic, the surficial marine waters of the Neuquén Basin were strongly oxic, allowing a faunal richness and diversity. Toxic conditions were restrained to the bottom waters, near the sediment:water interphase, due to a high nutrient supply caused by upwelling,

and an extremely reduced vertical circulation of sea water. The environmental shift from surficial oxic to bottom anoxic, and the decrease of the vertical circulation, are related to a marked thermopycnocline; that is, a marine water zone with rough variation in temperature and density, separating a surficial, warm and low density mass, from another cooler, denser and anoxic layer, in the depth.

Though not all the Trincajuera reptiles were studied yet, some taxa are the same as other Tithonian assemblages of the Neuquén Basin (Gasparini & Fernández 1997). *Neusticemys neuquina* was recorded in the Early Tithonian (Cerro Lotena), Middle Tithonian (Los Catutos) and Late Tithonian (Trincajuera). *Geosaurus* has the same geographical and temporal distribution. From a palaeobiogeographic point of view, whereas the Tithonian ichthyosaurs, plesiosaurs and crocodiles of the Neuquén Basin share several genera with those of the Middle and Late Jurassic European Tethys (*Ophthalmosaurus*, *Liopleurodon*, *Pliosaurus*, *Metrriorhynchus*, *Geosaurus*) (Gasparini & Fernández op. cit.), the turtles are undoubtedly endemic to western South America, though *Notoemys* is closer related to the Gondwanan pleurodires (Lapparent & de la Fuente in study).

Abbreviations: BMNH (the Natural History Museum, London); BSP (Bayerische Staatsammlung für Paleontologie und historische Geologie of Munich); MLP (Museo de La Plata); MOZ (Museo Olsacher, Zapala); QM (Queensland Museum, Brisbane); SMNS (Staatliches Museum für Naturkunde in Stuttgart).

Acknowledgements - The authors thank the staff of the Museo Olsacher of Zapala (S. Cocca, R. Cocca and D. Carbó) and Dirección General de Minería of Neuquén, their help in fieldwork. Dr. Ralph Molnar (Queensland Museum) for the casts of *Notochelone costata*. Dr. Angela Milner (the Natural History Museum, London) for the access to the pliosaurid collection under her care. Dr. Stephen Johnson for reading the English version. Fossil vertebrates were prepared by O. Molina and J. Laza from the Departamento de Paleontología Vertebrados, Museo de La Plata. C. Tremouilles and M. Lezcano made the drawings, F. Castets, the photographs and C. Deschamps helped with the edition of the text. This work was supported by NGS Grant 5178-94 and partly by grants of Universidad Nacional de la Plata to L. Spalletti and Z. Gasparini.

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