

The Jurassic Thalattosuchia (Crocodyliformes) of Chile : a paleobiogeographic approach

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Key words. – Jurassic, Thalattosuchia, Chile, Systematic, Paleobiogeography.

Abstract – The thalattosuchian fossils from the Jurassic of Chile are revised. Some specimens, dating from the Lower Lias (Sinemurian), are the oldest known thalattosuchians, but are too fragmentary to establish a precise taxonomic placement. New specimen related to the genus *Metriorhynchus* is described from the lower Bajocian. It is the oldest representative of the genus and fills an important gap in our knowledge of the paleogeographic history of this group. Other new cranial fragments, related to the Callovian species *Metriorhynchus casamiquelai*, are described and this species is revised in the light of new studies on the intraspecific variability in extant crocodylians. Up until now, the known distribution of Liassic Thalattosuchia suggested a circumpacific distribution with minimally episodic passages through the Caribbean Corridor. Nevertheless, the close affinities between the South American and the European Metriorhynchidae from the Callovian to the Tithonian suggest the possibility that more and more frequent communications were made via the Caribbean Corridor. The new data corroborate the hypothesis formulated from the invertebrate faunas.

Les Thalattosuchia (Crocodylomorphes) du Jurassique du Chili : une approche paléobiogéographique

Mots clés. – Jurassique, Thalattosuchia, Chili, Systématique, Paléobiogéographie.

Résumé – La révision des Thalattosuchia du Jurassique chilien est réalisée. Certains restes, datés du Lias inférieur (Sinémurien) correspondent aux plus anciens thalattosuchiens connus mais sont encore trop fragmentaires pour permettre une définition précise. Un nouveau crâne, rapporté au genre *Metriorhynchus*, est décrit dans le Bajocien inférieur. Il s'agit du plus ancien représentant du genre et permet ainsi de combler une importante lacune de connaissance dans l'histoire paléobiogéographique du groupe. De nouveaux fragments de crânes, rapportés à l'espèce callovienne *Metriorhynchus casamiquelai* sont décrits et la révision de cette espèce est proposée à la lumière des récents travaux sur la variabilité intraspécifique chez les crocodyliens. La répartition actuellement connue des Thalattosuchia liasiques suggère une dispersion circum-pacifique avec passages, au moins épisodiques, par le Corridor caraïbe. A partir du Callovien, et jusqu'à la fin du Jurassique, les fortes similitudes anatomiques entre les Metriorhynchidae sud-américains et ouest-européens suggèrent la possibilité de communications de plus en plus fréquentes par le Corridor caraïbe. Ces nouvelles données corroborent les hypothèses formulées à partir des faunes d'invertébrés.

VERSION FRANÇAISE ABRÉGÉE

Dans le Jurassique inférieur d'Amérique du Sud, les restes de reptiles marins sont encore très rares et fragmentaires. Par contre, la découverte de nombreux reptiles (ichthyosaures, plésiosaures, crocodyliens métriorhynchidés et tortues) lors de récentes fouilles dans le Jurassique moyen et supérieur du Bassin de Neuquén (Chili-Argentine, fig. 1) permet de montrer les importantes affinités taxonomiques des faunes sud-américaines et européennes et de préciser leurs relations paléobiogéographiques. Parmi les thalattosuchiens, les plus anciens représentants du genre *Metriorhynchus* dans le Bajocien inférieur et de nouveaux restes post-calloviens permettent d'apporter un nouvel éclairage sur la dispersion paléogéographique de ces formes.

La présence de Thalattosuchia dès le Sinémurien du Chili est signalée par Chong-Diaz et Gasparini [1972] mais ces restes de métatarsiens sont très fragmentaires (fig. 2), et ne permettent pas une définition taxonomique plus précise. Par contre, le réexamen de la position des orbites et du développement des préfrontaux sur un fragment de crâne provenant du Bajocien inférieur et initialement rapporté à *Ichthyosaurus acutirostris* par Tavera [1981] montre qu'il s'agit en fait du plus ancien représentant connu du genre *Metriorhynchus* (fig. 3).

La découverte de nouveau matériel dans le Callovien moyen et la prise en compte des données issues de l'étude de la variabilité intraspécifique chez les crocodyliens actuels [Vignaud, 1995] permettent de préciser les affinités phylogénétiques de l'espèce *Metriorhynchus casamiquelai* (fig. 4 et 5). La validité de cette espèce fut contestée par Adams-Tresman [1987] en raison notamment de l'existence d'intermédiaires entre les caractères distinguant *M. casamiquelai* de *M. brachyrhynchus* comme par exemple l'ornementation des os crâniens et la forme de la suture prémaxillaire / maxillaire. Les caractères diagnostiques sont donc discutés puis redéfinis. Parmi les autapomorphies de l'espèce, la distance séparant les prémaxillaires des nasaux, l'absence d'ornementation sur les préfrontaux, la forme du frontal et des narines internes entièrement cloisonnées permettent de distinguer *M. casamiquelai* des formes brévirostrées européennes telles que *M. brachyrhynchus*. L'espèce sud-américaine *M. westermanni* fut créée sur un crâne incomplet et mal préservé (fig. 6). Le réexamen des caractères montre que certains d'entre eux peuvent être interprétés comme correspondant à des caractères juvéniles (orientation de la face occipitale, forme du pilier postorbitaire) alors que l'absence de division des narines internes est en fait due à la médiocre conservation du matériel. L'holotype de *M. westermanni* est interprété comme un spécimen juvénile et l'espèce *M. westermanni* doit donc être mise en synonymie avec l'espèce *M. casamiquelai*.

Approche paléobiogéographique

Dans le Jurassique inférieur, la distribution des restes de Thalattosuchia montre que ces formes peuplaient les bordures de la Téthys et la bordure est du Paléopacifique (France, Inde, Chine, Chili et Argentine). Les données anatomiques et

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l'analyse sédimentologique des gisements indiquent clairement que ces premiers *Thalattosuchia* devaient être encore très inféodés aux milieux littoraux. Leur dispersion à travers le Paléopacifique paraît donc très improbable. Comme le montrent les affinités entre certaines faunes d'invertébrés (céphalopodes, lamellibranches, brachiopodes et ostracodes) d'Europe occidentale et d'Amérique du Sud [Schmidt-Effing, 1976; Hillebrandt, 1981; Hallam, 1983; Manceñido and Dagys, 1992; Boomer and Ballent, 1996; Rubilar, 1998; Jakobs and Smith, 1998; Liu *et al.*, 1998], la présence d'une mer épicontinentale, nommée Corridor hispanique ou Corridor caraïbe, est probable dès le Jurassique inférieur bien que non documentée dans les sédiments. Ainsi, ce bras de mer aurait pu constituer un passage privilégié facilitant la dispersion des *Thalattosuchia*.

Dans le Jurassique moyen, les premiers représentants du genre *Metriorhynchus* sont connus dès le Bajocien inférieur du Chili et peut-être même dès l'Aalénien de l'Orégon [Stricker and Taylor, 1989]. En Europe occidentale, les restes de Teleosauridae sont fréquents mais parmi les Metriorhynchidae, seul le genre *Teleidosaurus* est représenté au Bajocien et Bathonien; les premiers spécimens rapportés au genre *Metriorhynchus* ne sont datés que du Callovien inférieur [Vignaud *et al.*, 1994]. Dès le Bajocien, la présence de sédiments marins au Venezuela [Bartok *et al.*, 1985] atteste l'existence d'un bras de mer séparant l'Amérique du Nord de l'Amérique du Sud. Cette communication marine est confirmée par les importantes affinités taxonomiques des faunes d'invertébrés entre l'Europe et la bordure Pacifique de l'Amérique du Nord et du Sud [Westermann et Ricciardi, 1985; Manceñido et Dagys, 1992; Rubilar, 1998]. Parmi les Metriorhynchidae, les affinités taxonomiques sont très importantes dès le Callovien moyen (*M. brachyrhynchus* en Europe et *M. casamiquelai* en Amérique du Sud) et jusqu'au Tithonien (*Geosaurus* et *Dakosaurus*). Durant cette période, les Teleosauridae sont restreints à l'Europe occidentale. Jusqu'à la fin du Jurassique, la dispersion des Metriorhynchidae et de certains autres reptiles marins est favorisée par la fragmentation du Gondwana et l'ouverture de voies de communication marines [Gasparini, 1992; Gasparini et Fernández, 1997].

INTRODUCTION

The largest number and greatest taxonomic diversity of Jurassic marine reptiles is found in Europe. Outside of Europe the records are both temporally and geographically scant, except for the herpetofauna from western South America in northern Chile and central-western Argentina (Neuquén Basin) (fig. 1). In these regions, the record ranges from the Hettangian to the Tithonian, with a significant taxonomic diversity in the middle Jurassic (ichthyosaurs, plesiosaurs and metriorhynchid crocodiles) as well as in the Tithonian (the three mentioned groups plus the only marine turtles from the eastern Pacific) [Gasparini and Fernández, 1996, 1997]. Most of these reptile taxa are related to European forms. This fact prompted one of us to propose different paleobiogeographic hypothesis [Gasparini, 1985, 1992].

The record of marine reptiles from the early Jurassic in western South America is very poor due to the lack of methodical field work. The material is fragmentary and most of what has been cited up to 1970 has been lost [Casamiquela, 1970; Chong-Diaz and Gasparini, 1976; Gasparini, 1985]. Consequently the taxonomic information is limited. However, intensive work in early Bajocian exposures of the Neuquén Basin yielded the greatest diversity hitherto known of marine forms from the middle Jurassic (pre-Callovian). These forms are transitional between those from the European Liassic and Dogger, covering part of the gap in the knowledge of the evolution and geographic distribution of plesiosaurs and ichthyosaurs [Gasparini, Spalletti and Fernández, 1997; Fernández, 1997; Gasparini, 1997].

In the Callovian formation of northern Chile and the Neuquén Basin, the reptiles are closely related to those of western Europe, especially from the Oxford Clay (*Metriorhynchus*, cf. *Muraenosaurus*, cf. *Cryptoclidus*). Consequently, the South American herpetofauna is especially significant from a paleobiogeographic standpoint [Gasparini and Chong-Diaz, 1977; Gasparini and Spalletti, 1993]. Finally, except for unconfirmed reports of ichthyosaurs and plesiosaurs from the Oxfordian and Kimmeridgian of Chile [Chong-Diaz and Gasparini, 1976], all the marine reptiles from the late Jurassic of western South America are from Tithonian sediments from the Neuquén Basin, that includes Lo Valdés area in central-west Chile. Taxonomic studies of these off-shore forms led to the proposal of paleogeographic



FIG. 1. — Map of Chile with Jurassic marine crocodilian localities (symbol).

FIG. 1 — Carte du Chili et localisation des sites à crocodiliens marins du Jurassique.

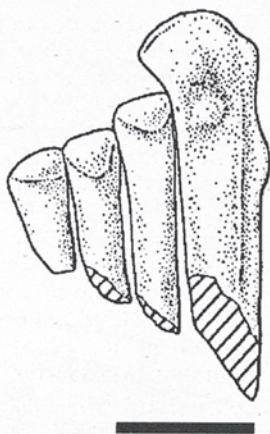


FIG. 2. – MGHF 3601 (87-1) *Thalattosuchia* indet., metatarsals 1-4, Sinemurian, scale bar : 2 cm.

FIG. 2. – MGHF 3601 (87-1) *Thalattosuchia* indet., métatarses 1-4, Sinémurien, barre d'échelle : 2 cm.

distribution hypotheses and paleoenvironmental analyses [Gasparini and Fernández, 1997; Gasparini Spalletti and de la Fuente, 1997; Gasparini *et al.*, 2000].

In this context, the paleofauna from Chile is particularly interesting. It includes, the oldest marine crocodylian known in the eastern Pacific domain [Chong-Diaz and Gasparini, 1972], and the first undoubted Callovian metriorhynchid outside of western Europe [Gasparini and Chong-Diaz, 1977]. The discovery of new material of *Metriorhynchus* sp. from early Bajocian cited in this paper is the oldest record of this genus. Therefore, Chilean crocodylians from the early and middle Jurassic complete the knowledge of South American forms focussed mainly in those of the Tithonian of Neuquén Basin.

The objectives of this paper are : the taxonomic review of Jurassic crocodylians from Chile, the reassignment of the Bajocian materials originally referred to Ichthyosauria [Tavera, 1981] to the Metriorhynchidae, and the analysis of the paleobiogeographic significance of these records.

Systematic paleontology

Crocodyliformes Clark [*in* Benton and Clark, 1988]
 Thalattosuchia FRAAS, 1902
 Gen. et sp. indet. (fig. 2)

Material. – MGHF 3601 (87-1). Right metatarsals 1-4 [Chong-Diaz and Gasparini, 1972]. MGHF : Museo Geológico H. Fuenzalida, Universidad Católica del Norte, Antofagasta, Chile.

Geographic and stratigraphic provenance. – Alto de Varas, Domeyko Cordillera, II Region (24°49'N; 69°10'W) (fig. 1). Sinemurian.

Discussion. – The four metatarsals are joined in natural position. Because of its stratigraphic position, it was tentatively referred to the Teleosauridae [Gasparini, 1985]. However, there are no characters for determining whether it belongs to the families Teleosauridae or Metriorhynchidae [Gasparini, 1996].

The oldest marine crocodylians known are from the Sinemurian of Lorraine, France [Huene and Maubeuge, 1952, 1954] and the Sinemurian of northern Chile. Other Liassic (*s.l.*) remains have been found in several localities of central Chile and Argentina [Gasparini, 1985], in the Kota Forma-

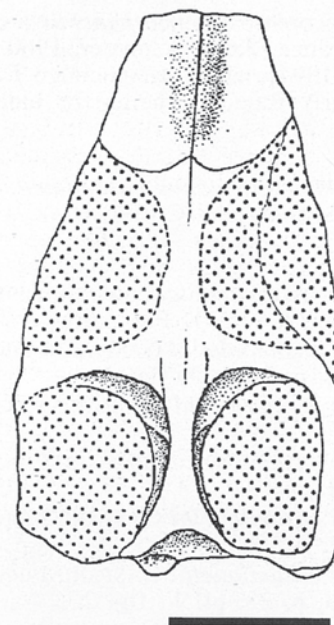


FIG. 3. – T 330 *Metriorhynchus* sp., posterior part of a skull in dorsal view, early Bajocian, scale bar : 5 cm.

FIG. 3. – T 330 *Metriorhynchus* sp., partie postérieure d'un crâne en vue dorsale, Bajocien inférieur, barre d'échelle : 5 cm.

tion of India [Krishna, 1987; Kutty *et al.*, 1987], and in the Ziliujing Formation (upper Lias ?) in the Sichuan Basin of China [Li, 1993]. Except for the Teleosauridae *Peipehsuchus teleorhinus* (YOUNG, 1948) of the Sichuan Basin, the remaining Liassic crocodylians are represented by fragmentary materials, and consequently the taxonomic determinations, even at familial level, are dubious.

Metriorhynchidae Fitzinger, 1843
Metriorhynchus MEYER, 1830
Metriorhynchus sp. (fig. 3)

Material. – T 330. Small badly preserved skull [Tavera, 1981, Pl.I]. Department of Geology and Geophysics, Facultad de Ciencias Físicas y Matemáticas, Universidad de Chile, Santiago.

Geographic and stratigraphic provenance. – Quebrada La Iglesia, 100 km SSE from Copiapo, III Region (28°07'S; 69°58'W) (fig. 1). Upper part of the Lautaro Formation (Seggerstrom), assigned by Jensen and Vicente [1976] and Hillebrandt [1977] to the early Bajocian.

Discussion. – Tavera [1981, Pl. I, 1-3] described part of a badly preserved skull, and referred it to *Ichthyosaurus acutirostris* OWEN. However, the specimen belongs to a marine crocodylian. The material was not prepared and much of the bones had been removed by erosion, leaving the filling of the cavities such as the orbits, the supratemporal fenestrae and the inside of the prefrontals exposed. This fact may have caused the misinterpretation by Tavera. Notwithstanding, these fillings, in dorsal and right lateral views, demonstrate the lateral position of the orbit and the expansion and lateral enlargement of the prefrontals, both synapomorphies of the Metriorhynchidae. The supratemporal fenestrae are subcircular, slightly shorter than the orbits, and the dorsal bars of the postorbitals and the squamosals give them the quadrangular frame characteristic of the Metriorhynchidae [Vignaud, 1995].

The oldest records of *Metriorhynchus* are from the early Callovian of France [Kuhn-Schnyder, 1960; Brunet, 1969; Vignaud *et al.*, 1994], while the specimen T 330 from northern Chile is early Bajocian, being the oldest specimen of the genus.

Metriorhynchus casamiquelai
GASPARINI and CHONG-DIAZ, 1977
(figs. 4, 5, 6)

Metriorhynchus casamiquelai nov. sp.; GASPARINI and CHONG-DIAZ, 1977, p. 341, Figs. 2-5.

Metriorhynchus casamiquelai GASPARINI and CHONG-DIAZ; Gasparini, 1978, p. 4, pl. 1, fig. A.

Metriorhynchus westermanni GASPARINI; Gasparini, 1980, p. 97, pl. I, II.

Metriorhynchus casamiquelai GASPARINI and CHONG-DIAZ; Gasparini, 1981, p. 181.

Metriorhynchus casamiquelai GASPARINI and CHONG-DIAZ; Buffetaut, 1982, p. 28.

Metriorhynchus casamiquelai GASPARINI and CHONG-DIAZ; Gasparini, 1985, p. 28, pl. 1; fig. 2.

Metriorhynchus westermanni GASPARINI; Gasparini, 1985, p. 28, pl. 1; fig. 3.

Metriorhynchus casamiquelai GASPARINI and CHONG-DIAZ; Adams-Tresman, 1987, pp. 192-193.

Metriorhynchus casamiquelai GASPARINI and CHONG-DIAZ; Gasparini, 1992, p. 361.

Metriorhynchus westermanni GASPARINI; Gasparini, 1992, p. 361.

Metriorhynchus casamiquelai GASPARINI and CHONG-DIAZ; Vignaud, 1995, pp. 222-223, pp. 228-229.

Metriorhynchus casamiquelai GASPARINI and CHONG-DIAZ; Gasparini, 1996, pp. 162, 163, 171, 181.

Metriorhynchus casamiquelai GASPARINI and CHONG-DIAZ; Gasparini and Fernández, 1996, p. 445.

Metriorhynchus casamiquelai GASPARINI and CHONG-DIAZ; Hua, 1997, pp. 133, 135.

Material. – Holotype MGHF 1-08573. Currently the Museo Fuenzalida at the Universidad Católica del Norte, Antofagasta, Chile. Skull with mandible (Figs. 4 a-c)

Geographic and stratigraphic provenance. – Quebrada Sajasa, 70 km NNE from Chuquicamata, El Loa Department, II Region (21°46'S; 69°15'W) (fig. 1). Middle Callovian [Gasparini and Chong-Diaz, 1977].

Emended diagnosis. – The skull is massive with a broad and short rostrum. The distance between premaxillae and nasals is proportionally long. It is 12 percent the skull length and 33 percent the width between quadrates. In *M. brachyrhynchus* these values are 4-6 percent (on nine specimens) and 9-18 percent (on eight specimens), respectively. No ornamentation is present on frontal and prefrontals. The supratemporal fossae are quadrangular and the postorbital arcades are massive. The frontal is very wide between the orbits, and its posterior width, completely perpendicular to the anteroposterior axis of the skull, is considered an autapomorphy of this species. The orbit is circular, the lacrimal and the antorbital foramen are well developed. The internal nares are completely separated and closed posteriorly, this latter character also considered an autapomorphy. The pterygoid fossae are as wide as long. The foramina of the occipital face are large. The dental formula is 20-21/20-23.

Referred material. – MGHF 1-181097. Anterior part of a large skull (fig. 5), from Sierra Candeleros (fig. 1), Callo-

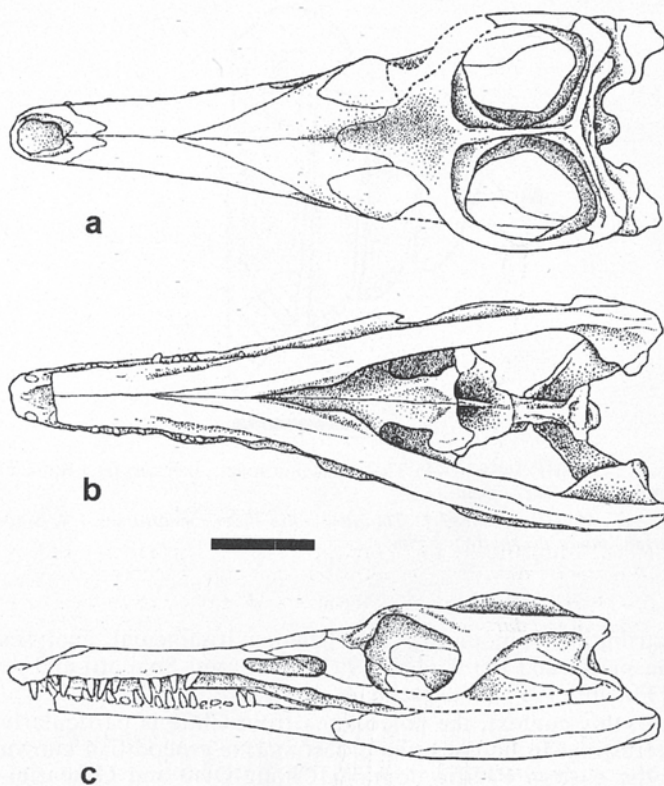


FIG. 4. – MGHF 1-08573, holotype, *Metriorhynchus casamiquelai*, Callovian. 3a, dorsal view; 3b, ventral view; 3c, lateral view, scale bar: 10 cm.

FIG. 4. – MGHF 1-08573, holotype, *Metriorhynchus casamiquelai*, Callovien. 3a, vue dorsale; 3b, vue ventrale; 3c, vue latérale, barre d'échelle: 10 cm.

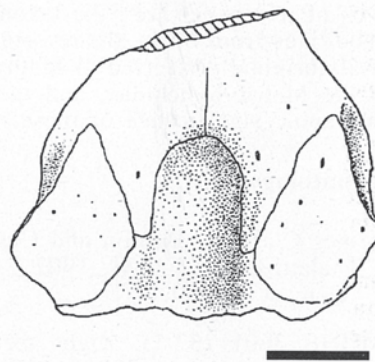


FIG. 5. – MGHF 181097 *Metriorhynchus casamiquelai*, Callovian, part of a skull in dorsal view, scale bar: 5 cm.

FIG. 5. – MGHF 181097 *Metriorhynchus casamiquelai*, Callovien, fragment d'un crâne en vue dorsale, barre d'échelle: 5 cm.

vian. MGHF 1-010199 (McMJ 1151r) original material (fig. 6) designed as *M. westermanni* holotype [Gasparini, 1980], from Placilla de Caracoles (23°00'S; 69°00'W) (fig. 1); Mina Chica Fm (Harrington), referred to the Lower-Middle Callovian [Gasparini, 1980]. The MGHF 1-010199 was originally referred as McMJ 1151r from the Mc Master University (Canada). Currently it belongs to the Museo Geológico H. Fuenzalida, Chile.

The MGHF 1-181097 (fig. 5) extends from the antorbital wall to a brief section in front of the prefrontals. These are longer (105 mm) than wide (80 mm). The suture between

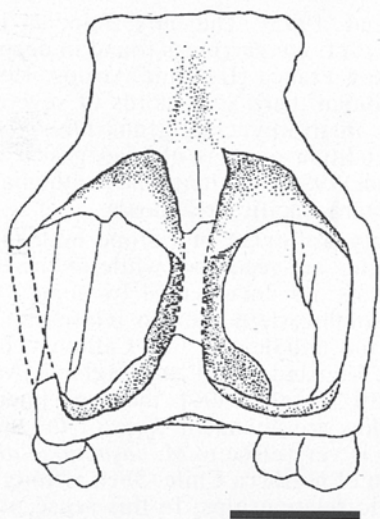


FIG. 6. – MGHF 1-010199 *Metriorhynchus casamiquelai*, posterior part of a skull in dorsal view, Early-Middle Callovian, scale bar : 5 cm.

FIG. 6. – MGHF 1-010199 *Metriorhynchus casamiquelai*, partie postérieure d'un crâne en vue dorsale, Callovien inférieur ou moyen, barre d'échelle : 5 cm.

the frontal and nasal has the same shape as in the holotype of *M. casamiquelai*. Likewise, they are alike in that the frontal is markedly deep between the orbits, and the prefrontals are smooth. The high porosity of the bones is worthy to be noted, suggesting the advanced osteoporosis of adults of metriorhynchids, ichthyosaurs and plesiosaurs [Hua and Buffrénil, 1996].

Discussion. – Adams-Tresman [1987] included *M. casamiquelai* in the synonymy of *M. brachyrhynchus*. In her opinion, the characters selected by Gasparini and Chong-Diaz [1977] to define *M. casamiquelai* (lack of ornamentation on the cranial and rostral bones; premaxillar-maxillar suture with form of an M) are not valid because they exhibit a wide and continuous range of variation in *Metriorhynchus*. Adams-Tresman [op. cit. : 192] pointed out that there are faint striae on the nasals, and a portion of the frontal and prefrontal has been restored, reducing the amount of morphological details that can be retrieved from this vital area.

However, the frontal and the restored area of the right prefrontal is small and does not prevent inferring the complete lack of ornamentation. The specimen MGHF 1-181097 (fig. 5), 25 percent larger than the holotype, confirms the lack of ornamentation. Vignaud [1995] observed that in the brevirostral species of *Metriorhynchus* the ornamentation is progressively stronger in adults (specimens with skull and rostrum larger than 600 mm). The holotype of *M. casamiquelai* is 618 mm in length and the new specimen is even longer.

Regarding the maxillary-premaxillary suture in dorsal view, both Adams-Tresman [1987] and Vignaud [1995] point out that it is V-shaped rather than W-shaped in *Metriorhynchus*. The latter is seen occasionally both in "broad-skulled" (brevirostrine) species such as *M. brachyrhynchus* and "narrow-skulled" species such as *M. superciliosus* [Adams-Tresman, 1987, Text-fig. 9; Vignaud 1995, fig. 37]. The shape of the suture is linked to the allometric growth of the anterior part of the rostrum [Vignaud, 1995]. While the V-shaped suture in most Thalattosuchia may respond to a dominant anteroposterior growth, the W-shaped suture may reflect a mediolateral growth, particularly significant in *M. casamiquelai*. Mediolateral

growth is also observed in the fronto-nasal relationship and in the extreme development of the frontal between the orbits [Gasparini and Chong-Diaz 1977].

The specimen MGHF 1-181097 (fig. 5) is similar to the holotype of *M. casamiquelai* in the size and shape of the sutures of prefrontals, frontal and nasals. Despite being an older specimen, the anteroposterior length of the prefrontal is still larger than the mediolateral (9.6 cm / 6.1cm). Likewise, the frontal extends between the nasals with a curved suture. A similar suture is seen in the specimen BM(NH)R 3321 referred by Adams-Tresman [1987] and Vignaud [1995] to *M. brachyrhynchus* [Deslongchamps, 1868].

Among the "broad-skulled" species of *Metriorhynchus* (*M. brachyrhynchus*, sensu Adams-Tresman and *M. brachyrhynchus* and *M. casamiquelai*, sensu Vignaud), *M. casamiquelai* is the one in which the participation of the maxillae in the rostrum reaches its maximum. Consequently, it has the longest distance between nasals and premaxillae [Vignaud, 1995; fig. 57 f]. On the contrary, the nasals of some adults of *M. brachyrhynchus* extend anteriorly into the external nares [Leeds, 1908].

The frontal of *M. casamiquelai* is very distinct and its posterior base is very large. This particular shape of the frontal is an autapomorphy of the species, because it is proportionately much larger than any of the other species, independently of size of the animal [Vignaud, 1995 : 145].

Vignaud [1995] recognized two morphotypes of internal nares in Callovian *Metriorhynchidae*. One of them is triangular, with the apex anteriorly directed, as in *M. superciliosus*. In the other morphotype the palatines form an M in the anterior edge of the nares (*M. brachyrhynchus* and *M. casamiquelai*). Though this character is slightly variable inter- and intraspecifically, the main difference is that *M. casamiquelai* has completely divided internal nares, closed posteriorly by a complete septum formed by the pterygoids (a character considered an autapomorphy). In other species of Callovian *Metriorhynchus* the nares open over the pterygoids.

The shape of the supratemporal fenestrae is linked to the allometric growth of the posterior part of the skull. When comparing individuals similar in size, the supratemporal fenestrae of *M. casamiquelai* are similar in length to those of the brevirostral species of Europe, but are much wider [Vignaud, 1995 : 149]. In this way, the ratio of supratemporal fenestrae width versus skull length in skulls 570 mm and 680 mm long, is 18 percent in *M. casamiquelai*, 14 percent in *M. brachyrhynchus* (on 5 specimens), and 12 percent in *M. superciliosus* (on 12 specimens).

Finally, the validity of *M. casamiquelai* claimed by Vignaud [1995] and Gasparini [1996] is here supported by the following unique derived features : posterior part of the frontal very wide, straight and perpendicular to the sagittal axis of the skull; completely divided internal nares closed posteriorly; nasals and premaxillae more widely separated; absence of ornamentation on the frontals and prefrontals.

The specimen MGHF 1-010199 (fig. 6), was designated the holotype of *M. westermanni* GASPARINI 1980. When this specimen was described, the mandible was attached with the skull [Gasparini, 1980, Plate I, II]. Now, the skull and the mandible are separated, and probably it has been treated with acid, as some of the characters mentioned in the original description cannot be observed.

The specimen MGHF 1-010199 (= *M. westermanni*), like *M. casamiquelai*, has no ornamentation (fig. 6). Although several authors [Buffetaut and Thierry, 1977; Adams-Tresman 1987; Vignaud 1995] do not accept this character because they consider it related either to sex or to ontogenetic development, in the Chilean specimens of *Metriorhynchus*

it is independent of the size of the specimen. In this way, *M. westermanni* is approximately half the size of the holotype of *M. casamiquelai*, while the new specimen from Sierra Candeleros (MGHF 1-181097) is 25 percent larger than the holotype of *M. casamiquelai*. However, none of them has the ornamentation characteristic of any of the ornamented European species.

Other characters mentioned by Gasparini [1980] to support the validity of *M. westermanni* were: the lack of division in the internal nares, the position of the occipital table more vertical than in the holotype of *M. casamiquelai*, and the narrower postorbital pillar. The lack of division in the internal nares may be a consequence of poor preservation; however, the more vertical disposition of the occipital table [Vignaud, 1995] and the narrower postorbital pillar correspond to ontogenetic variations in extant crocodylians. Vignaud [1995: 229] pointed out that *M. westermanni* might be a synonym of *M. casamiquelai*. In this review, we conclude that it is a juvenile specimen of *M. casamiquelai* because of the two characters mentioned (vertical disposition of the occipital table and shape of the postorbital pillar).

PALEOBIOGEOGRAPHIC APPROACH

The remains of an indeterminate thalattosuchian found in the Sinemurian from Alto de Varas are the oldest records of marine crocodylians in the eastern Pacific. Although the record of early Jurassic marine crocodylians is scant, it demonstrates that they already inhabited the whole Tethys and the eastern Pacific. According to some paleogeographic reconstructions [Smith *et al.*, 1995] the dispersal of these marine reptiles may have been circumpacific. However, an epicontinental Sinemurian corridor, in Central America (Caribbean or Hispanic Corridor) [Hillebrandt *et al.*, 1992] may have aided on the dispersal of marine reptiles, in particular the crocodylians [Gasparini, 1978, 1985]. This seems to be the most plausible hypothesis, as the first marine crocodylians are Teleosauridae (probably the first crocodylian specimens of western South America were also Teleosauridae). Anatomical characters suggest that these forms must have been restricted to coastal environments and especially continental margins. Crossing the Paleopacific would have been an unsurmountable ecological barrier. The close affinities observed in some groups of ammonites, bivalves, brachiopods, and ostracods in western South America and western Europe have also been cited as evidence supporting the existence of an at least intermittent Caribbean Corridor, very early in the Jurassic [Schmidt-Effing, 1976; Hillebrandt 1981; Hallam, 1983; Manceñido and Dagys, 1992; Boomer and Ballent, 1996; Rubilar, 1998; Jakobs and Smith, 1998; Liu *et al.*, 1998].

Some indeterminate fragments of plesiosaurs and ichthyosaurs, and the skull of *Metriorhynchus* sp. were found 100 km SSE from Copiapo, in early Bajocian levels [Jensen and Vicente, 1976]. Prior to this, the oldest records of *Metriorhynchus* came from the lower Callovian of Poitou, France [Vignaud *et al.*, 1994]. Consequently, the specimen T.330 extends range of the metriorhynchids to the early Jurassic in the eastern Pacific. An unstudied skull, possibly related to *Metriorhynchus*, is reported from early Alalenian rocks of Oregon [Stricker and Taylor, 1989]. Previously, Buffetaut [1979] had described a Teleosauridae indet. from the early Bajocian of Oregon, though the material is too fragmentary to conclude its familial determination. Fossil crocodylians are scarce in the European Bajocian and belong mainly to teleosaurids, which is consistent with the regional regressions suggested age [Enay *et al.*, 1980; Cariou *et al.*,

1985; Vignaud, 1995]. The only Bajocian metriorhynchid (*Teleidosaurus* cf. *gaudryi*) was found in deep-sea sediments of southeastern France [Hua and Atrops, 1995]. In the European Bathonian there are records of several teleosaurids, but a single metriorhynchid genus (*Teleidosaurus*), while the few crocodylian remains of Madagascar are Teleosauridae [Vignaud, 1995]. Hitherto no Bathonian crocodylians from the eastern Pacific are known.

In the early Callovian of Europe both teleosaurids and metriorhynchids are recorded, while in the eastern Pacific, thalattosuchians are documented by some vertebrae found in Oaxaca, southwestern Mexico [Gasparini, 1992]. But it is not until the middle and late Callovian of France [Hua *et al.*, 1994; Vignaud 1995] and England [Adams-Tresman, 1987; Martill *et al.* 1994] that specimens referred to *Metriorhynchus* are abundant. One of the species, *M. brachyrhynchus* is very close to *M. casamiquelai* from the middle Callovian of northern Chile. Such affinity supports close biogeographic relationships. In this sense, it has been proposed that a Caribbean Corridor could be the dispersal route of *Metriorhynchus* and other marine reptiles [Gasparini, 1985, 1992; Gasparini and Fernández 1996], coincidental with the tecto-eustatic transgression of the beginning of the Callovian [Fourcade *et al.*, 1995]. Marine Bajocian sediments have been recorded in northern Venezuela [Bartok *et al.*, 1985] suggesting at least the existence of an arm of sea between North and South America. Again, the close taxonomic affinity among some ammonite, bivalve and brachiopod groups [Westermann and Riccardi, 1985; Manceñido and Dagys 1992; Rubilar, 1998] from the west of South America, and north of Africa and Europe support the hypothesis of the Caribbean corridor in the pre-Callovian middle Jurassic. Buffetaut [1979] also suggested the hypothesis of a Caribbean Corridor to explain the presence of marine crocodylians in the Bajocian of Oregon.

Finally, a marine crocodylian vertebra, similar to those of *Geosaurus araucanensis*, was found in the Tithonian of the Lo Valdés area, Chile. According to the paleogeographic reconstruction, this area belonged to the retroarc of Neuquén Basin [Legarreta and Uliana, 1991], where *Geosaurus araucanensis* is the most frequent Tithonian metriorhynchid of this basin. All the Tithonian crocodylians of the eastern Pacific come from the Neuquén Basin, and are exclusively metriorhynchids: *Metriorhynchus potens* (RUSCONI, 1948), *Dakosaurus andiniensis* VIGNAUD and GASPARINI, 1996 and *Geosaurus araucanensis* GASPARINI and DELLAPÉ, 1976. In accordance with the inferred habits [Hua, 1994; Hua and Buffetaut, 1997], they occur in off-shore facies of the Neuquén Basin [Gasparini *et al.*, 2000]. In the European Tithonian *Geosaurus* and *Dakosaurus* are recorded in addition to teleosaurids [Buffetaut, 1982; Vignaud, 1995]. Toward the end of the Jurassic, and as a consequence of the fragmentation of Gondwana, other seaways opened and favored the dispersion of crocodylians and other marine reptiles together with the Caribbean Corridor [Gasparini, 1992; Gasparini and Fernández, 1997].

CONCLUSIONS

The first marine crocodylians of the eastern Pacific are recorded in the Sinemurian of northern Chile. Previous records of Liassic crocodylians of Chile and Argentina are dubious and cannot be determined at the family level [Gasparini, 1985]. If they were, as those of the European and Asian Lias, members of the family Teleosauridae, their transpacific dispersion was impossible, as the postcranium and osteoderms suggest that they had to live, at least in part, on land. In this case, the Liassic crocodylians of the

Tethys may have had biogeographic connections with those of the eastern Pacific through intermittent Caribbean connections.

According to the record, it is quite probable that the Metriorhynchidae have been present in the late Aalenian of Oregon [Stricker and Taylor, 1989]. But it is in the early Bajocian of northern Chile when *Metriorhynchus* appeared, supporting the hypothesis of Vignaud [1995] of an extra-Tethyan origin for this genus. Besides, in this paper, *M. westermanni* GASPARINI, 1980 from the early-middle Callovian of Chile is considered a synonym of *M. casamiquelai*, also from the middle Callovian of northern Chile. Likewise, it is demonstrated that *M. casamiquelai* is a valid species, related to *M. brachyrhynchus* from the European Callovian [Vignaud, 1995; Gasparini 1996]. The close affinity between these species supports close paleobiogeographic relationships, and in this sense the Caribbean Corridor must have played a major role as it was for other nektonic organisms.

Finally, a vertebra probably referable to *Geosaurus*, found in the Tithonian of central Chile, expands westwards the rich record of Tithonian crocodylians of the Neuquén Basin, in which *Geosaurus* is the most common. Toward the end of the Jurassic the Caribbean Corridor could be still used as a dispersal route way by several pelagic reptiles, among them the metriorhynchid crocodiles. But other new seaways appeared, as a consequence of the fragmentation of Gondwana cannot be discarded. For example the Weddellian Corridor where ichthyosaurs have been recorded [Gasparini, 1992; Gasparini and Fernández, 1997].

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