

FIRST RECORD OF *METRIORHYNCHUS* (REPTILIA: CROCODYLIFORMES) IN THE BATHONIAN (MIDDLE JURASSIC) OF THE EASTERN PACIFIC

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INTRODUCTION

JURASSIC MARINE reptiles are best known from the study of European Jurassic collections. The record of these reptiles encompasses most of the period, but that of Aalenian–Bathonian rocks is quite incomplete (Andrews, 1913; Brown, 1981; Buffetaut, 1982; Godefroit, 1994; Bardet, 1995; O’Keefe, 2001; McGowan and Motani, 2003). South American marine reptiles of the early Middle Jurassic are especially significant because they

contribute to fill this gap of taxonomic and paleogeographic information (Fernández, 1994, 1999, 2003; Spalletti et al., 1994; Gasparini, 1997; Gasparini et al., 2000).

The largest amount and diversity of Jurassic marine reptiles of the Southern Hemisphere was found in northwestern Patagonia, in the Neuquén Basin (Yrigoyen, 1991; Fig. 1). These reptiles dominate in Tithonian rocks cropping out at numerous sites of the basin (Gasparini and Fernández, 1996; Spalletti et al., 1999). On the contrary, Middle Jurassic marine reptiles are restricted to Chacaico Sur area, southeast of the Neuquén Province (Fig. 1). There, until present, ichthyosaurs, plesiosaurs, and a crocodile vertebra were found in the upper part of Los Molles Formation, Cuyo Group (Lower Bajocian), and plesiosaurs and plesiosauroids were found in the lower part of Lajas Formation, Lower Callovian (Gasparini and Spalletti, 1993; Fernández, 1994, 1999; Spalletti et al., 1994; Gasparini, 1997).

Recently, during field work performed by the biostratigraphy students of the Geological Sciences Department (University of Buenos Aires) in the area of Chacay Melehue, Neuquén Province (Fig. 1), two of the authors (MC and DL) took part in the finding and extraction of the skull and postcranium of a marine crocodile from Upper Bathonian sedimentites. This specimen confirms the presence of marine crocodiles in the Middle Jurassic of Argentina, and is the first record of a metriorhynchid in the Late Bathonian of the Eastern Pacific.

GEOLOGICAL SETTING

The Neuquén Basin is located in west-central Argentina between latitude 34° and 41°S. It is developed in Neuquén and part of Mendoza, Río Negro, and La Pampa Provinces (Fig. 1). Its infill exceeds 6,000 m of marine and continental sedimentary rocks, which range from Late Triassic to Paleocene in age (Yrigoyen, 1991; Legarreta and Uliana, 1999). Over a great part of the basin, marine conditions prevailed from the Sinemurian until the Late Callovian. During this interval the Los Molles Formation was deposited. The maximum extent of the area with marine deposition occurred during the Bajocian. From then onwards, the area of sedimentation was gradually reduced until, during the mid-Callovian, the basin became virtually cut off from the open sea, resulting in the deposition of evaporites in the center (Gulissano and Gutiérrez Pleimling, 1994).

The crocodile remains proceed from the middle to upper part of the Los Molles Formation, at the classical Chacay Melehue section (Fig. 1). At the base of the outcrop, there are epiclastic and pyroclastic deposits, which lack a formal name and correspond to the base of the Cuyo Group (Gulissano and Gutiérrez Pleimling, 1994). These beds are overlain conformably by the Los Molles Formation (Fig. 2). This unit is composed of more than 850 m of black shales, claystones, sandstones, and limestones of Toarcian to Callovian age. It has been interpreted as having been deposited in an offshore, inner basinal to turbiditic basinal environment (Gulissano and Gutiérrez Pleimling, 1994).

The remains studied here have been found in a level within the interval V proposed by Gulissano and Gutiérrez Pleimling (1994)

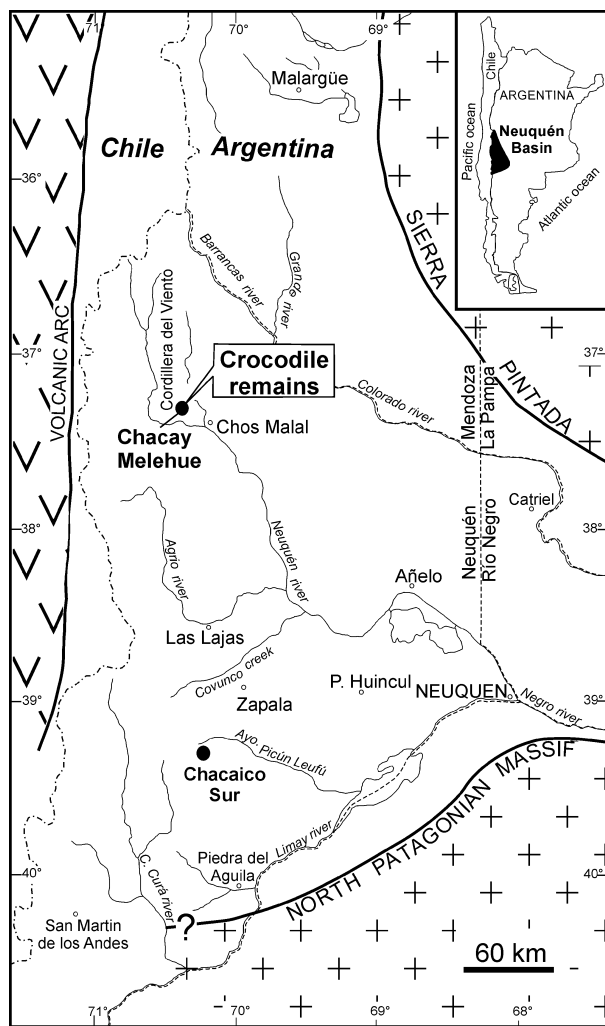


FIGURE 1—The Neuquén Basin in west-central Argentina, showing the location of Chacay Melehue section. The crocodile remains proceed from Los Molles Formation. Base map from Digregorio et al. (1984).

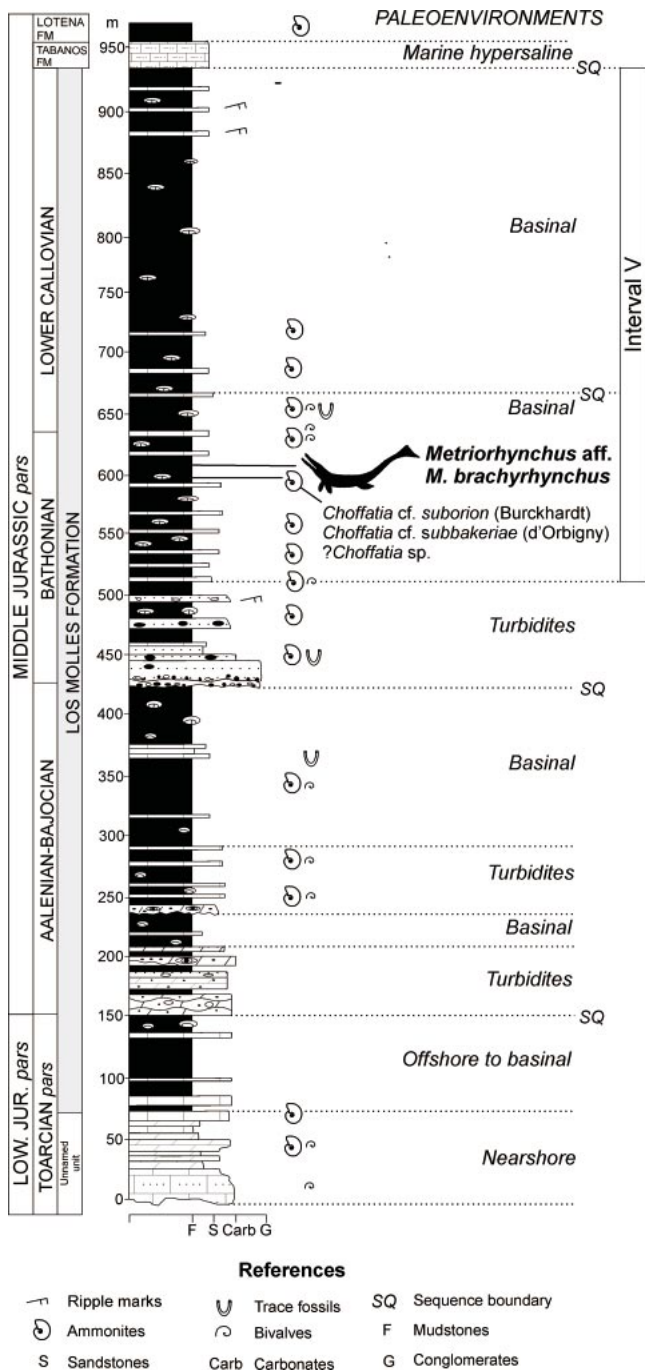


FIGURE 2—Detailed stratigraphic section of the Los Molles Formation in Chacay Melehue, showing the position of the crocodile remains and associated ammonites in the Upper Bathonian. Base column and paleoenvironments from Gulisano and Gutiérrez Pleimling (1994).

in the middle to upper part of the Los Molles Formation. This interval has slightly more than 400 m, and is characterized by a monotonous succession of black shales, with calcareous concretions and intercalations of tabular tuff and tuffaceous sand beds, and its mode of deposition has been interpreted as an inner basinal environment. The crocodile remains were found articulated within a black shale level.

SYSTEMATIC PALEONTOLOGY

Repository.—The described and figured material is deposited in the following collection under the catalog number listed in the text: Museo Juan Olsacher. Dirección General de Minería de la Provincia de Neuquén. Olascoaga 421, (8340) Zapala, Neuquén, Argentina.

Superorder CROCODYLOMORPHA emend. Walker, 1968
 Order CROCODYLIFORMES Benton and Clark, 1988
 Family METRIORHYNCHIDAE Fitzinger, 1843
 Genus METRIORHYNCHUS Meyer, 1830
 METRIORHYNCHUS AFF. *M. BRACHYRHYNCHUS*
 (Deslongchamps, 1867)

Metriorhynchus brachyrhynchus DESLONGCHAMPS, 1867.
Metriorhynchus brachyrhynchus DESLONGCHAMPS, 1867, p. 333.
Metriorhynchus brachyrhynchus (DESLONGCHAMPS). ADAMS-TRESMAN, 1987, p. 193.
Metriorhynchus brachyrhynchus (DESLONGCHAMPS). VIGNAUD, 1993, p. 255.

Description.—Skull: only the anterior part of the rostrum articulated with the mandibular symphysis was recovered. Although this part of the snout is quite damaged, it preserves two fragments of teeth, one on the left premaxillary and the other on the left dental. Both are circular in section. The dorsal area of the premaxillaries is missing, but it may be observed that they join at a wide angle (Fig. 3.1). A wide depression behind them represents the bottom of the external nares. Some fragments of the right and left maxillae were also recovered. The left maxillary fragment presents six alveoli with very narrow interalveolar space (Fig. 3.2), and exhibits strong ornamentation in dorsal and lateral views (Fig. 3.1, 3.2). The preorbital fenestra is surrounded by the left maxillary and the channel-shaped, anterodorsally oriented nasal (Fig. 3.2), a typical Metriorhynchidae feature (Wenz, 1968; Adams-Tresman, 1987). The left lachrymal is lateral (Fig. 3.2). Although incomplete, there is an expansion behind and over the preorbital fenestra that belongs to the prefrontal. The longitudinal anteroposterior ornamentation is conspicuous on the anterior left sector of the frontal. The dorsal border of the orbital cavity, formed by the prefrontal, frontal, and postorbital, is also preserved. As in all the Metriorhynchidae, the upper arch of the orbit is strongly excavated, leaving the prefrontal laterally exposed. The posterior part of the dorsal bar of the parietal is very damaged and welded to the squamosals. In dorsal view, the squamosals are partially located inside the supratemporal fenestrae (Fig. 3.1). In occipital view, the squamosals are subvertical and the paraoccipital processes are not well exposed. Consequently the adjacent sector of the quadrate is slightly concave (Fig. 3.3). The foramen magnum is subcircular, wider than high. The occipital condyle has no neck (Fig. 3.3), and the foramina for the carotid are large as in all the Metriorhynchidae. On the left side of the left basioccipital, there is a slight expansion, suggesting that there were two tubera. The basisphenoid and the palate are very damaged by postmortem flattening.

Mandible: the posterior part of the right hemimandible is preserved. It is very damaged, broken, and displaced. Externally a line is visible, that belongs to the angular-surangular suture (Fig. 3.4). There is no external mandibular fenestra. The glenoid fossa is wide but not very deep, and the retroarticular process, which is oriented slightly inwards, is very incomplete (Fig. 3.5).

Vertebrae: several fragments of vertebral centra were recovered, 12 of which are relatively complete. One of them belongs to a cervical (Fig. 3.6) in which height and length of the body are similar (2.1 cm). The rest are dorsal vertebrae, spool or sandglass-shaped, in which the height is half the length (Fig. 3.7). In

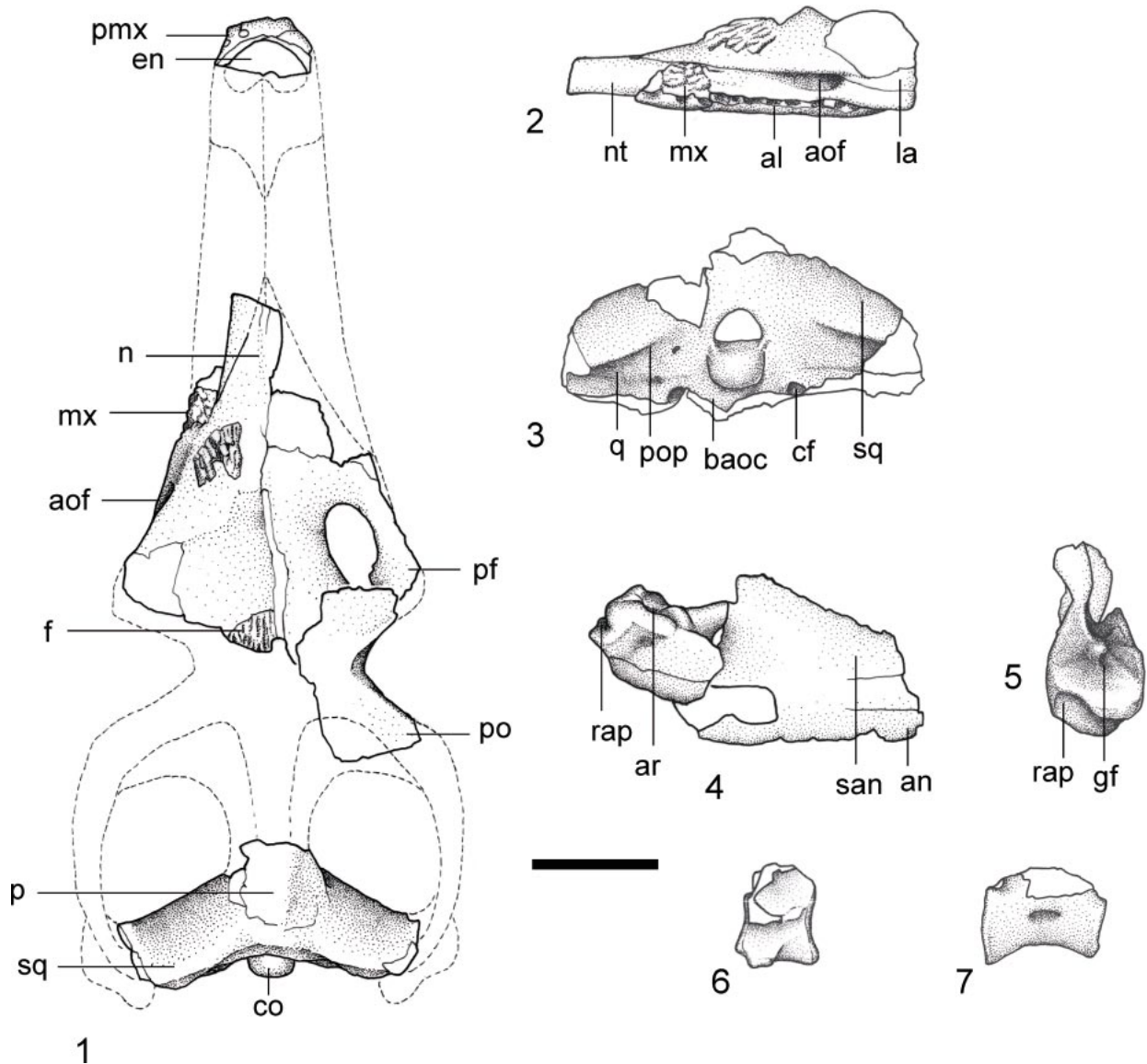


FIGURE 3—*Metriorhynchus* aff. *M. brachyrhynchus* (Deslongchamps, 1867), PV-6913-MOZ, 1, skull in dorsal view; 2, rostrum in lateral view; 3, skull in occipital view; 4, right mandible in dorsal view; 5, articular area of the right mandible in lateral view; 6, cervical vertebra in lateral view; 7, dorsal vertebra in lateral view. Scale: 5 cm. Abbreviations are as follows: al, alveoli; an, angular; aof, antorbital fenestra; ar, articular; baoc, basioccipital; cf, carotid foramen; co, condyle; en, external nares; f, frontal; gf, glenoid fossa; la, lacrimal; mx, maxillar; n, nasal; nt, nasal tubes; p, parietal; pf, prefrontal; pmx, premaxillar; pop, paraoccipital process; po, postorbital; q, quadrate; rap, retroarticular process; san, surangular; sq, squamosal.

some of them, the lower part of the neural arch is welded and preserves the cast of the neural channel.

Material examined.—PV-6913-MOZ, fragments of skull, mandible, and vertebral centra of a single specimen (Fig. 3). This specimen was articulated in situ. The mechanical extraction of the surrounding rock was made while repairing the route 43, and broke it in such a way that it could only be partially recovered. Some areas of the skull, such as the occipital table or the filling of the narial tubes, are preserved without deformation. Others, such as the posterior part of the rostrum, which collapsed over the palate, show postmortem deformation.

Occurrence.—Chacay Melehue section (37°15.799'S, 70°29.555'W), located 27 km northwest of Chos Malal village, on the margin of provincial route 43, at the southern end of the Cordillera del Viento (Fig. 1). The material proceeds from

the middle to upper part of the Los Molles Formation (Weaver, 1931), within the interval V of Gulisano and Gutiérrez Pleimling (1994). It is associated with the next ammonites: *Choffatia* cf. *subbakeriae* (d'Orbigny, 1842–1851), *Choffatia* cf. *suborion* (Burckhardt, 1903), and *Choffatia?* sp., Upper Bathonian (Riccardi, personal commun., 2003; Fig. 2).

DISCUSSION

PV-6913-MOZ is referred to the *Metriorhynchidae* because of the following characters: preorbital fenestra elongate and oriented anteriorly and upward, lacrimal small exclusively lateral in position, lacrimal with a depression on the lateral side that marks the support for the prefrontal expanded outwards, upper margin of the orbit strongly excavated, and absence of external

mandibular fenestra (Buffetaut, 1982; Vignaud, 1995; Gasparini et al., 2000).

Likewise, the specimen is referred to *Metriorhynchus* sp. because, in occipital view, the squamosals are more posteriorly inclined and the occipital condyle lacks a marked neck (Vignaud, 1995). In other metriorhynchids such as *Geosaurus* Cuvier, 1824 and *Dakosaurus* Quenstedt, 1852, the squamosals are almost vertical and the occipital condyle has a very conspicuous neck (Gasparini and Dellapé, 1976, and new material of *Dakosaurus* sp. in study by ZG). The type and degree of ornamentation of the skull dorsum of *Metriorhynchus brachyrhynchus* (Deslongchamps, 1867) and *M. superciliosus* de Blainville, 1853 is variable (Adams-Tresman, 1987), but there is no ornamentation in *M. casamiquelai* Gasparini and Chong, 1977 from the Callovian of Chile (Gasparini et al., 2000). Accordingly, none of the metriorhynchids discovered in Argentina and Chile have dorsal ornamentation (*Geosaurus*, *Metriorhynchus*, *Dakosaurus*), except for PV-6913-MOZ from the Late Bathonian of Chacay Melehue. Accordingly, this is the first evidence of strongly ornamented forms for the eastern Pacific. In addition, the anterior portion of the snout of PV-6913-MOZ is wide, with proportionally large teeth that are circular in section, suggesting it belongs to a short-rostrum species, with the characteristics of *M. brachyrhynchus*. Since there are no other characters that undoubtedly certify the assignment to this species, PV-6913-MOZ is referred to *Metriorhynchus* aff. *M. brachyrhynchus*. The oldest record of *Metriorhynchus* outside South America is *M. brachyrhynchus* and *M. superciliosus* from the Lower Callovian of Poitou, France (Vignaud, 1995).

The largest diversity of metriorhynchid crocodiles outside Europe has been recorded in Jurassic rocks of Argentina and Chile. The oldest record of *Metriorhynchus* is that of the Lower Bajocian of Chile (Gasparini et al., 2000), whereas one vertebra assigned to Metriorhynchidae indet. was found in the upper part of the Los Molles Formation (Lower Bajocian) in Chacaico Sur, Neuquén Province (Spalletti et al., 1994). *M. casamiquelai*, a species very close to *M. brachyrhynchus* (Gasparini et al., 2000), was found in rocks of the Early–Middle Callovian age of northern Chile. Finally, in the Tithonian of the Neuquén Basin prevails *Geosaurus araucanensis* Gasparini and Dellapé, 1976, although *Metriorhynchus potens* (Rusconi, 1948) and *Dakosaurus andiniensis* Vignaud and Gasparini, 1996 have also been reported. The presence of these marine crocodiles in the eastern Pacific is consistent with their capability as offshore predators. A set of ecophysiological modifications such as the loss of dermal scutes, the modification of limbs as equilibrium elements, and the heterocercal to hypocercal tail as the main element of propulsion (Hua and Buffetaut, 1997), together with the strong osteoporosis (Hua and Buffrénil, 1996) and the presence of hypertrophied salt glands (Fernández and Gasparini, 2001), suggest a degree of adaptation to sea life within the Metriorhynchidae unequalled by any other marine crocodilian clade.

The oldest record of *Metriorhynchus* is from the Early Bajocian of Chile (Gasparini et al., 2000). *Metriorhynchus* is first known in Europe in the Lower–Middle Callovian (Buffetaut, 1982; Vignaud, 1995). All of the Metriorhynchidae previously known from western South America are forms without ornamented skulls. *Metriorhynchus* aff. *M. brachyrhynchus* from the Late Bathonian of the Neuquén Basin is the first record of a strongly ornamented form in the eastern Pacific, and, together with *Metriorhynchus* sp. from the Lower Bajocian of Chile, is the oldest record of the genus.

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