

A vertebrate assemblage of Las Curtiembres Formation (Upper Cretaceous) of northwestern Argentina

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Abstract: We describe an association of fossil vertebrates from the Morales Member of the Las Curtiembres Formation (Campanian) near Puente Morales, Salta Province, NW Argentina. The fossils include teleostean fishes, pipid frogs, pleurodiran turtles, mesoeucrocodylians, non-avian theropod dinosaurs, and enantiornithine birds. The vertebrate record is dominated by freshwater taxa. With the exception of pipid frogs, all taxa here described constitute new records for this sedimentary unit. Among them, the turtles are reported for the first time in the Cretaceous of northwestern Argentina (Salta Group). Additionally, the recently published small enantiornithine *Intiornis inexpectatus* enlarges the diversity of cretaceous birds from South America. Despite the fragmentary nature of the specimens, the information provided by this Late Cretaceous assemblage sheds new light on the composition of the continental vertebrate fauna in a paleontologically poorly known region of South America.

Key words: Vertebrates, Las Curtiembres Formation, Upper Cretaceous, Argentina.

Resumen: Una asociación de vertebrados de la Formación Las Curtiembres (Cretácico Superior) del Noroeste de la Argentina. Aquí describimos una asociación de fósiles de vertebrados proveniente del Miembro Morales de la Formación Las Curtiembres (Campaniano) exhumada en la localidad de Puente Morales, provincia de Salta, Argentina. Esta asociación se encuentra conformada por peces teleosteos, anuros pipidos, tortugas pleurodiras, mesoeucrocodilidos, dinosaurios terópodos no avianos y aves Enantiornithes. Este registro de vertebrados se encuentra dominado por taxa de agua dulce. Con la excepción de los anuros pipidos, todos los demás taxa aquí descriptos constituyen nuevos registros para esta unidad sedimentaria. Entre ellos, el registro de tortugas resulta ser el primero para el Grupo Salta. Adicionalmente, el Enantiornithes *Intiornis inexpectatus* amplía la diversidad de aves cretácicas de América del Sur. Más allá de la naturaleza fragmentaria de algunos de los especímenes, la información proporcionada por esta asociación del Cretácico Superior aporta novedosa información acerca de la composición de la poco conocida fauna de vertebrados continentales de esta región de América del Sur.

Palabras clave: Vertebrados. Formación Las Curtiembres, Cretácico Superior, Argentina.

INTRODUCTION

The Cretaceous-Paleogene Salta Group, which crops out extensively in northwestern Argentina, has yielded a large number of relevant fossil vertebrates. Most of these fossils, however, are from the middle and upper sections of this unit, the Balbuena and Santa Bárbara subgroups. By con-

trast, the lower section, the Pirgua Subgroup, has only produced fishes, anurans, and dinosaurs, most of which are represented by scarce remains.

The first discovery of vertebrates in the Pirgua subgroup, generally considered Upper Cretaceous in age, was made by Ibáñez (1960), who discovered numerous, but poorly preserved,

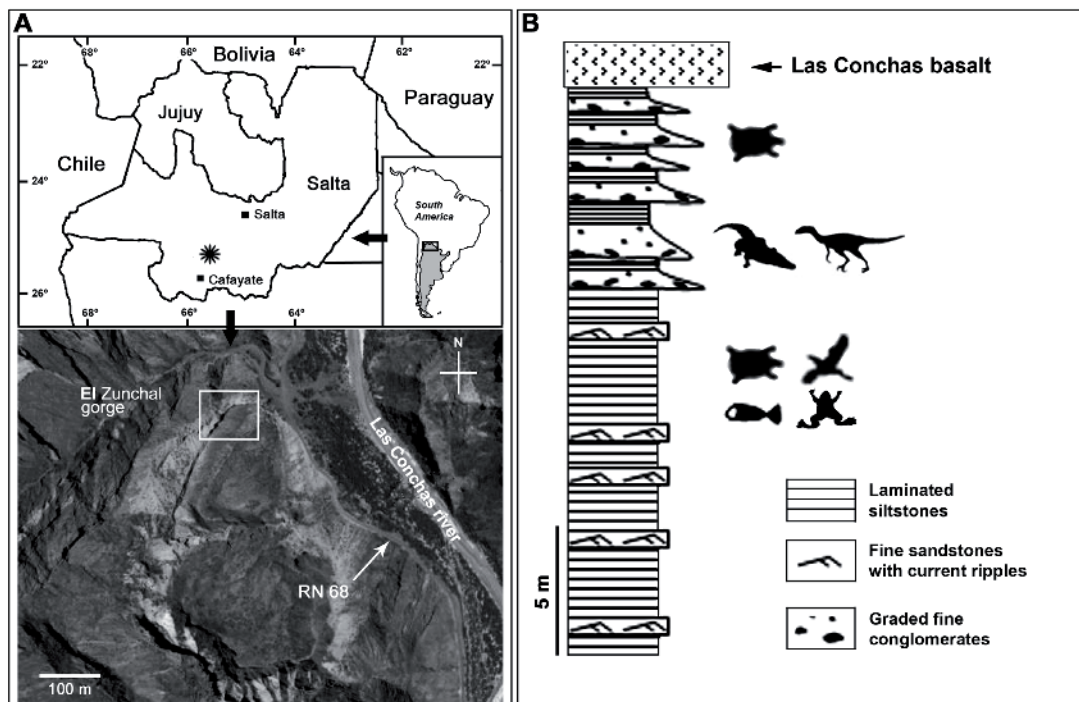


Fig. 1. A, Geographic location of Puente Morales area. In the upper map the asterisk indicates the location of Puente Morales. In the photograph the square marks the position of the quarry; B, stratigraphic section exposed in the quarry where the specimens were collected.

frog remains in the Las Curtiembres Formation at the Puente Morales locality, in the Las Conchas River valley, Salta province. These specimens were briefly described and named by Reig (1959) as *Saltenia ibanezi* (see below). Subsequently, Bonaparte & Bossi (1967) described a few disarticulated postcranial bones of sauropod dinosaurs collected from the overlying Los Blanquitos Formation in the Sierra de la Candelaria. Powell (1979) also reported titanosaurian bones and described a large theropod of uncertain relationships based on an isolated pubis, named as *Unquillosaurus ceibali* (Powell, 1979; Novas & Agnolin, 2004).

During the years 2005 and 2006, the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" made several field trips to Puente Morales fossil site. In these expeditions, new specimens of the pipoid frog *Saltenia ibanezi* and remains of a variety of vertebrates were collected. Herein we describe this material, which constitutes the first vertebrate assemblage known for the Las Curtiembres Formation. All specimens are housed in the paleontological collection of the Museo de Antropología de Salta, Salta province, Argentina.

GEOLOGICAL SETTING AND LOCALITY

The fossiliferous beds of the Las Curtiembres Formation were attributed to the Pirgua Formation by Reig (1959). Subsequently, Reyes & Salfity (1973) considered the Pirgua Formation as a subgroup of the Salta Group and subdivided it into three formations, La Yesera, Las Curtiembres, and Los Blanquitos, previously considered as members. These units constitute the infill of an extensional basin that extends along several provinces of NW Argentina, Bolivia, Paraguay, and Chile. In Argentina, a number of sub-basins controlled by active faults have been recognized (Gómez Omil *et al.*, 1989; Salfity & Marquillas, 1981, 1999).

The Las Curtiembres Formation is a succession of continental red siltstones and lithic sandstones that filled the southern sub-basins (Alemania, Brealito, and Metán). According to Salfity & Marquillas (1999), this succession records the accumulation in meandering fluvial and lacustrine settings. The development of local lacustrine depocenters was favored by tectonic activity that occurred during the early synrift stage of the basin, producing slope changes and

associated alkaline volcanism. The middle to upper section includes alkaline volcanic and pyroclastic rocks (Las Conchas Basalt) that originated during an extensional phreatomagmatic episode along north-south faults (Galliski & Viramonte, 1988). Thickness varies from hundreds to more than 2000 m and was controlled by the subsidence rate of each depocenter of the Las Curtiembres Formation. The Morales Member, a siliciclastic subunit recognized in the Las Curtiembres Formation at the Alemania sub-basin, is in the middle to upper part of the succession intercalated with the aforementioned volcanic rocks. It is nearly 78 m thick and consists of yellowish green siltstones, fine conglomerates, and subordinated sandstones.

The Las Conchas Basalt in the upper part of the Las Curtiembres Formation was dated to 78–76 my (K/Ar method) and thus is contemporaneous with the Peruvian diastrophism (Valencio *et al.*, 1976; Reyes *et al.*, 1976; Galliski & Viramonte, 1988); hence, the age of the fossil-bearing Morales Member appears to be Campanian according with new information provided by palynological analysis (Narváez & Sabino, 2008).

All the fossils described here come from the Morales Member, at the locality of Abra El Zunchal, north of Puente Morales (Fig. 1A). The material was collected from two quarries excavated in rocks of differing lithology. One quarry is located near the National Road 68; only the frog *Saltenia ibanezi* and fishes were found in the green laminated siltstones there. The second quarry is located nearly 150 meters to the west of the first site. Frogs, birds, and isolated turtle shell elements were found in laminated siltstones, whereas complete turtle specimens along with crocodile scutes and dinosaur bones were discovered in fine conglomerates.

A section approximately 30 m thick (Fig. 1B) is exposed in the second, more fossiliferous quarry. The lower part is composed of green laminated siltstones with diagenetic nodules and subordinated yellowish fine-grained sandstones with current ripples. The upper part includes finning-upward cycles, with erosive bases. Each cycle comprises normal graded, matrix-supported sandy conglomerates, which pass into rippled medium-to-fine sandstones, and finally to laminated siltstones. The conglomerates are fine, with angular extra- and intraformational (shale) clasts, up to 7 mm in diameter. Dinosaur bones and some turtle remains occur in these coarse facies. More delicate specimens, such as those of birds, frogs (including tadpoles), and fishes,

come from the laminated siltstones.

The Morales Member records the sedimentation in a lacustrine environment. The presence of limestones in other localities was interpreted as reflecting alkaline-brackish water conditions, caused by chemical interaction between the lake water and phreatomagmatic activity (Marquillas *et al.*, 2005). The fine laminated siltstones of the lower part accumulated by slow deposition in quiet conditions, away from lake shore. Short pulses of increased energy are indicated by interbedded rippled sandstones. Deposition of the upper part was dominated by debris-flows that transported gravel clasts and eroded the substrate. These events were frequent and probably related to an increase of seasonal drainage.

Due to the nature of the lamination of siltstones, fish, anuran, and avian remains were found in two dimensions. The fishes, represented only by bones, were found articulated, with scarce signs of displacement or scattering (Fig. 2A,B). The total lengths of the specimens range among 3–5 cm. In turn, pipid tadpoles were found lacking signs of having been transported (Fig. 2E). Most adult frogs (nearly 3 cm of snout-vent length) are articulated (Fig. 2C), but some specimens show some disarticulation and scattering to a varying degree. Moreover, some levels include isolated and partially disarticulated anuran bones, the most frequent of which are braincases (Fig. 2D) and fused sacrum and urostyle complexes. The hind limb corresponds to the enantiornithine bird was found fully articulated, with a carbonized cover around the bones that might represent soft tissue (Fig. 4C).

SYSTEMATICS

Actinopterygii Klein, 1885

Neopterygii *sensu* Patterson & Rosen, 1977

Teleostei *sensu* Arratia, 1997

Unnamed taxon Elopomorpha + more advanced teleosts *sensu* Arratia, 1997

Genus and species indet.

Referred material. MAS-P/2 2 to 8, seven specimens on slabs (part and counterpart) (Fig 2A,B).

Remarks. We here follow the phylogenetic parsimony analysis for basal teleosts of Arratia (1997, 1999, 2000a, 2004). Arratia (2000a,b) excluded the taxa †Pachycormiformes and †Aspidorhynchiformes from the Teleostei (for a different view, see Patterson & Rosen, 1977; Patterson,

1993). We have been able to observe several of the characters of Arratia (2000a) in the material.

The following characters, including synapomorphies and homoplasies, suggest that they are teleosts more advanced than †Ichthyodectiformes (Arratia 2000a): both epaxial and hypaxial fulcra absent, each hypural articulates with few caudal rays, probably mobile premaxilla present, cephalic sensory canals with simple tubules, fewer than 20 principal caudal rays, cycloid scales, midcaudal autocentra strongly constricting the notochord, fringing fulcra preceding the first principal caudal ray absent, epipleural intermuscular bones developed in abdominal region, and dorsal scute preceding caudal fin absent. The specimens are referable to Teleostei following both Arratia (2000a) or Patterson & Rosen (1977) and Patterson (1993) and most likely to the unnamed group Elopomorpha + more advanced teleosts following Arratia (1999, 2000a). Besides, the morphology of cranial bones without large teeth in parasphenoid does not appear to correspond to that of those Elopiformes or Osteoglossiformes known from South America.

The absence of series of abdominal or dorsal scutes suggests that they are not clupeomorphs. Within the sister group of clupeomorphs, the ostariophysans, Las Curtiembres specimens do not belong either to Siluriformes or to Gymnotiformes. Cypriniformes are unknown in South America (Arratia & Cione, 1996; Nelson, 2006).

Regarding the most advanced fishes, they are not acanthomorphs because they lack true dorsal and anal fin spines and the shape of mouth bones differs considerably (Johnson & Patterson, 1993; Johnson & Wiley, 2006).

Specimens most closely resemble ostariophysan Anotoptysi (Gonorhynchiformes) and ostariophysan Otoptysi such as Characiformes (see Filleul & Maisey, 2004), and perhaps pertain to an unknown taxon. Due to the poor preservation, we did not find characters of generic or specific value. We do not discount that more than one species could be present in the material. However, neither morphology nor meristic data support this hypothesis.

Batrachia Latreille, 1800
Anura Fischer von Waldheim, 1813
Pipimorpha Ford & Cannatella, 1993
Pipidae Gray, 1825

Saltenia ibanezi Reig, 1959

Referred material. MAS-P/2 unnumbered, 30 postmetamorphic specimens (articulated, fairly

complete skeletons preserved as both bone and bone impression, and disarticulated, but associated, bones) and 3 tadpoles (Fig. 2C-E).

Remarks. A large collection of anurans from the Puente Morales site was first made by geologists of the Comisión Nacional de Energía Atómica and studied simultaneously by Reig (1959) and Parodi Bustos *et al.* (1960). These authors concluded that the specimens belong to a pipoid taxon but disagreed over the interpretation of many features and, as a result, the taxonomic placement within Pipoidae. Whereas Reig (1959) considered that these specimens might belong to a new aglossal genus and species close to the extant African pipid *Xenopus* and the extinct *Eoxenopoides* and *Shelania*, Parodi Bustos *et al.* (1960) referred this material to a new species of the African genus *Eoxenopoides* described by Haughton (1931). Subsequent revision of *Eoxenopoides* (Estes, 1977) and study of numerous additional specimens from the Puente Morales locality (Báez, 1981) revealed that the latter differs from the former in several features, such as the morphology of the elements of the maxillary arch, the lack of ossification of the platum antorbitale, and the number of presacral vertebrae. These features justify the referral of Salta's specimens to a separate genus.

The occurrence of an azygous frontoparietal and parasphenoid lacking subotic alae indicates that the collected material represents a pipoid taxon, according to recent phylogenetic analyses (e.g., Báez & Pugener, 2003). Moreover, it is a member of Pipimorpha (a stem-based name that includes those taxa more closely related to crown-group Pipidae than to crown-group Rhinophrynidae) in possessing elongate metapodials, a long cultriform process of the parasphenoid, and free ribs in larvae and subadults. The fused sacrum and urostyle, the excavated anteroventral surface of the prootics to accommodate the Eustachian tubes, the optic foramen completely enclosed in the sphenethmoidal ossification, and the parasphenoid partially incorporated into the floor of the braincase are derived features that *Saltenia* shares with crown pipids and might indicate that it is within this clade (Báez & Pugener, 2003). *Saltenia* has been interpreted as a basal member of the pipid lineage represented at present by the African *Silurana* and *Xenopus*. However, its position within Pipidae is still debatable partly due to the poor preservation that precludes confident scoring of many characters that have been used in parsimony analyses of extant and extinct pipoids.

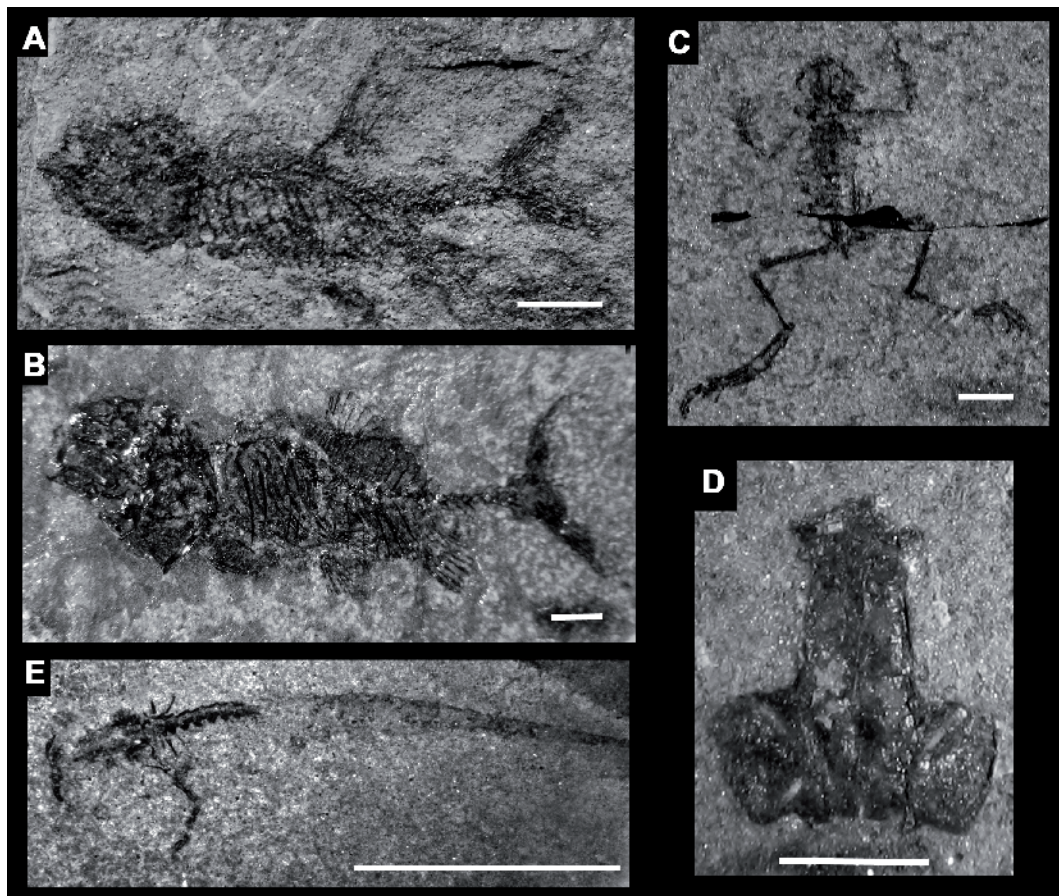


Fig. 2. A-B, teleostean fishes; C-E, *Saltenia ibanezi*; C, complete postmetamorphic individual; D, isolated braincase; E, tadpole. Scale bar 5 mm.

Testudines Batsch, 1788

Pleurodira Cope, 1865

Genus and species indet.

Referred material. MAS-P/2 9 and 10, two neural arches of cervical vertebrae of an adult specimen; MAS-P/2 11 and 12, two partially complete carapaces (part and counterpart) of two juvenile specimens, one of them with scarce skull remains, and isolated postcranial remains such as an anterior portion of carapace and plastron; MAS-P/2 13 and 14, scapula and a left humerus of different juvenile specimens (Fig. 3A,B).

Remarks. Although there is not enough evidence to get an accurate determination of these specimens, because of the absence of diagnostic characters in poorly preserved skull and shell remains, the type of attachment between of pelvic girdle and carapace (iliac scars on the visceral surface of carapace) and the morphology of cervical

vertebrae suggest pleurodiran affinities (Broin, 1977). The two neural arches preserved show that the transverse processes of cervical vertebrae are strongly developed and are located at the middle of the axial length, and their postzygaphyses are supported by a common elevated process. These conditions are recognized in post-Jurassic pleurodires (Fernández & de la Fuente, 1994; de la Fuente & Iturralde Vinent, 2001; Lapparent de Broin, 2000; de la Fuente, 2003; Lapparent de Broin *et al.*, 2007). Because of the centra of these cervical vertebrae are not preserved, the cervical vertebrae formula cannot be determined (*sensu* Williams 1950), which is important in distinguishing between pelomedusoids and chelids. Moreover, the morphology of the type of vertebral arch is also similar to the cervical vertebrae found in large extant species of Podocnemididae (e.g., *Podocnemis expansa*, *P. unifilis*). In contrast to the condition recognized in juvenile specimens of chelid and other turtles, the carapace of the juvenile

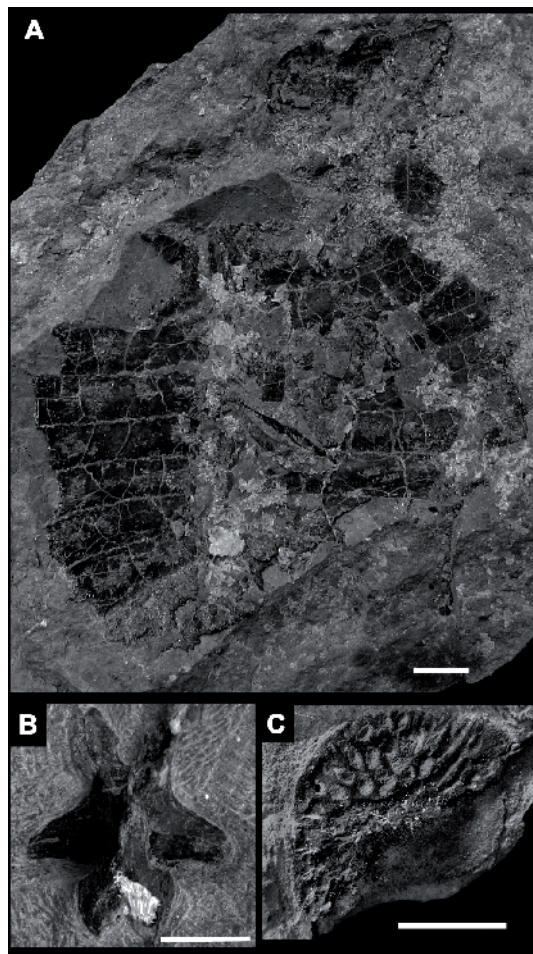


Fig. 3. A-B, Pleurodiran turtles. A, visceral view of carapace and remains of the skull; B, neural arch of cervical vertebra in dorsal view; C, Mesoeucrocodylian osteoderm in dorsal view. Scale bar 10 mm.

specimens of Las Curtiembres turtles are ossified enough to preclude the formation of large pleuro-peripheral fontanelles. This condition is seen in juvenile specimens of podocnemidid turtles.

Crocodylomorpha Walker, 1970

Mesoeucrocodylia Whetstone & Whybrow, 1983

Genus and species indet.

Referred material. MAS-P/2 15 and 16, two incomplete dorsal scutes (Fig. 3C).

Remarks. The available osteoderm shows a straight posterior margin, indicative of mesoeucrocodylian affinities (Ortega *et al.*, 2000). The absence of a median dorsal keel and of anterolat-

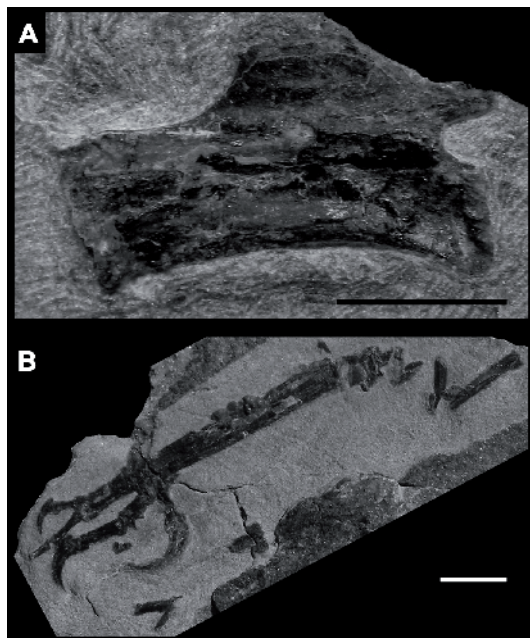


Fig. 4. Archosaurian remains. A, posterior caudal vertebra of a possible coelurosaurian theropod in lateral view; B, left articulated foot of the enantiornithine bird *Intiornis inexpectatus*. Scale bar 10 mm.

eral processes excludes this specimen from basal mesoeucrocodylians and Goniopholidae (Pol, 2000; Sereno *et al.*, 2001). A pitted dorsal surface was recognized in the gondwanan peirosaurids (Marinho *et al.*, 2006), but the presence of this character together with an anterior surface for the articulation with preceding osteoderm are characters found in Neosuchia (Ortega *et al.*, 2000).

Dinosauria Owen, 1842

Theropoda Marsh, 1881

?Coelurosauria Huene, 1920

Genus and species indet.

Referred material. MAS-P/2 17, an isolated posterior caudal vertebra, with distal tip of prezygapophyses missing (Fig. 4A).

Remarks. Although the present specimen is poorly preserved, it may be referred to Theropoda on the basis of the elongate and depressed centrum, and the dorsoventrally tall and well-developed prezygapophyses (see Rauhut, 2003). This specimen differs from the large sized Gondwanan Abelisauridae, Noasauridae and gigantic Carcharodontosauridae on the basis of subhorizontal orientation of the base of the prezygapophyses, and non-dorsal orientation of the postzygapophyses (see Novas *et al.*, 2004; Coria

& Currie, 2006). In both features, the Salta specimen is reminiscent of Coelurosauria, and in consequence is referred with doubts to that theropod group.

Aves Linnaeus, 1758

Enantiornithes Walker, 1985

Intiornis inexpectatus Novas, Agnolin & Scanferla, 2010

Holotype. MAS-P/2 1, one specimen preserved in a slab and counter slab, comprising a right foot articulated with the distal end of corresponding tibiotarsus (Fig. 4B).

Remarks. This recently discovered bird clearly belongs to the Enantiornithes because of the presence of a large medial condyle of the tibiotarsus and distal shaft of the metatarsal IV laterally compressed (Chiappe & Walker, 2002). Also, it is referred to the family Avisauridae on the basis of its cranially convex third metatarsal. Several features suggest close relationships between *Intiornis* and the avisaurid *Soroavisaurus*, from the Lecho Formation (Maastrichtian; North-West Argentina). *Intiornis* was the size of a sparrow, thus representing the smallest Enantiornithes known from South America. In Northern Argentina, a large variety of Enantiornithes was recovered in the Lecho Formation (Maastrichtian), but it consists mainly of isolated bones (Walker, 1981).

DISCUSSION

To date, the only fossil described from the Las Curtiembres Formation was the frog *Saltenia ibanezi*. Herein we expand the fossiliferous content of this unit, including: teleostean fishes, pleurodiran turtles, crocodylomorphs, non-avian dinosaurs, and enantiornithine birds. The new discoveries invite to review some relevant aspects of Cretaceous vertebrate diversification in the Southern continents.

There are many reports of Late Cretaceous fishes from South America (e.g. Cione, 1987; Arratia & Cione, 1996; Gayet & Meunier, 1998; Gayet et al., 2003; Cione et al., 2007). However, most fish records of this age consist of poorly preserved or incomplete specimens (e.g. Santos, 1984; Gallo & Brito, 2004; López-Arbarelo et al., 2003; Martinelli & Forasiepi, 2004) in contrast with older and younger records (Arratia & Cione, 1996; Cione & Báez, 2007). Consequently, although important cladogenetic events may have occurred in the South American continental ichthyofauna during the Late Cretaceous, there is almost no fossil documentation of them. This is why

discovery of articulated fishes, such as those from Las Curtiembres Formation, is relevant and stimulates additional collecting in Late Cretaceous outcrops to shed light into the origin and evolution of the South American extant ichthyofauna.

The remains described here represent the first Cretaceous record of turtles from the Salta Group that belongs to Pleurodira. The record of podocnemidoid pleurodiran turtles in Late Cretaceous deposits of northwestern Argentina is consistent with the paleobiogeographic scenario proposed by Broin (1988), Broin & de la Fuente (1993 a,b) and de la Fuente (2003), which suggests that the differentiation of pelomedusoids occurred in northern Gondwana whereas that of chelids took place in the southern part of this supercontinent. This hypothesis is supported by the record of the podocnemidoid clade in the Cretaceous of Brazil and in the Paleocene of northwestern Argentina and Bolivia (Broin, 1991; de la Fuente & Lapparent de Broin, 1997; Lapparent de Broin, 2000; Franca & Langer, 2005; Romano & Azevedo, 2006), and the restriction of the chelid record to Patagonia during the Cretaceous (Broin & de la Fuente 1993b; Lapparent de Broin & de la Fuente, 2001).

The archosaurian record of Las Curtiembres Formation is currently composed of mesoeucrocodylians, small non-avian theropod dinosaurs (perhaps coelurosaurians), and enantiornithine birds. Regrettably, the crocodile and non-avian dinosaur specimens recorded here are rather fragmentary, and only allow us to demonstrate the presence of these taxa in the unit. With respect to the enantiornithine bird *Intiornis* (Novas et al., 2010), its minute size clearly contrasts with the usually larger and more robust proportions of Late Cretaceous taxa (Zhou & Zhang, 2006), including previous records in the Salta Group (Lecho Formation; Chiappe, 1993). The fossil bird reported here constitutes the first avian record from the Pirgua Subgroup and the oldest record for the whole Salta Group. Curiously, Enantiornithes was not found in well-known Campanian-Maastrichtian fossiliferous deposits from Patagonia (e.g. Los Alamitos Formation, Allen Formation; Bonaparte, 1987; Martinelli & Forasiepi, 2004; Agnolin & Martinelli, 2009).

Previous environmental interpretations of the Morales Member sequence proposed that it represents a perennial, brackish water body of around 300 km², deposited possibly under dry and warm climatic conditions (Marquillas et al., 2005). The vertebrate association reported here (especially fishes, the fully aquatic pipid frogs

and pleurodiran turtles) supports the perennial condition of this lake. Living pipid frogs and pleurodiran podocnemid turtles are currently mostly distributed in intertropical environments of Africa, Madagascar, and South America (Iverson, 1992; Cannatella & Trueb, 1988). Thus, their presence in the Morales Member lake is congruent with the climatic inferences made by previous authors based on geological and paleobotanical evidence (Marquillas *et al.*, 2005). Recently, Narváez & Sabino (2008) proposed semiarid conditions and a warm paleoclimate based on palynological data. These authors also inferred more humid conditions at the base of the Morales Member based on the abundance of green shales and micritic limestones. Thus, the environmental reconstruction of the Morales Member remains unresolved until more paleoclimate indicators will be found. The presence of articulated small-sized fishes and frogs (and, more surprisingly, delicate tadpoles) suggests a rapid burial and absence of scavengers. However, the faunal assemblage indicates an oxygenated environment with abundant alimentary resources for the maintenance of the tadpoles and fishes, but these environmental conditions imply benthic activity (and consequently disarticulation of the carcasses by scavengers). This is contradicted by the preservational conditions, which suggest poor benthic activity. This contradiction, in turn, possibly indicates stratification of the water column, with a well-oxygenated upper stratum and an anoxic lower one.

In summary, as noted previously, the paleontological evidence for Late Cretaceous vertebrate assemblages of northwestern Argentina is very patchy and biased. Thus, despite the fragmentary condition of many specimens described here, the new information provided by the Campanian assemblage of the Morales Member (Las Curtiembres Formation) at the Puente Morales locality offers a broader view of the Late Cretaceous faunal composition in this region of South America.

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