DINOSAURS AND OTHER VERTEBRATES OF THE LAKE EZEQUIEL RAMOS MEXIA AREA, NEUQUÉN - PATAGONIA, ARGENTINA

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Abstract  Lake Ezequiel Ramos Mexia is an artificial reservoir built in the Rio Limay Valley. This river forms the border between Neuquén and Rio Negro provinces. The outcrops adjacent to the Neuquén coast of the lake are continental red beds, mostly the Candeleros Member of the Rio Limay Formation. The age of this Member has been dated as Albian based on the vertebrate fauna. The coastal outcrops have yielded one of the most important Mesozoic faunas found in South America during the last 10 years. The Candeleros Member has yielded the largest theropod ever found (Gigantosaurus carolintii), the most primitive diplodocid sauropod (Rebbachisaurus tessonei), the most primitive titanosurid sauropod, (Andesaurus delgadoi). Among dinosaur tracks, the area has given the first evidence of iguanodontids in Argentina (Sousaichnium monettae and Limayichnus major), the first sauropod tracks in Argentina (Saupodichnus giganteus) and other new theropod tracks (Deferrariichnium mapuchensis, Bressanichnus patagonicus, Abelichnus astigarrae, and Picunichnus benedettoi). Among other vertebrates recorded in this fauna is the oldest known specimen of the Chelidae (turtle); the oldest Pipidae (Anura) from South America and a new species of crocodile (Araripesuchus sp.). Finally this area has yielded the first evidence of pterosaur tracks on the Southern continents. A short review and description of each specimen is given, and a listing of all the new findings in the area is presented. A new diagnosis is given based on best material of Sauropodichnus giganteus. The ichnospecies Bonaparteichnium tali is here shown to be a junior synonym of Limayichnus major.

Introduction  
Lake Ezequiel Ramos Mexia (Fig. 1) is a giant water reservoir created to produce hydroelectric energy. It was formed by building a dam across the Limay River in 1972 at El Chocón. The lake is 60 km. long, and its greatest width is 15 km. It occupies 816 square kilometers. Cropping out on all sides of the lake are sedimentary rocks of the Candeleros and Huincul members of the Rio Limay Formation, Neuquén Group (Fig. 2). The Candeleros Member is composed of reddish sandstones and mudstones that represent environments as different as floodplains and sand dunes. The Huincul Member, on the other hand, has only yellowish, coarse sandstones and conglomerates deposited on alluvial fans. The age of the Candeleros and Huincul members has been determined as Albian-
Cenomanian (Calvo, 1991), but the Candeleros Member is likely to be Albian in age (Calvo and Salgado, 1996).

Many Cretaceous fossils have been collected from this region. Three papers have previously been published on the vertebrate fossils of this area: descriptions of *Andesaurus delgadoi* (Calvo and Bonaparte, 1991), *Rebbachisaurus tessonei* (Calvo and Salgado, 1995) and *Giganotosaurus carolinii* (Coria and Salgado, 1995). The known fauna is very important because it shows strong resemblances with that of northeastern Brazil and Africa. Therefore, these fossils from Argentina are relevant as paleobiogeographic data regarding the opening of the South Atlantic Ocean (Calvo and Salgado, 1996).

Since the first description of sauropod remains at El Chocón (Calvo and Bonaparte, 1988), the fauna in the area has been substantially increased. However, many other specimens collected have not been mentioned in the literature. This paper is a contribution towards the better understanding of the fossil fauna of the Lake Ezequiel Ramos Mexia, usually known as the El Chocón fauna. In an attempt to provide an accurate description of the Lake Ezequiel Ramos Mexia fauna as a whole, a short description with comments about each specimen is given, and an up-to-date list of the taxa discovered in the area is presented. A new diagnosis is given based on the best material of *Sauropodichnus giganteus*. The ichnospecies *Bonaparteichnium tali* is here shown to be a junior synonym of *Limayichnus major*.

Fig. 1. Map showing Neuquén Province (1), study area (2) and surrounding area of the Lake Ezequiel Ramos Mexia (3).
History

The first dinosaur bones in the Lake Ezequiel Ramos Mexia area were collected by the Austrian Captain Zapalowicz in 1889. While working for a German University, he discovered a dorsal vertebra of a dinosaur on the Alarcón Ridge, today a peninsula in Lake Ezequiel Ramos Mexia. This material was described in 1902 by Baron von F. Nopcsa as probably belonging to the sauropod Bothriopodylus. In 1903, Hatcher stated that the morphology of Nopcsa's dorsal vertebra was not generically distinguishable from that of Haplocanthosaurus priscus. Later, Macintosh (1990) was correct in interpreting this as
belonging to a species closely related to *Rebbachisaurus garasbae* (Lavocat, 1954). The specimen collected by Captain Zapalowickz is now thought to be the sauropod *Rebbachisaurus tessonei* (Calvo and Salgado, 1995). Ninety years later, in 1979, a field party from the National Sciences Museum of La Plata investigated the southern margin of the lake across from Picún Leufú. This resulted in new discoveries. Gasparini and Musacchio (1979), in a brief report, noted the presence of dinosaur tracks discovered by Mr. Santiago Astigarraga that year. In spite of that discovery, there was no published paleontological description between 1902 (Nopcsa, 1902) and 1988 (Calvo and Bonaparte, 1988).

In 1987 paleontologists from the National University of Comahue made several field trips to the area surrounding Lake Ezequiel Ramos Mexía. The same year, Mr. Alejandro Delgado (from the Hidronor State Company) rediscovered Zapalowickz's dinosaur-bearing strata near El Chocón on the north side of the lake. Since 1987 several more field trips under the direction of the author were taken, funded by the University. The area prospected extended from Neuquén City to the Lake Ezequiel Ramos Mexía area resulting in the discovery of dinosaur tracks in the Picún Leufú area (Calvo, 1991), as well as skeletal material of two different kinds of sauropods: *Andesaurus delgadoi* (Calvo and Bonaparte, 1991), and *Rebbachisaurus tessonei* (Calvo and Salgado, 1995). These discoveries are important because they have filled the gap between Early and Late Cretaceous dinosaur faunas in Patagonia. The complete faunal list of the Lake Ezequiel Ramos Mexía area is given below:

**Theropoda**

- *Giganotosaurus carolinii* Coria and Salgado, 1995

**Sauropoda**

- *Andesaurus delgadoi* Calvo and Bonaparte, 1991
- *Rebbachisaurus tessonei* Calvo and Salgado, 1995
- Titanosauridae indet., this paper

**Crocodylia**

- *Araripesuchus* sp. Gasparini, Buscalioni, Ortega and Calvo, 1998

**Turtles: Pleurodira**

- Chelidae indet. de Broin, de la Fuente and Calvo, 1997

**Anura**

- Pipidae indet. Baez and Calvo, 1990

**Dinosaur tracks**

**Theropoda**

- *Abelichnus astigarrae* Calvo, 1991
- *Picunichnus benedettii* Calvo, 1991
- *Deferrariischnium mapuchensis* Calvo, 1991
- *Bressanichnus patagonicus* Calvo, 1991
- Coelurosauria indet. Calvo, 1989

**Sauropoda**
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*Sauropodichnus giganteus* Calvo, 1991

Ornithischia

*Sousaichnium monettae* Calvo, 1991

*Limayichnus major* Calvo, 1991

**Pterosaurs tracks**

Pteraichnidae

*Pteraichnus* sp. Calvo and Moratalla, 1998

**Geological Framework**

The Neuquén Basin of western Argentina has deposits ranging in age from Late Triassic to Tertiary. The sedimentary filling of this basin has been subdivided into three supercycles (Groeber, 1946): “Jurásico” (Late Triassic to Early Jurassic), “Andico” (Early Jurassic to Early Cretaceous) and “Riogránico” (Late Cretaceous to Paleocene) (Fig. 2). The latest supercycle is divided into the “Neuqueniano” Cycle, corresponding to the deposition of the Neuquén Group (Albian to Early Maastrichtian times) and the “Malalhueyano” Cycle during which the Malargue Group was deposited (Late Campanian-Paleocene). The Neuquén Group is composed of sediments deposited in a continental, fluvial environment (Uliana and Dellapé, 1989). The Malargue Group represents the first incursion of the Atlantic Ocean into the Neuquén Basin (Uliana and Dellapé, 1981). The Neuquén Group is represented, in the southeastern sector of the Neuquén Basin, by thick sequences of siliciclastic red beds. The lowest unit in the Rio Limay Formation, is composed of three members, from bottom to top: Candeleros, Huincul and Lisandro (Cazau and Uliana, 1972). Up to now, 80% of the vertebrate fossil remains have come from the Candeleros Member. Siltstones and fine sandstones are the most common rocky components of these thick sequences of siliciclastic red beds that form the Candeleros Member. Most of the outcrops on the margins of Lake Ezequiel Ramos Mexia are formed of continental deposits of the Candeleros Member.

A preliminary stratigraphic study of the Candeleros Member has been made by Spalletti and Gazzera (1989). The sequence begins with deposits of single transverse aeolian dunes (barchans) inferred from huge (up to 13 meters thick) cross-bedded sandstone sets. Other aeolian deposits are interpreted as dry, interdune to extradune fields. Plane-bedded sandstones and mudstones were formed by distal, fast, poorly channeled ephemeral flows. Heterolithic, pelite, and chert interlaminations, suggest fall-out playa and playa-lake deposits. There are some thicker intervals of fine grained loessic and ephemeral flow deposits interpreted as extradune settings. There is one facies representing an arid to semiarid phase in the lower part of the section of the Candeleros Member. On the basis of paleontological and sedimentological evidence, Calvo and Gazzera (1989) concluded that for the most of the deposition of the Candeleros Member, a temperate climate with alternate rainy and dry periods prevailed.

The age of the Candeleros Member based on dinosaur tracks has been determined as Albian-Cenomanian (Calvo, 1991). However, the occurrence of a more primitive vertebrate fauna collected in the last 10 years (Calvo and Bonaparte, 1991; Calvo and Salgado, 1995;
Coria and Salgado, 1995; de Broin et al., 1997; Gasparini et al., 1998) together with new discoveries in Africa (Congleton et al., 1992; Jacobs et al., 1993; Werner, 1993; Sereno et al., 1996; Russell, 1996; Jacobs et al., 1996) allow us to confirm that this member is Albian in age (Calvo and Salgado, 1996).

Dinosaurs from the Aptian-Albian of Brazil come from the Araripe Basin. The age of these dinosaurs has been established through palynological studies (Pons et al., 1990). Among the rock units of the Araripe Basin is the Romualdo Member, from which comes a well known assemblage of plants, fish, crocodiles, pterosaurs, and some dinosaur remains. The age of the Romualdo Member has been determined as Middle Albian. It is interesting to note that from this member comes the crocodile Araripesuchus gomesii, a species closely related to the new material of Araripesuchus sp. from Lake Ezequiel Ramos Mexia. This implies an Albian age for the Candeleros Member (Calvo, 1991; Calvo and Salgado, 1996).

Abbreviations

The abbreviations used in the text and figures are as follows:
MRF-Muséum d’Histoire naturelle, Paris, France
MUCPv-Geology and Paleontology Museum of the National University of Comahue, Neuquén, Argentina.
MMChPv-Museo Municipal El Chocón, Argentina.

The Fauna of the Rio Limay Formation at Lake Ezequiel Ramos Mexía

Most of the specimens from the Candeleros Member described to date have ranged from partial to almost completely articulated skeletons. Only a few specimens from the Huincul Member consist of associated skeletal remains. In the following faunal descriptions from the Lake Ezequiel Ramos Mexia area, the previous record of each group is treated first, followed by a brief discussion of the new material now housed in the collection at the Museum of Geology and Paleontology of the National University of Comahue. Finally, the main characteristics of each species is given.

Dinosauria Owen, 1842
Sauropoda Marsh, 1878
Rebbachisauridae Calvo and Salgado, 1995
Rebbachisaurus tessonei Calvo and Salgado, 1995
(Figs. 3 and 4)

Materials: Rebbachisaurus tessonei is known from at least six specimens (MUCPv-153, 205, 206, 272, 273 and unnumbered; Nopcsa, 1902). The holotype (MUCPv-205) is the most complete, articulated specimen from the Candeleros Member, Río Limay Formation, and the most complete sauropod ever found in South America. It was excavated in 1988, by a joint field party from the Natural Sciences Museum of the National University of Comahue
(Neuquén) and the Argentine Museum of Natural Sciences “Bernardino Rivadavia” Buenos Aires. The site lies 10 km SW of El Chocón Locality. The specimen was briefly reported on by Calvo and Bonaparte (1988) and Calvo and Salgado (1991), and was formally named by Calvo and Salgado (1995).

The holotype (MUCPv–205) of the species is an articulated and well-preserved skeleton. Its skull includes teeth, a basicranium, frontal, parietal, lacrimal, squamosal, postorbital, prefrontal, supraoccipital, exoccipital, basioccipital, laterosphenoids, basisphenoids, basipterygoid processes, prootic, anhtotic, opisthotic, nasals, quadratojugal, quadrate and jugal. The specimen also has 8 cervical vertebrae, 12 dorsal vertebrae (6 of them articulated), 40 articulated caudal vertebrae, ribs, a complete pelvis and a pectoral girdle, nearly complete hind and forelimbs (lacking a manus) and gastroliths. Aside from the holotype, *Rebbachisaurus tessonei*
is also known by less complete specimens (MUCPv–153, 205, and 206) that shed relevant complementary anatomical information (Calvo and Salgado, 1995).

Specimen MUCPv–206 of *R. tessonei* was found by the author in 1987 in the same stratigraphic level but approximately 1,000 meters away from MUCPv–205. MUCPv–206 is a partial skeleton, collected in 1988, composed of two posterior and two anterior cervical vertebrae, one posterior dorsal vertebra, one sternal plate, four metacarpals, partial ribs and gastroliths.

Specimen MUCPv–153 is represented by a partial, articulated skeleton found by Mr. Ruben Carolini in 1987 and collected in 1990. It is composed of two sacrals, the first 6 caudals, a pubis and an ischium. It is the only specimen found in the lower part of the Huincul Member.

From the Candeleros Member comes an unnumbered dorsal vertebra collected by Captain Zapalowicz in 1889 and described by Nopcsa (1902), now stored in Geneva, Switzerland.

In 1993 Mr. Ruben Carolini found another specimen of *R. tessonei* in the Candeleros Member, 15 km. south of the El Chocón Locality, close to where the holotype of *Giganotosaurus carolinii* was discovered. The excavation was conducted by the author in 1996 resulting in more material of *Rebbachisaurus tessonei*. The specimen (MUCPv–273) consists of two anterior, two middle, and one posterior caudal vertebrae (Fig. 3).

Finally, four articulated dorsal vertebrae, a pubis, an ischium, and 6 gastroliths (MUCPv–272) were found by Mr. Ruben Carolini and collected by the author and L. Salgado in 1996. This specimen comes from the Candeleros Member, 8 km. south of the El Chocón Locality. The height of the neural arch and the morphology of the pubis and ischia are similar to those elements described for the holotype and paratype.

*Comments:* The genus *Rebbachisaurus* was erected by Lavocat (1954) to describe sauropod remains from the Albian of Morocco. Among the diagnostic characters listed for this genus by Calvo and Salgado (1995) are the following: paddle-like scapular blade (fig. 4); V-shaped angle between the acromion and the scapular blade; dorsal vertebrae: absence of hyposphene-hypantrum, tall neural arch, single neural spine, and parapophysis directed upward at approximately 45°. Two species of this genus have been recognized: *Rebbachisaurus garasbae* and *Rebbachisaurus tessonei*. Most of the characters listed by Lavocat (1954) are now considered as synapomorphies of *Rebbachisaurus*. Bonaparte (1998) recognized the presence of an accessory suprapostzygapophysial lamina in *R. garasbae* in order to propose a different genus for *R. tessonei*. However, this character is also present in the posterior dorsal vertebrae of *R. tessonei*, but, unfortunately, it was not illustrated in the original description of that species (Calvo and Salgado 1995). Therefore, this new character increases the strong affinities between these two species of *Rebbachisaurus*. A monograph on *R. tessonei* is in preparation by the author (Calvo, in prep.).

The following derived character states are present in *Rebbachisaurus tessonei*: basipterygoid process very thin and short, posterior process of the postorbitals absent, anteroposteriorly elongated articular condyle of the quadrates, toberas very reduced, paroccipital process not distally expanded, neural spine in the posterior cervical vertebrae and anterior dorsal vertebrae possessing an accessory lamina connecting with both the
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Diapoposyzygapophyseal laminae and the supraprezygapophyseal laminae, anterior dorsal vertebrae with supraprezygapophyseal laminae contacting the top of the neural spine. At present, the states of these characters are unknown in *Rebbachisaurus garasbae*. *R. tessonei* differs from *R. garasbae* in that the former has a transverse process in the anterior caudals formed by a dorsal and ventral bar of bone directed upward (Fig. 3); *R. garasbae* instead has a true wing-like transverse process.

The discovery of nearly complete skeletons of *Rebbachisaurus tessonei* allows for a reconsideration of the phylogenetic relationships of the genus *Rebbachisaurus*. *Rebbachisaurus* is the latest Diplodocimorpha so far known (Calvo and Salgado, 1995) and it exhibits many synapomorphies that justify its position as the primitive sister group of the Diplodocidae. Recently, Bonaparte (1996) described a new sauropod, *Rayososaurus agrioensis* from the Rayoso Formation, Aptian of Neuquén, Argentina, based on a scapula and a few other fragmentary bones. The broad distal scapular blade and the direction of the acromial process seen in *R. agrioensis* are regarded as autapomorphies of *Rebbachisaurus* by McIntosh (1990) and Calvo and Salgado (1995). These characters were the basis for Bonaparte (1996) establishing *R. agrioensis*. Therefore, *R. agrioensis* was considered as a nomen dubium by Calvo and Salgado (1996) and its holotype, MACH-N 41, was regarded as *Rebbachisaurus* sp.

More recently Wilson and Sereno (1998) stated that, "...enough differences exist between...", *Rebbachisaurus garasbae* and *Rebbachisaurus tessonei* to justify the new name *Rayososaurus tessonei*. However, they mentioned only two characters to support such differences: 1) presence of accessory infradiapophyseal and infrazygapophyseal laminae on the dorsal vertebrae of *R. garasbae*, and 2) the neural spine of the dorsal vertebrae broadens to nearly twice their minimum width through the proximal two-thirds of their height, and then taper sharply towards their summit. Character 1) could possibly be significant if it could be assessed in *R. tessonei*. Unfortunately, the dorsal vertebrae of *R. tessonei* have suffered post mortem deformation and the condition of the two laminae cannot be determined. Character 2) has been misinterpreted by Wilson and Sereno (1998). The maximum width of the preserved neural spine of *R. garasbae* is only one-third wider than its minimum width and therefore is similar to *R. tessonei*. On the other hand because the top is missing from the neural spine of the holotype of *R. garasbae*, it is not known whether or not it tapers sharply to its dorsal tip. On two specimens referred to *R. garasbae*, MRS 1991 and MRS 2000, it is possible to see that the end is slightly rounded as in *R. tessonei*. Calvo and Salgado (1995) recognized an autapomorphic character on the anterior dorsal vertebrae of *R. tessonei*: the two supraprezygapophyseal laminae are directed upward and contact one another at the top of the neural spine. This character state is also present in the referred specimen of *R. garasbae*, MRS 2000. But it is impossible to establish for certain that the two laminae which contact one another are both supraprezygapophyseal laminae. But in any case, the same character state occurs in both species. I propose this character state as an autapomorphy of *Rebbachisaurus*. On the other hand, Wilson and Sereno (1998) did not mention that Calvo and Salgado (1996) recognized the strong similarities between *Rayososaurus agrioensis* and the species of *Rebbachisaurus* so that the former genus was invalidated (see discussion above). Therefore, I continue to maintain the original name for
this Diplodocimorpha: *Rebbachisaurus tessonei* Calvo and Salgado 1995.

Finally, Wilson and Sereno (1998) allocate *Rebbachisaurus* to the Diplodocoidea and place *Haplocanthosaurus* in a new clade called Macronaria. Wilson and Sereno (1998, pages 49–50) listed only three characters to typify the Macronaria: (86) middle and posterior dorsal neural spines with transversely flared distal ends, (87) anterior caudal chevrons with open proximal articulation, and (88) ischial distal shafts nearly coplanar. These features are present in *Rebbachisaurus tessonei* (Calvo and Salgado 1995) and yet Wilson and Sereno (1998) regard that species as a member of the Diplodocoidea. In that case, either *Rebbachisaurus* "Rayosaurus" is a member of the Macronaria or *Haplocanthosaurus* belongs within the Diplodocoidea, and the Macronaria must be rejected. I prefer to follow the phylogenetic hypothesis presented by Calvo and Salgado (1995) where *Haplocanthosaurus* is probably a DiplodocoidMarsh, 1884 (=*Haplocanthosaurus*+Diplodocimorpha) and *Haplocanthosaurus* is the sister group of Diplodocimorpha Calvo and Salgado 1995 (=*Rebbachisaurus*+Diplodocimorpha).

Titanosauriformes Salgado, Coria, and Calvo, 1997  
Titanosauria Bonaparte and Coria, 1993  
*Andesaurus delgadoi* Calvo and Bonaparte, 1991  
(Figs. 5–7)

*Andesaurus delgadoi* (MUCPv–132) was the first dinosaur collected from the area surrounding Lake Ezquiel Ramos Mexia. It was found by Mr. Alejandro Delgado in 1987 and collected the same year by the author and Mr. Pablo Puerta. The holotype was found 7 km southwest of El Chocón. A short, preliminary description of this find assigned it to the Titanosauridae (Calvo and Bonaparte, 1988). Calvo and Bonaparte (1991) described all the material of the specimen, erecting a new member of the Titanosauridae, *Andesaurus delgadoi*, placed in its own subfamily, Andesaurinae.

The holotype includes four articulated posterior dorsal vertebrae, twenty-seven articulated caudal vertebrae, an almost complete ischia and a left pubis, and an incomplete right humerus and a femur. There are also several incomplete ribs. Salgado et al. (1997) recognized two long metacarpals as part of the holotype specimen.

A second specimen of *Andesaurus* is now available (MUCPv–271). The material includes only a partial pelvis and some caudal vertebrae. The specimen was found by Mr. Rubén Carolini in 1995 and collected by the author and his team in 1996. All the material is currently in a jacket waiting to be prepared and studied (Calvo, in prep.). The pubis in this referred specimen of *Andesaurus* is laminar with an oval pubic foramen as is the case in the holotype (Fig. 5). Eleven rounded gastroliths associated with this referred specimen are similar in size and composition to those found in *Rebbachisaurus tessonei*.

Comments: Among the most important characters of *Andesaurus delgadoi* are: tall posterior dorsal vertebrae; the presence of a hyposphene-hypanthrum; amphiplatian or flattened midcaudal vertebrae (Fig. 6); broad laminar neural spines on middle posterior caudal vertebrae; wide proximo-lateral processes on the pubis; and a short iliac contact with the ischia (Fig. 7). Salgado et al. (1997) correctly stated that the anterior caudal centra have shallow anterior faces and posterior faces that are only slightly convex. This last observation
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Fig. 5. *Andesaurus delgadoi* (MUCPv–271). Lateral view of the right pubis and some of the 11 gastroliths. Scale bar, 10 cm.

Fig. 6. *Andesaurus delgadoi* (Holotype, MUCPv–132). Lateral view of a middle caudal vertebra. Scale bar, 10 cm.

is contrary to observations made by Calvo and Bonaparte (1991), who proposed that all the caudals were amphiplatian. This condition was interpreted as an incipient procoely of the anterior caudals.

Calvo and Bonaparte (1991) created a new subfamily, Andesauroidea, to include all the titanosaurids with midcaudal amphiplatian vertebrae having laminar neural spines, and dorsal vertebrae with a hyposphene-hypantrum. Later, the name Titanosauria (Bonaparte and Coria, 1993) was erected to accommodate sauropods lacking some titanosaurid features such as procoelous caudals; Andesauroidea was erected to include *Andesaurus*. Finally, Salgado et al. (1997) maintained the name Titanosauria, but they separated the rest of the Titanosauridae from *Andesaurus*; therefore, Andesauroidea was rejected. They recognized that *A. delgadoi* should be considered a basal Titanosauria, because it has all titanosaur synapomorphies but lacks unequivocal synapomorphies diagnosing Titanosauridae (for instance caudal vertebrae being strongly procoelous, having ball and socket articular facets).

*Andesaurus delgadoi* shares with *Malawisaurus dixeyi* (Jacobs et al., 1993), from the Aptian of Malawi (Jacobs et al., 1996), undivided dorsal vertebrae; an ischium that is transversely expanded; anterior caudal vertebrae that are procoelous; amphiplatian middle and posterior caudal vertebrae, and proximally open haemal arches. This combination of
characters is only present in these two taxa, but, *Malawisaurus* lacks a hyposphene-hypantrum articulation in the dorsal vertebrae (Jacobs et al., 1993). As stated by Salgado et al. (1997), the relationships of *M. dixeyi* and *Epachthosaurus sciuttoi* (Powell, 1990) remains unresolved, because *M. dixeyi* does not have a hyposphene-hypantrum, while *E. sciuttoi* does not have amphiplatian mid and posterior caudal vertebrae. Both species are the sister taxa of *Andesaurus*. In sum, very probably *Andesaurus* and *Malawisaurus* are basal members of the Titanosauria, but *Epachthosaurus* should be included as a true Titanosauridae.

Titanosauridae Lydekker, 1885

*Titanosauridae* gen. et. sp. indet.

From the top of the Candeleros Member, Calvo and Salgado (1995) collected a new specimen of a titanosaurid sauropod. The specimen was found by Mrs. Viviana Moro of El Chocón, 300 meters north of the tourist office entrance to El Chocón. The material (MUCPv-244) consists of one anterior, four middle, and two posterior caudal vertebrae, metacarpals, one haemal arch, one distal end of a tibia, and one tooth. All the caudals are characterized by having procoelous centra (Fig. 8), the metacarpals are very long resembling those of *Andesaurus* (Calvo and Bonaparte, 1991) and those of other titanosaurs (Salgado et al., 1997). The midcaudal vertebrae have anteriorly placed neural arches and plate-like
neural spines, as in *Andesaurus* (Fig. 9). The posterior caudal vertebrae have neural arches well displaced anteriorly. A single incomplete tooth, MUCPv–244 (Fig. 10) shows a morphology very distinct from that present in derived titanosaurids such as *Alamosaurus* (Kues et al., 1980), *Ampelosaurus* (Le Loeuff, 1995), *Nemegtosaurus* (Nowinsky, 1971), *Titanosaurus* and *Antarctosaurus* (Huene, 1929). The tooth is a compressed cone-chisel-like tooth (*sensu* Calvo, 1994). Its length is 21 mm, the labio-lingual width is 8 mm., the anteroposterior length at the crown is 11.4 mm., and at the bottom of the preserved crown, is 10.4 mm. A smooth lingual carina is present. The tooth is bent lingually and does not have lateral facets, so the teeth did not interlock as in *Camarasaurus* (Gilmore, 1925; Fiorillo, 1991; Calvo, 1994). *Rebbachisaurus* is characterized by having almost unworn, thin,
long, curved peg-like teeth (Calvo, 1994). Derived titanosaurids have long, thin, straight, chisel-like teeth (Huene, 1929; Calvo, 1994), with some having the apical moiety of the crown slightly compressed labiolingually. They also have a wear surface inclined at a very sharp angle. The shape and morphology of this tooth together with the postcranial evidence suggest that this specimen belongs to a clade of sauropods previously unknown in the Lake Ezequiel Ramos Mexía region.

Teeth of *Andesaurus delgadoi* are unknown. It is expected, however, that its teeth will be more similar to those present in *Brachiosaurus* (Janensch, W. 1935–1936; Calvo, 1994) and *Pleurocoelus* (Leidy, 1865; Calvo, 1994), which are compressed cone-chisel-like teeth (Calvo, 1994). Martínez (1998) announced the discovery of a new sauropod skull with compressed cone-chisel-like teeth from the Bajo Barreal Formation, Albán of Chubut Province. He interpreted the collected material (also including a partial neck) as belonging to a titanosaurid. According to this evidence it is probable that the Chubut skull may belong to a member of the Titanosauria, closely related to *Andesaurus delgadoi*. Therefore, *Andesaurus* is likely to have had compressed cone-chisel-like teeth. The new specimen of Titanosauridae (MUCPv-244) with compressed cone-chisel-like teeth probably represents a new taxon more derived than *Andesaurus*, but more primitive than the rest of the Titanosauridae.

**Sauropoda** gen. et sp. indet.

In 1996, Mr. Prebiterio Pacheco, a technician of University of Comahue found a giant vertebra and a partial rib (MUCPv–251) 8 km south of El Chocón. The remarkable aspect of this sauropod specimen is its gigantic size. The proximal half of a rib, lacking the vertebral articulations, measures 175 centimeters in length. The dorsoventral width at the proximal end is 21 cm. The preserved distal end has a section of 12 cm. dorsoventrally by 6 cm antero-posteriorly. The vertebra recovered probably is a dorsal. Further studies (Calvo, *in prep.*) will establish if it has some relationships with the largest known sauropod, *Argentinosaurus*.

**Theropoda** Marsh, 1881
**Carcharodontosauridae** Sereno et al., 1996

*Giganotosaurus carolinii* Coria and Salgado, 1995

(Figs. 11, 13–15)

The first evidence of giant theropods in the area was discovered in 1987 by Mr. A. Delgado, who found a large theropod tooth (MUCPv–52), a description of which is given below. The material was collected on the coast of the Lake Ezequiel Ramos Mexía approximately 5 km. south of El Chocón. The tooth closely resembles that of *Giganotosaurus carolinii* (MUCPv-Ch1, personal observation). The second specimen collected consists of a left dentary containing some unworn teeth (MUCPv–95). It does not come from the area near the lake but from the same geological unit, the Candeleros Member of the Rio Limay Formation. It was collected by the author in 1988 at Los Candeleros, 50 km. west of El Chocón. The third specimen, the holotype (MUCPv-Ch1), was found by R. D. Carolini in 1993, 15 km. south of El Chocón. The specimen is very well preserved, and
it includes nearly 70% of the skeleton. It is represented by a partial skull, most of the vertebral column, complete pectoral and pelvic girdles, both femora, left tibia and fibula.

The presence of carnivorous dinosaurs at the Candeleros Member of the Rio Limay Formation was first published by Calvo (1989). Calvo noted that the huge incomplete dentary (MUCPv-95), 61 cm. in length, had the unusual feature that the anterior end of the dentary was dorsoventrally expanded and had the ventral process and the symphysial surface flattened (Fig. 11). I also noted that these characters were present to a lesser degree on the theropod *Piatnitzkysaurus floresi* (Bonaparte, 1986) (Fig. 12), so there is some resemblance to the Allosauroidea (Sereno et al., 1996). The preliminary study of MUCPv–95 (Calvo, 1989) suggested that it probably belonged to a new theropod taxa, now recognized as *Giganotosaurus carolinii* (Coria and Salgado, 1995), with a size close to that of *Tyrannosaurus rex* (Osborn, 1905). Thus, it is the largest theropod ever found in the southern continents. Calvo and Coria (in press) provide a complete description of this material, recognizing it as the largest specimen of *Giganotosaurus carolinii* ever found, with

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**Fig. 11.** *Giganotosaurus carolinii* (MUCPv–95). Lingual view of the dentary. Scale bar, 10 cm.

**Fig. 12.** *Piatnitzkysaurus floresi*. Drawing in lingual view of the dentary showing the ventral process and the anteroventrally directed Meckelian Groove.
a skull length of approximately 195 cm.

Comments: Coria and Salgado (1995) described the most complete specimen of *Giganotosaurus carolinii*, the holotype (Fig. 13). *Giganotosaurus* is characterized by having dorsoventrally deep maxilla, with subparallel dorsal and ventral edges; a cave-like supraorbital lacrimal-postorbital contact; two pneumatic foramina on the internal side of the quadrate; the symphyseal end of the dentary dorsoventrally expanded, bearing a ventral process (Fig. 12); the proximal end of the scapula forwardly projected above the coracoid (Fig. 14); a lobe-shaped obturator process of the ischium; a dorsally projected femoral head (Fig. 15) and a posterior intercondylar groove on the proximal end of the tibia.

*Giganotosaurus* was considered as the sister group of the Allosauroidea by Coria and Salgado (1995); however, Sereno et al. (1996) include it within Allosauroidea in the Carcharodontosauridae, based on its having a broad orbital shelf (formed by the lacrimal and postorbital bones) and a squared anterior end of the lower jaw. Very recently, Novas (1997) noted the strong resemblance among the different South American, Malagasy, and Indian theropod taxa, suggesting a Gondwanan origin for both the abelisaurids and the carcharodontosaurids. According to Novas (1997), *Giganotosaurus carolinii* and *Carcharodontosaurus saharicus* exhibit many derived characters in common with abelisaurids suggesting that they are more closely related than previously supposed.

A single incomplete tooth (MUCPv-52) is tentatively referred here to *Giganotosaurus* sp. because it is laterally compressed (Fig. 16) and oval in cross-section being mediolaterally compressed in the holotype. The root is missing, but the crown shows close resemblance with that of the holotype. The tooth has the typical theropod features with serrated anterior

![Fig. 13. *Giganotosaurus carolinii* (Holotype, MUCPv-Ch-1). Partial view of the skeleton.](image-url)
Fig. 14.  *Giganotosaurus carolinii* (Holotype, MUCPv-Ch-1). Lateral view of the scapula and coracoid. Scale bar, 10 cm.

Fig. 15.  *Giganotosaurus carolinii* (Holotype, MUCPv-Ch-1). Medial view of the femur. Scale bar, 10 cm.

and posterior borders. The preserved crown is 90 mm. in length, its maximum width is 45 mm., and its thickness in the labio-lingual direction is 21 mm. There are 9 to 12 serrations present per 5 mm.

Crocodylomorpha Walker, 1970 *sensu* Benton and Clark, 1988
Crocodyliformes *sensu* Benton and Clark, 1988
Mesoeucrocodylia *sensu* Benton and Clark, 1988
Genus *Araripesuchus* Price, 1959

*Araripesuchus* sp. Gasparini, Buscalioni, Ortega and Calvo, in press e
In 1988 Lic. Cesar E. Gazzera discovered fossil remains of an undetermined vertebrate 5 km. south of El Chocón. The site is located where the Cañadón de Coria intersects the Lake Ezequiel Ramos Mexia. Three specimens were collected in the same year by the author, and in 1989 the remaining material was collected by the author and J. F. Bonaparte's team. At least five partially articulated specimens of a new species of the crocodilian genus *Araripesuchus* were collected (Gasparini et al., 1998; Gasparini et al., in press a).

The specimen MUCPv-269 includes the mandibles and the anterior half of an articulated skull lacking the most anterior part of the rostrum. The specimen also includes the precaudal dorsal armour and bones of both shoulder girdles (scapulae) and forelimbs (humeri, radius and ulnae). Specimen MUCPv-267 consists of the anterior half of an articulated individual preserving an almost complete skull and attached mandibles. Specimen MUCPv-268 is made up of postcranial, articulated elements. Specimen MUCPv-268 consists of the distal fragments of a tibia and a fibula. Specimen MUCPv-270 is the distal portion of a left femur in articulation with a tibia and a fibula, and specimen MUCPv-283 is an isolated anterior fragment of a rostrum comprising the premaxillae and anterior tip of the maxillae, nasals, and dentaries. All referred specimens have been found in association with the holotype (Gasparini et al., in press a).

Comments: *Araripesuchus* sp. (Gasparini et al., 1998) has a skull with a tubular rostrum slightly wider than high, without alveolar ornamentation, and with a sharp anterior tip to the rostrum. The orbits occupy one-third of the skull length and project laterally and dorsally. The orbits are covered by two palpebral bones. Four premaxillary teeth are present. The teeth are heterodont. *A. gomesii* (Price, 1959) differs from *Araripesuchus* sp. in the...
degree of the dorsal extension of the lacrimal and prefrontal bones that modifies their relationships with the nasals.

Araripesuchus sp. and A. gomesiiare are mesoeucrocodyles more advanced than Notosuchus because the vomer is not exposed on the palate and the quadrate lacks multiple fenestrae. Gasparini, et al. (1998) recognized that it is very difficult to establish the phylogenetic position of Araripesuchus with respect to other mesoeucrocodyiles because it has a mixture of derived and primitive characters. Araripesuchus was originally referred to Notosuchidae (Price, 1959; Hecht, 1991), a family composed of Notosuchus, Araripesuchus and Uruguaysuchus. But, Gasparini et al. (in press b) recognized that Notosuchus is the sister group of Araripesuchus plus Neosuchia. On the other hand, the African species Araripesuchus wegeneri (Buffetaut, 1981) does not share the diagnostic traits of the genus, and it should be placed in a new genus (Gasparini et al., in press b).

Crocodylomorpha

Araripesuchus ?

Another specimen of a Crocodylomorpha was found 3 km. north of El Chocón by the geologist C. E. Gazzeria in 1990. A partial articulated specimen was collected the same year by Gazzeria and the author (MUCPv–248). This material remains unstudied. This specimen is twice the size Araripesuchus sp., so could belong to a new taxa of Araripesuchidae, different from Araripesuchus.

At least two more crocodile specimens were collected 12 km. south of El Chocón. They were excavated in 1997 by Mr. Cristian Albornoz and Mr. Rogelio Zapata, technicians of the El Chocón Museum. One of them, (MMChPv–01) is a partial skull; the other one, (MMChPv–02) is an articulated skeleton with a skull, cervical vertebrae, and part of the dorsal vertebrae. Some limb bones are present. All the specimens are still in the matrix, but the evidence suggests that they could be referred to Araripesuchus sp. based on morphology of the dentary teeth, cervicals, dorsal plates, and the pointed snout. They were found at the same stratigraphic level as Araripesuchus sp. MUCPv–269.

Testudines Linnaeus, 1758
Casichelydia Gaffney, 1975
Pleurodira Cope, 1864
Chelidae Gray, 1825
Gen. and sp. indet. (de Broin, de la Fuente and Calvo, 1997)

This is the oldest known record of the family Chelidae, and supports the hypothesis that this family originated in Gondwana. In 1988 several turtle plates were collected by J. O. Calvo from the area surrounding the Rebbachisaurus tessonei site. The presence of turtle plates in the area was first mentioned by Calvo and Gazzeria (1989). Since that time, hundreds of turtle plates have been recovered, and these have been assigned to Chelonii indet. and later to the Chelidae (de Broin et al., 1997).

At El Chocón there are at least two species of fresh-water turtles differentiated from one another by the morphology of the carapace, particularly by the suprapygal and entoplastron (de Broin et al., 1997). All the specimens are small, no more than 20 cm in
length. The presence of mesoplastron, the elongated surface of the ischia insertions, and the extension of the neural series, among other features, indicate that these remains are from primitive turtles. However, these specimens show derived characters, such as cervical scutes: broad and large in some nuchals but narrow in others. The turtles in the fauna from El Chocón are readily distinguished from other Late Cretaceous turtles by their low diversity and lack of well decorated scutes.

Amphibia Linnaeus, 1758  
Lissamphibia Haeckel, 1866  
Anura Giebel, 1847  
Pipidae Bonaparte, 1831  
Gen and sp. indet. Báez and Calvo, 1990

The anuran specimen from Lake Ezequiel Ramos Mexia is the oldest record of the Pipidae in South America. It occurs outside the tropical area where living pipids are found in South America. In 1989 Mr. Rubén D. Carolini found at the El Gigante Locality, on the east side of Lake Ezequiel Ramos Mexia (Rio Negro Province), small bones belonging to an undetermined animal. The same year, the author collected all the available material of this fossil and recognized it as a frog in the family Pipidae (Báez and Calvo, 1990).

The material consists of some partial articulated bones. This anuran shares with the Pipidae the presence of opisthocoelous, dorsoventrally flattened vertebral centra. The anterior and posterior branches of the pterygoid form an otic plate, probably the floor of the Eustachian Canal. The sacrum and urostyle are fused. The ilium has a dorsal prominence. The atlas has a transverse process fused to the succeeding cervical vertebrae. This specimen has characters on the pelvic girdle that are present in some living pipids.

**Dinosaur Tracks**

Dinosaur tracks are very abundant on the Neuquén coast of the Lake Ezequiel Ramos Mexia. The first evidence of them was noted by Gasparini and Musacchio in 1979 on the south end of the lake at Picún Leufú. The first mention of these tracks was made by Leonardi (1981). Field work in this area was carried out by Calvo in 1987 and 1988. In 1989 Calvo published the first description of some of these dinosaur tracks from the island of Cerrito del Bote, a new site discovered by him in 1988. More discoveries of dinosaur tracks were made on Peninsula Nueva where Calvo recognized 8 new ichnospecies (Calvo, 1991). In his paper, Calvo presented a classification of dinosaur tracks. New track sites were discovered along the Neuquén coast of the lake by Lic. Cesar Gazzera and the author at El Chocón Beach, on the northwest side of the lake (Calvo et al., 1990; Calvo and Salgado, in press). A brief description of the tracks already published (Calvo, 1989, 1991) is given below along with some mention of new evidence from other sites.

Ornithopoda Marsh, 1881  
Iguanodontidae Cope, 1869  
*Limayichnus major* (Calvo, 1991)  
(Fig. 17)
This is the most abundant dinosaur track type in the area. The trackways belong to a tridactyl bipedal animal, the pace angulation is over 150° and less than 170°. The tracks are symmetrical, lacking impressions of heel and claws. The impressions of the toes are short, with rounded distal ends. The largest digit is III. The holotype (MUCPv–65) and three more trackways (MUCPv–66, 70 and 73) come from Peninsula Nueva. At the El Chocón Locality, 14 trackways have been identified (Calvo and Salgado, in press) as belonging to this ichnotaxon, and three more could probably belong to Limayichnus also. In 1990, the author found another track with pes morphology and shape identical to that of Limayichnus at the Cañadon de Coria, located 3 km. southwest of the El Chocón Locality.

“Bonaparteichnium tali” (Calvo, 1991)

(Fig. 18)

Calvo recognized a new Iguanodontidae track morphotype characterized by having a very long heel. He named it as the holotype of Bonaparteichnium tali (MUCPv–64). The anterior part of the track looks very similar to that of Limayichnus major, but the posterior part has an unusual extension of the heel. In light of the present knowledge of dinosaur tracks it is possible to see this pattern of long heel in a wide variety of dinosaurs (Kuban, 1989). Kuban (1989) concluded that long heels are related to behavior patterns of walking and posture in some dinosaurs that results in the formation of impressions of the metatarsals. This plantigrade track type may have been made occasionally by a variety of bipedal dinosaurs whenever they walked low to the ground, which would decrease the angle between the metatarsus and the substrate. Accordingly, I currently interpret that Bonaparteichnium tali is a nomen vanum, and this track must be referred to Limayichnus major.

Sousaichnium monettae (Calvo, 1991)

This is the only record of this ichnospecies in the area. The track (MUCPv–71) is asymmetrical with a very large, somewhat prominent heel that is displaced internally. The toes are relatively longer than those of Limayichnus, and Digit III is also displaced internally. Differences with S. pricei (Leonardi, 1979) from Brazil are related to digit distributions, general shape, and morphology of the heel.

Sauropodomorpha von Huene, 1932
Sauropoda Marsh, 1878
Sauropodichnus giganteus (Calvo, 1991)

(Fig. 19)

This ichnospecies was the first evidence of sauropod tracks discovered in Argentina. The diagnosis given in the original paper (Calvo, 1991) recognized that the trackway was left by a giant quadrupedal animal. These tracks have a semicircular shape and no evidence of digits and heels (MUCPv–145–146). The diameter of each track reaches 90 cm traced laterally from the midline of the trackway. Calvo (1989) and Calvo and Salgado (in press) recognized the existence of better impressions of sauropod tracks at the Cerrito del Bote and El Chocón localities. These latter trackways have good manus prints. They were made by an
animal with widely separated left and right limbs, because the footprints do not overlap the midline of the trackway. These footprints are wider than long, and are liver-shape with a convex anterior border and a concave posterior one. The pes tracks have subtriangular and almost subcircular shapes. The wider section is at the front. A new diagnosis of the ichnogenus is given as follows:

**New Diagnosis:** Wide trackway of a gigantic sauropod. The pace angulation is more than $60^\circ$. The internal border of left and right tracks are well separated from the midline of
the trackway, as in Brontopodus (Farlow et al., 1989). Pes tracks have a length of between 60 to 100 cm., the shape is subtriangular when well-preserved and circular when poorly-preserved. Manus tracks are wider (40 cm.) than long (25 cm.), but always smaller than the pes tracks. Manus tracks are crescent-shaped with the posterior border concave and anterior border convex (Fig. 19).

This same pattern and morphology have been observed at the El Chocón locality (Calvo and Salgado, in press). At El Chocón nine sauropod trackways were identified; but, there are many more poorly preserved ones. Calvo and Salgado (in press) recognized the presence of two morphotypes: Sauropodichnus giganteus and aff. Breviparopus sp. As a result of a closer study, all these sauropod tracks are now interpreted as belonging to Sauropodichnus giganteus, also found at Cerrito del Bote (see above). The main difference between these two ichnogenera is that Breviparopus belongs to a sauropod in which the footprints are close to the midline of the trackway, and in Sauropodichnus the footprints lie further from the trackway midline. Several manus footprints were recognized at Cañadon de Coria, but they are very badly preserved.

According to the record of sauropod bones in the area, I believe that all these tracks and trackways could have been left by the sauropod Andesaurus delgadoi. The support of this interpretation is that brachiosaurids and titanosaurs would have had footprints that would have been displaced far from the midline of the trackway. Andesaurus is a primitive titanosaurid closely related to Brachiosaurus and Pleurocoelus (Salgado et al., 1995, 1997). Moreover, probably Andesaurus, as in all other titanosaurids known (Salgado et al., 1997), did not have phalanges and claws on its fore foot; so that, the track morphologies could have been liver-shaped like on the manus. A similar footprint named Brontopodus birdi (Farlow et al., 1989) could have been left by the sauropod Pleurocoelus. Salgado et al. (1997) refer Brontopodus to a basal titanosauriform. In the same manner, the shape and morphology of Sauropodichnus giganteus from Lake Ezequiel Ramos Mexia could have been left by a dinosaur like Andesaurus. Additional evidence supporting this inference is that Andesaurus was found at the same stratigraphic level as the sauropod tracks, just 500 meters south of the El Chocón Beach Site.

Theropoda Marsh, 1881
Abelichnus astigarrae Calvo, 1991
(Figs. 20, 21)

These tracks belong to a huge theropod. There are two trackways at Peninsula Nueva, the larger tracks (MUCPv–74) are 50 cm in length and the pace of it is 130 cm. The smallest track (MUCPv–148) is 36 cm. in length and the pace is almost 100 cm. Tracks are tridactyl with large and coarse digits. Claw impressions are very prominent. Digit impressions occupy most of the length of the track. The pace angulation is almost 150°.

Another track has been identified at Cañadon de Coria, in which the claws are very well preserved. The length of this track reaches 45 cm. At Balneario El Chocón Locality two more trackways were identified as Abelichnus, and both of them are represented by three tracks, the best preserved is 40 cm. long. One of the trackways has tracks with a thin and relatively long heel. Finally, another track (MUCPv–139) was found at Cerrito del Bote
(Calvo, 1989); the length of the track is 48 cm. (Fig. 21), and digit and claw impressions are very prominent, indicating that it belonged to *Abelichnus astigarrae*.

I infer that these huge theropod tracks were made by very large carnivorous dinosaurs. The only osteological evidence for such a dinosaur recorded up to now in the area is *Giganotosaurus carolinii*. The bulk of the *G. carolinii* specimens has been found at a higher stratigraphic level in the Rio Limay Formation than the theropod trackways. However, Mr. A. Delgado collected a huge theropod tooth referred to *Giganotosaurus* (Calvo, this paper) from the coast of the lake. From the strata in which *Giganotosaurus* was found, we have also collected most of the specimens of the sauropod *Rebbachisaurus tessonei* and one partial skeleton of *Andesaurus delgadoi*. Therefore, if *Andesaurus* lived with *Giganotosaurus*, probably the theropod tracks could have been left by *Giganotosaurus*.

*Bressanichnus patagonicus* (Calvo, 1991)

These are small theropod tracks (MUCPv–60, 61, 68, 69) characterized in being tridactyl; all digits have very sharp claw impressions. The impression of the Digit III is curved interiorly. The posterior border of the track is small and rounded. At the El Chocón Locality, six trackways have been identified (Calvo and Salgado, *in press*). Four of them were assigned to this ichnogenus.

*Deferrariischnium mapuchensis* (Calvo, 1991)

These tracks belong to a small theropod dinosaur characterized by having the impression of a long Digit III with a sharp claw. Digit III occupies more than 50% of the track length. The lateral digits are small and poorly preserved, so that it is difficult to see claw impressions. The posterior border of the track is somewhat acute having a small heel (MUCPv–62, 63, 66). At the Chocon Locality we have recognized just one, poorly preserved track of this ichnogenus characterized by having a very long Digit III and small Digits II and IV.

*Picunichnus benedettoi* (Calvo, 1991)

The only record of this ichnogenus is based on a single track. The track is tetradactyl with good impressions of claws. Digit I is directed medially and is very small. It is placed on the posterior half of the heel. Digit III is the longest.

Ichnogen. and ichnosp. indet.

(Fig. 22)

Small theropod tracks (Calvo, 1989): At Isla Cerrito del Bote five long trackways belonging to small theropods were found. The pace between two tracks is 45 cm., the length of each track was approximately 10 cm. The longest track is 12 cm. (Fig. 22). Digits are very well preserved. They are long and thin with sharp claw impressions. I interpret that these tracks belong to a new ichnogenus not described before in the area. The five trackways run in the same direction, and they are separated by just 20 to 40 cm. Probably all theropods were running together as a pack to protect themselves or to attack prey. The record of this theropod track type is evidence that this taxon probably lived and moved socially, as has
Fig. 20. *Abelichnus astigarrae*. Drawings of the footprints at Peninsula Nueva. Scale bar, 10 cm.
Fig. 21. *Abelichnus astigarrae*. Drawings of the footprint at Cerrito del Bote island. Scale bar, 10 cm.
Fig. 22. *Theropoda indet*. Drawings of the footprints. Scale bar, 1 cm.
Fig. 23. *Pteraichnus sp*. Manus track. Scale bar, 1 cm.
Fig. 24. *Pteraichnus sp*. Pes track. Scale bar, 1 cm.
been inferred for some herbivorous dinosaurs. Some plastotypes are MUCPv=133, 134, 135.

**Pterosaur Tracks**

*Pteraichnidae*

**Pteraichnus** sp. Calvo and Moratalla, 1998

(Figs. 23, 24)

In 1987, Mr. F. Tessone found some unusual tracks on the Neuquén coast of Lake Ezequiel Ramos Mexia, a site located 15 km. southwest of El Chocón. One year later, the author collected several blocks containing some of these vertebrate tracks. The description and interpretation of this material as belonging to a pterosaur was done by Calvo and Moratalla (1998).

The trackway is wide, belonging to a small semierect, and lightly built quadrupedal animal. The manus is tridactyl (Fig. 23), strongly asymmetric, with three digit impressions showing strong outward (positive) rotation. Digit II is the shortest, subtending an angle of about 90° relative to the trackway axis. Digit III is intermediate in length with respect to Digits II and IV, subtending an angle of 130° relative to the trackway axis. Digit IV is the longest; it is slightly curved with an angle of 175° to 180° relative to the trackway axis. The pes is very elongated (Fig. 24), about three times longer than wider (10 and 3 cm. respectively) and plantigrade. The pes is subtriangular-shaped, with the lateral borders of the heel almost parallel or slightly inclined toward the midline of the foot. The axis of the footprint shows positive (outward) rotation of about 25° relative to track axis. The pes are functionally tetradactyl with digit impressions II and III slightly longer than Digits I and IV. Digit IV is wide, and Digit I very reduced.

Pterosaur fossil trackways have been controversial since their first description by Stokes (1957). Recently, a comprehensive review of the pterosaur tracksites from several European and American localities of Jurassic and Cretaceous age have improved substantially the knowledge of this type of tracks and how they were made (Lockley *et al.*, 1995). Up to now, the record of pterosaur tracks is limited to twelve localities (Lockley *et al.*, 1995 and references in there). Based on the pes and manus morphology the pterosaur trackways found in Neuquén belong to the family *Pteraichnidae*. The Neuquén tracks show a similarity to *Pteraichnus*. *Pteraichnus* from Neuquén constitutes the first record of pterosaur tracks in southern continents.

**Paleogeographic Considerations**

The Albian-Cenomanian fauna of Lake Ezequiel Ramos Mexia area is taxonomically very similar to what little has been in northeastern Brazil and North-Central Africa (Egypt, Morocco, Algeria, Niger, Cameroon, Sudan, and Malawi).

The evidence of an African-South American faunal connection during Aptian through Cenomanian times is based on both geological and paleontological data. At that time the place of connection between South America and Africa appears to have been northeastern
Brazil and Nigeria-Cameroon (Mabesoone, 1996). It is apparent that up to the latest Cretaceous, the Atlantic Ocean was divided into separate parts, Equatorial and Southern. These were separated by the remains of continental crust in the form of a submerged sill during worldwide transgressive phases, or as a landbridge during regressive periods (Mabesoone, 1996). Evidence of shallow marine environments is recorded during Aptian-Albian times in the Araripe-Potiguar Depression and AfroBrazilian Depression. This was the result of regional subsidence in those areas. Later, at the end of the Albian, there is a well marked return to continental conditions in which fluvial systems became established over the whole area. As a consequence, the AfroBrazilian and Araripe-Potiguar depressions merged, and they lost their separate identities (Lima Filho et al., 1996). Therefore, freshwater sediments were simultaneously deposited in northeastern Brazil (Fonseca, 1966) and Gabon (de Klasz, 1965) that are very similar indicating that they were deposited in the similar environments.

K/Ar dating of basic magmatic rocks that occur in Brazilian sedimentary basins, which are related to the opening of the South Atlantic Ocean, led Pimentel Mizusaki et al. (1996) to suggest that the definitive separation between South America and Africa, probably was more recent than 100 Ma. Therefore, the effective separation between the South and Equatorial Atlantic Ocean occurred either at the end of the Cenomanian or during the Turonian at the latest (Pimentel Mizusaki et al., 1996, Meister et al., 1996). It is known that during Coniacian-Santonian times a major oceanographic event occurred signalling the final structural detachment of the South American and African plates and the initiation of a deep-oceanic circulation regime (Koutsoukos et al., 1993; Koutsoukos, 1996).

In sum, geological evidence, both stratigraphic and magmatic, supports that during the end of Albian times and probably during part of the Cenomanian there was an emergent landbridge between northeastern Brazil and West Africa. This geological evidence is corroborated by paleontological data from different vertebrate groups. South America and Africa share many vertebrate taxa at that time, enumerated in Table I.

Both geological and paleontological data show that Africa and South America were connected by a land bridge at least up to Albian-Cenomanian times as was suggested by Taquet (1977) and Calvo and Salgado (1996). The strong similarities of the faunas are consistent with the presumed proximity of both continents at that time.

Conclusions

The area around Lake Ezequiel Ramos Mexia has yielded one of the most important Albian vertebrate faunas. In the last ten years several vertebrate taxa were recorded: the dinosaurs *Rebbachisaurus*, *Andesaurus* (sauropods), *Gigantosaurus*, (theropod), the crocodile *Araripesuchus*, the chelid turtles, and the pipid anurans. Moreover, an important associated ichnofauna is known, composed of theropod, ornithopod, sauropod, and pterosaur tracks. This fauna is important not only because it increases the knowledge of unknown species, but also helps to understand the phylogenetic relationships of the Mesozoic taxa. The species found in this area are also relevant in testing the accuracy of current paleogeographic reconstructions, mainly between Africa and South America.
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| *Araripesuchus gomesii*  
(Price, 1959) | Aptian      | Brazil (Buffetaut and Taquet, 1979) | *Araripesuchus sp.* | Aptian      | Cameroon (Congleton et al., 1992) |
|                               | Albian      | Argentina (Gasparini et al., 1998) |                                           |             |                                |
| *Sarcosuchus imperator*  
(de Broin and Taquet, 1966) | Aptian      | Brazil (de Broin and Taquet, 1966) | *Sarcosuchus hartii* | Aptian      | Niger (Buffetaut and Taquet, 1977) |
|                               |             |                                |                                           |             |                                |
| *Araripemyidae*  
|                               |             |                                |                                           |             |                                |
| Coelacanths  
*Mawsonia*  
(Wenz, 1980) | Aptian-Albian | Brazil (Wenz, 1980) | Coelacanths  
*Mawsonia* | Aptian-Albian | Niger and Gabon (Buffetaut and Taquet, 1977) |
|                               |             |                                |                                           |             |                                |
| fish *Lepidotus*  
|                               |             |                                |                                           |             |                                |
| *Andesaurus delgadoi*  
(Calvo and Bonaparte, 1991) | Albian      | Argentina (Calvo and Bonaparte, 1991) | *Malawisaurus deyevi* | Aptian      | Malawi (Jacobs et al. 1996) |
|                               |             |                                | (Haughton, 1928; Jacobs et al., 1993) |             |                                |
|                               |             |                                |                                           |             |                                |
| *Rebbachisaurus tessonei*  
|                               |             |                                | (Lavocat, 1954) |             |                                |
|                               |             |                                |                                           |             |                                |
| *Rebbachisaurus sp.*  
(Bonaparte, 1996; Calvo and Salgado, 1996) | Albian      | Brazil (Kellner and Campos, 1996; Kellner, 1996) | *Spinosaurus aegyptiacus* | Cenomanian | Egypt (Stromer, 1915) |
|                               |             |                                | (Stromer, 1915) |                         | Niger (Taquet, 1984), |
|                               |             |                                |                                           |             |                                |
|                               |             |                                |                                           |             |                                |
| *Angaturama limai*  
|                               |             |                                | (Russell, 1996) |             |                                |
|                               |             |                                |                                           |             |                                |
| *Irritator challenger*  
|                               |             |                                | (Russell, 1996) |             |                                |
|                               |             |                                |                                           |             |                                |
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