JURASSIC TETRAPODS AND FLORA OF CAÑADÓN ASFALTO FORMATION IN CERRO CÓNDOR AREA, CHUBUT PROVINCE

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ABSTRACT

The plant and tetrapod fossil record of the Cañadón Asfalto Formation (Middle to Late Jurassic) found in Cerro Cóndor area (Chubut Province) is summarized here. The flora is dominated by conifers (Araucariaceae, Cupressaceae sensu lato) but also includes ferns and equisetaleans. The tetrapod fauna is composed of dinosaur taxa described in the 70's as well as other remains recently described and other vertebrate groups such as amphibians, turtles, and mammals. The amphibian remains have been interpreted as representatives of a new species of *Notobatrachus*, considered one of the most basal members of the anuran lineage. Similarly, turtle remains have been recently recognized as a new species of basal turtle, bringing valuable information about the early evolution of this group. The dinosaur remains are largely dominated by saurischian taxa, represented by basal forms of Eusauropoda and Tetanurae. In addition, three different mammalian species have been identified and considered as early representatives of an endemic Gondwanan mammalian fauna. The fossil record of this formation represents the most completely known biota from the continental Middle to Late Jurassic of the Southern Hemisphere and one of the most complete of the entire world.

Keywords: *Jurassic, Patagonia, Paleobiogeography, Flora, Fauna.*

RESUMEN: *Flora y tetrápodos del Jurásico de la Formación Cañadón Asfalto en el área de Cerro Cóndor, provincia de Chubut.* Se resume brevemente el registro de plantas y tetrápodos fósiles de la Formación Cañadón Asfalto (Jurásico Medio a Superior) en el área de Cerro Cóndor, provincia de Chubut. La flora está conformada por coníferas de las familias Araucariaceae y Cupressaceae sensu lato dominando la asociación, la cual se completa con helechos y equisetales en proporciones menores. La fauna de tetrápodos se compone por los clásicos dinosaurios descriptos en los 70`s, a los que se suman nuevos restos pertenecientes a este grupo, así como anfibios, tortugas y mamíferos coleccionados en la última década. Los restos de anfibios han sido interpretados como representantes de una nueva especie de *Notobatrachus*, considerado uno de los miembros más basales del linaje de los anuros. De igual modo, los restos de tortugas han sido recientemente reconocidos como una nueva especie de tortuga basal la cual aporta valiosa información acerca de la evolución temprana de este grupo. Los restos de dinosaurios se encuentran mayormente dominados por saurisquios, representados por formas basales de Eusauropoda y Tetanurae. Asimismo, tres diferentes especies de mamíferos han sido identificadas y consideradas como representantes basales de una fauna de mamíferos endémica de Gondwana. El registro de las formas clásicas en conjunto con los grupos taxonómicos recientemente descriptos, representan la biota del Jurásico Medio a Superior continental más completa de Gondwana, y una de las más completas a nivel global.

Palabras clave: *Jurásico, Patagonia, Paleobiogeografía, Flora, Fauna.*

INTRODUCTION

The Jurassic Cañadón Asfalto Formation crops out along the middle Chubut river valley (Fig. 1). This unit transitionally overlies volcanic rocks of the Lonco Trapial Formation and is uncomformably overimposed by the Cretaceous Chubut Group (Page *et al.* 1999).

Silva Nieto *et al.* (2003) have identified two members in the Cañadón Asfalto Formation: Las Chacritas in the lower section and Puesto Almada in the upper portion of the unit. The lower member is mostly dominated by lacustrine sediments with volcanic intercalations at the base, while the upper one is mainly siliciclastic and it represents a prograding fluvial system on the lacustrine previous deposits (Cabaleri *et al.* 2005). Alternatively, some of the fluvial deposits traditionally referred to the Cañadón Asfalto Formation have been considered a different unit: the Cañadón Calcáreo Formation (Proserpio 1987, Figari and Courtade 1993). From a sequence stratigraphy viewpoint, Figari *et al.* (1996) interpreted

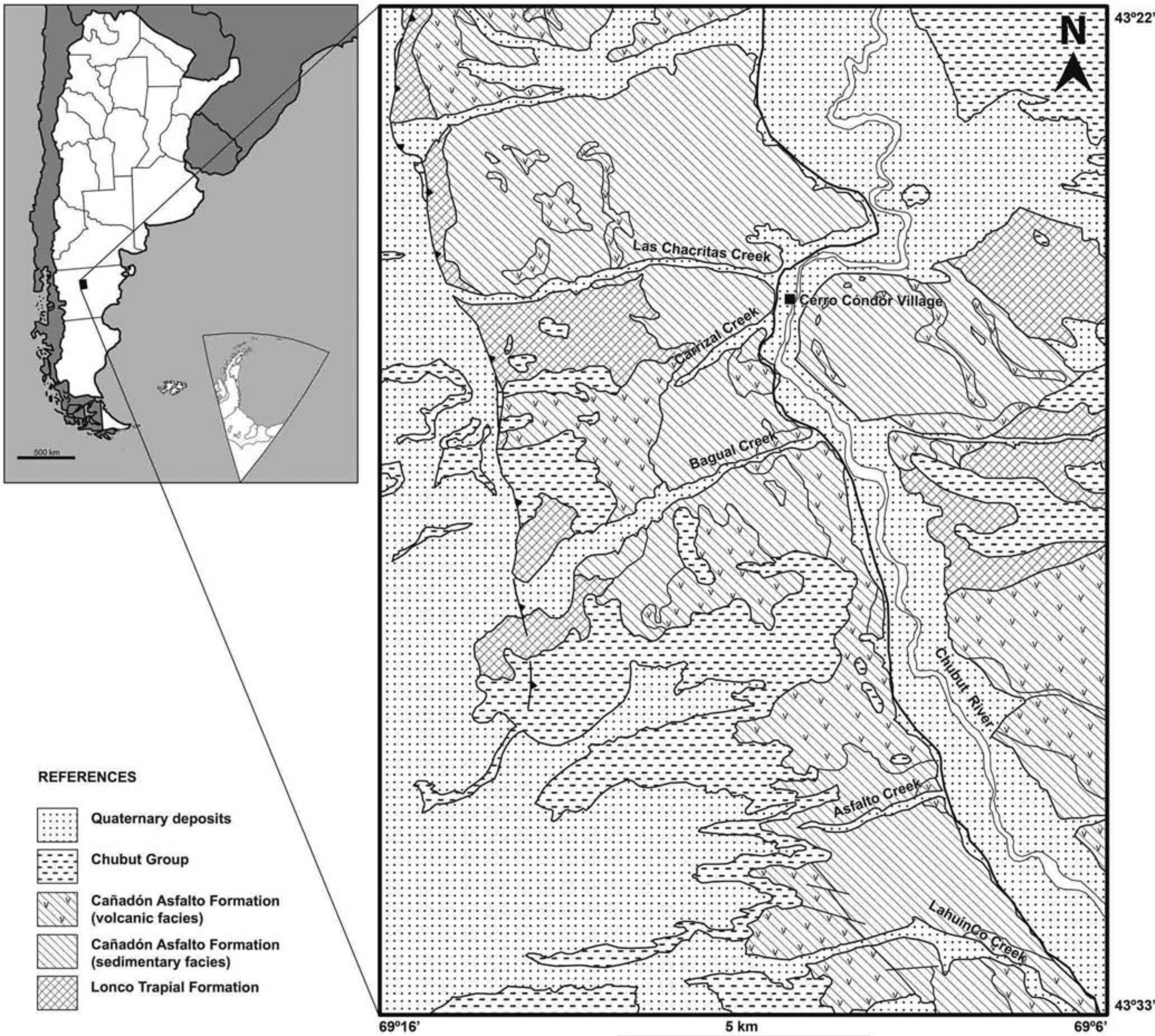

Figure 1: Geological map of the Cerro Cóndor area, Chubut Province. Modified from Silva Nieto *et al.* (2002).

the Cañadón Asfalto basin as a rift developed from the Triassic through the late Cretaceous. These authors recognized a series of four major megasequences, the second one corresponding with the Cañadón Asfalto Formation. More recently, Silva Nieto *et al.* (2007) suggested that the Cañadón Asfalto basin could be formed by several pull-apart depocenters which are not strictly contemporary. According to these authors, each one of the depocenters would constitute an isolated basin with its own evolutionary history.

In general, the Cañadón Asfalto Formation has been referred to the Middle to Upper Jurassic (Callovian-Oxfordian) based on its paleontological content (Frenguelli 1949a, Tasch and Volkheimer 1970, Volkheimer 1971, Silva Nieto *et al.* 2007). However, its age interpretation, which is mostly based on the fossils recovered around the type locality (Cerro Cóndor area), could not be entirely accurate for the remaining localities. For instance, recent palynological records from the upper section of the Cañadón Asfalto Formation in the northern area of Cerro Cóndor suggest an early Cretaceous age (Silva Nieto *et al.* 2007).

The aim of this work is to summarize recent advances in the knowledge of the Cañadón Asfalto Formation paleobiota in the Cerro Cóndor area, Chubut province. During the last ten years an intensive fieldwork has been conducted and numerous new fossil localities have been discovered. There, several new plant, reptile, mammal and amphibian taxa were unearthed from lacustrine sediments. In this contribution we are mainly focusing on fossil tetrapods and plants, although the record of fresh water invertebrates is also remarkable (Tasch and Volkheimer 1970, Silva Nieto *et al.* 2007).

Flora

Jurassic floras in southern Argentina are mostly known from Neuquén and Santa Cruz provinces, but not much has been accomplished from the Chubut province. However plant bearing sequences in Chubut province are widely distributed, including Early trough Late Jurassic deposits. Jurassic lithoestratigraphic units from Chubut province bearing plant assemblages are: 1) Taquetrén Formation (Bonetti 1964, Herbst and Anzótegui 1968, Escapa *et al.* 2008a), 2) Pampa de Agnia Group (Herbst 1966), 3) Lonco Trapial Formation (Cortés and Baldoni 1984) and 4) Cañadón Asfalto Formation (Frenguelli 1949a and b, Cortés and Baldoni 1984). In this regard, there have been constant discussions about the proper denomination of all of these geological units (see Silva Nieto *et al.* 2003 and citations therein) but no consensus has been achieved yet. For this reason, in this paper we follow the formational names such as were originally used in the description of these floras.

In particular the Middle to Late Jurassic Cañadón Asfalto taphoflora was initially reported by Frenguelli (1949a), who described a few specimens collected by Dr. Miguel Flores from probable lacustrine sediments at the Cañadón Asfalto locality (15 kilometers southern Cerro Cóndor village). Eleven taxa, including ferns, seed ferns and conifers were briefly mentioned from this locality. In a later paper, Frenguelli (1949b) described in more detail two species of the genus *Palyssia* (Coniferophyta). However, the interpretations and systematic assignations that Frenguelli made to these specimens have been highly questioned. In the same Cerro Cóndor area, from a new locality named "Frenguelli site", we collected and described numerous compression-impression plant specimens with preserved organic tissues. Along with plant remains fragmentary vertebrate remains and fresh water invertebrates have been found as well.

The new specimens from Cañadón Asfalto Formation are mostly dominated by conifer branches, seed and pollen cones and isolated seeds with minor amounts of equisetaleans, ferns and possible seed ferns. The conifers represent about 90 percent of the specimens recovered while all the remaining groups represent the 10 percent remnant. The high number of specimens collected has allowed a de-tailed description of some taxa, specialy conifers referred to Araucariaceae and Cupressaceae *sensu lato* families. One of the most relevant characteristics of the flora is the complete absence of Cycadophyta (Cycadales and Bennetittales) and Ginkgophyta, which are usually dominant in Early Jurassic floras. The anomalous absence of these plant groups during the Middle and Late Jurassic in Cerro Cóndor, which is reverted from the Early Cretaceous, could probably be a response to certain broad environmental/paleoclimatic changes associated with the dynamics of paleoclimatic belts during the Jurassic (Rees *et al.* 2000).

Equisetales: Several specimens of *Equisetum*-like (Equisetaceae) axis and foliage have been recovered from the Frenguelli site (Fig. 2e). The specimens collected are represented by articulate vegetative shoots, with internodes bounded by foliar whorls. The leaves show a basal sheath and a distal free part always shorter than the sheath.

Equisetalean remains of Jurassic-Cretaceous age have been normally referred to the form-genus *Equisetites*, even though not significant morphological differences distinguish it from the extant genus *Equisetum*. The low number of differences observed between them could have a taphonomic explanation more than a real morphological base. Other equisetalean genus mentioned from some Jurassic localities is *Neocalamites*, which is more common for Triassic outcrops. Opposite to our specimens, *Neocalamites* shows leaves with a reduced or absent foliar sheath and linear leaves always longer than the sheath.

Ferns: The ferns are a minor component at Frenguelli site, but they are represented by at least two morphospecies (see also Frenguelli 1949a). The low representation of Pteridophyta in this locality is probably related with taphonomic bias more than with a real representation of the original flora. Considering that this plant assemblage is dominated by plant parts with higher preservational potential (*e.g.* conifers branches, cones, seeds), a high degree of selection and allochthonous conditions ruled plant burying deposition.

Most of fern remains are assignable to the genus *Sphenopteris* (Fig. 2f), a morphotaxon used to characterize only vegetative parts. It is interesting to note that some additional fern-like remains are probably related to pteridosperms (seed ferns), a group that shows vegetative systems similar to true ferns.

Araucariaceae: Conifers of this family are represented in the Frenguelli site by numerous well preserved leafy twigs, female cones (Fig. 2d), and isolated ovuliferous complexes of at least two species, one of them previously reported as *Araucarites cutchensis* (Frenguelli 1949a). Even when ovuliferous complexes of Araucariaceae show relatively high size variation within individual species (see Harris 1979, Rees and Cleal 2004), it cannot explain the two principal morphologies observed in our specimens. Therefore, the size range and morphology between the Cañadón Asfalto Formation specimens do not correspond with two ontogenetic steps of the same species, since both present mature characters such as a prominent central seed and a distal ligule (Fig. 2a). The presence of Araucariaceae of at least two very distinctive sizes constitutes a common feature with other Mesozoic localities from Argentina (e.g. *Araucarites baqueroensis* and *A. minumus*, Archangelsky 1966).

The Araucariaceae family shows a Southern Hemisphere distribution, but during the Mesozoic it was present in both Hemispheres (see Florin 1940, Stockey

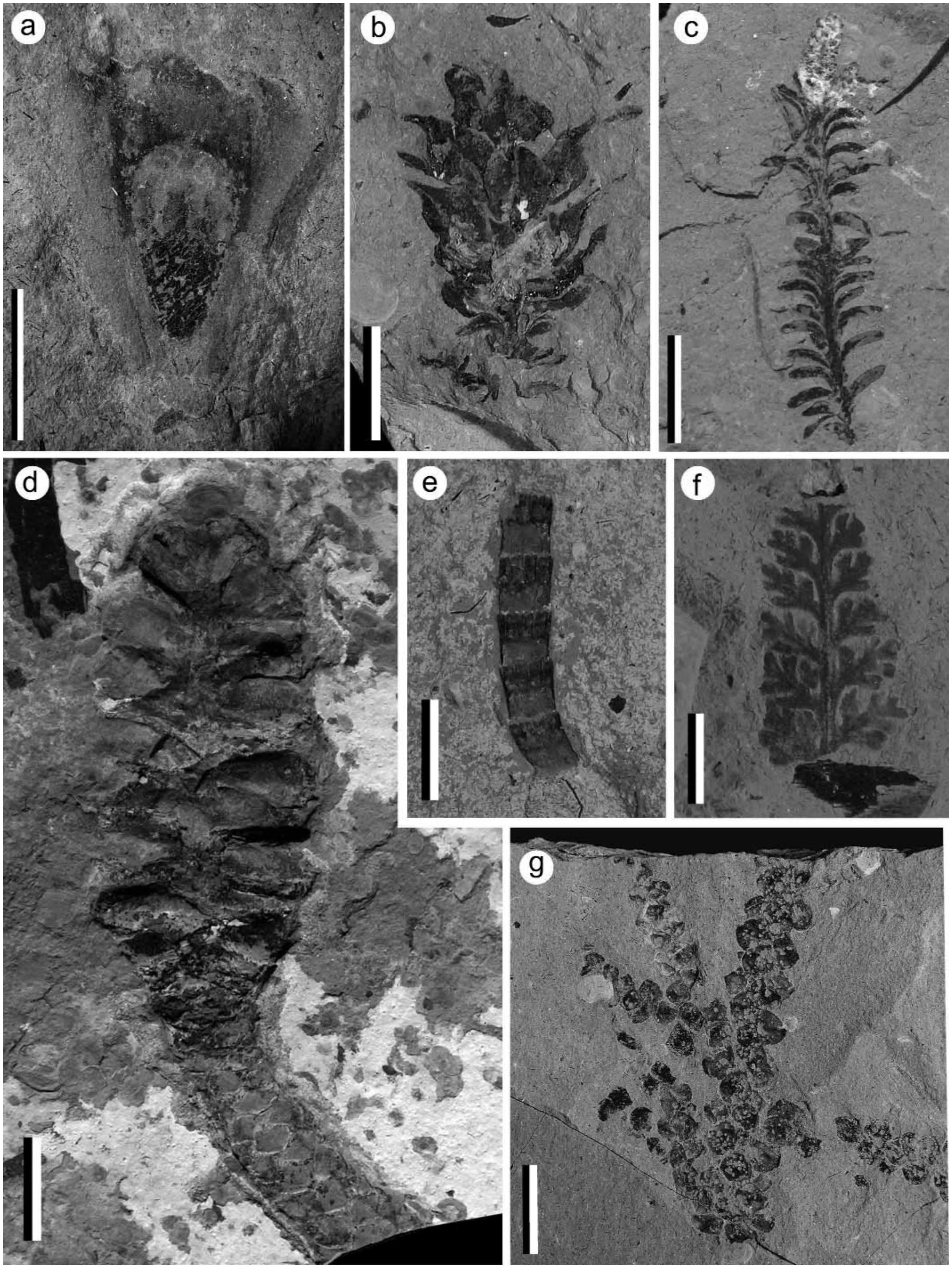

Figure 2: Flora of Frenguelli site, cañadón Lahuinco, Cerro Cóndor area. a) *Araucarites cutchensis ovuliferous* complex (MEF-Pb 1794). Scale bar 0.5 cm b) Cupressaceae *sensu lato* ovuliferous cone (MEF-Pb 2463). Scale bar 1 cm. c) Cupressaceae *sensu lato* pollen cones organically attached to leafy twigs of *Elatocladus* sp (MEF-Pb 2429). Scale bar 1 cm. d) *Araucaria* sp. Ovuliferous cone organically attached to a branch of *Brachyphyllum* sp. (MEF-Pb 1647). Scale bar 1cm. e) *Equisetum* sp. Fragment of ribbed axis showing foliar whorls on nodes (MEF-Pb 2008). Scale bar 1 cm. f) *Sphenopteris* sp. (MEF-Pb 2015). Scale bar 0.5 cm g) *Brachyphyllum* sp. (MEF-Pb 1803). Scale bar 1cm.

1982, 1994, Stockey and Ko 1986, Del Fueyo and Archangelsky 2002 and references therein), specially *Araucaria* (and associated morphogenera). Particularly in Patagonia, Araucariaceae played an important role in most Jurassic and Cretaceous environments as indicated by its wide distribution and abundance (see Spegazzini 1924, Frenguelli 1949a, Calder 1953, Stockey 1978).

In some particular cases, the ovuliferous cones have been found organically attached to leafy twigs. The general morphology of the branches is comparable to some species of *Brachyphyllum* morphogenus. Cuneate leaves are arranged in a helix closely appressed to the shoot axis. Isolated vegetative shoots present occasional branches that show an irregular arrangement.

Cupressaceae sensu lato: Conifers previously reported as *Palyssia* (Frenguelli 1949 a and b) have been recently included in Cupressaceae *sensu lato* (= Taxodiaceae + Cupressaceae *sensu stricto*) since the new specimens (Figs. 2b and c) show a combination of reproductive-vegetative characters typical for the basal forms of this family (Escapa *et al.* 2008b). The seed cones are normally single and terminally attached to distal branches. They show a simple organization, represented by helically disposed bracts, which support small, inverted ovules. The bracts are rhomboidal in shape with an acute apex and a quite distinctive abaxial keel. On the other hand, the pollen cones are terminally disposed in clusters. Vegetative organs are organized in two orders of branching that are covered by helically inserted univein leaves, dorsiventrally flattened with a decurrent insertion and a distal free part, mostly diverging from the axis in one plane producing a distichous appearance. Leafy twigs of this morphology, when are found isolated, are normally included into the morphogenus *Elatocladus*.

It is interesting to note that the oldest record of Cuppressaceae *s.l.* in the Southern Hemisphere is dated back to the late Early Cretaceous of Argentina (Halle 1913, Archangelsky 1963, Villar de Seoane 1998, Llorens and Del Fueyo 2003), represented by vegetative and reproductive organs of *Athrotaxis ungeri*. Following this, the Middle Jurassic Cupressaceae *s.l.* of Cañadón Asfalto Formation, together with another species recently described (Escapa *et al.* 2008b), could represent the oldest record of the family for the Southern Hemisphere, and one of the oldest at global level.

Other conifers: Some specimens bound vegetative shoots that due their morphology cannot be assigned to any of the mentioned families. The general morphology of these specimens is comparable with the morphogenera *Pagiophyllum* and *Brachyphyllum* (Fig. 2, g). However, without cuticular or reproductive characters it is not possible to relate these leafy twigs with any natural group because some species of this morphogenus have been found in organic connection with reproductive structures of different conifer families (*e.g.*, Araucariaceae, Cheirolepidaceae).

Tetrapod fauna

The tetrapod record of the Cañadón Asfalto Formation is the most diverse Jurassic assemblage in South America. In particular, this unit contrasts with the fragmentary remains recovered in other Jurassic units of Patagonia, including Roca Blanca (Lower Jurassic), Cerro Carnerero (Lower to Middle Jurassic), and Tordillo (Upper Jurassic) formations. The only possible exception is the Cañadón Calcáreo Formation where well preserved remains of three dinosaur taxa have been recently found (Rich *et al.* 1999, Rauhut *et al.* 2005, Rauhut 2006), although some authors have recently suggested that the age of this unit is Lower Cretaceous rather than Upper Jurassic (Silva Nieto *et al.* 2007).

The first tetrapod record of the Cañadón Asfalto Formation was published by Bonaparte (1979) who discovered a sauropod bone-bed in the vicinities of Cerro Cóndor village, from which he described three dinosaur taxa (*Patagosaurus fariasi* Bonaparte, *Volkheimeria chubutensis* Bonaparte, and *Piatnitzkysaurus floresi* Bonaparte). Subsequent field work conducted during the 80's by Bonaparte resulted in a large number of dinosaur remains from this unit (most of which have been referred to *P. fariasi*). The known tetrapod diversity from this unit has been significantly increased in the last five years, mainly through the development of collaborative projects conducted by Dr. Oliver Rauhut, Dr. Guillermo Rougier, and the Museo Paleontológico Egidio Feruglio (Trelew). The results of these projects have provided not only new dinosaur taxa but also new taxa from other taxonomic groups, including amphibians, mammals, turtles, and pterosaurs.

Amphibians: Frog remains recently collected from the Zitarroza site in the Cañadón Bagual locality have been interpreted as a new species of *Notobatrachus*, *N. reigi* Báez and Nicoli (2008). The holotype is represented by a single specimen preserved as partially articulated cranial (mandible, suspensorium and maxillary arch remains) and postcranial impressions. Additional cranial and postcranial disarticulated material, also referable to this species, has been found in sediments of the Queso Rallado and Frenguelli localities. *Notobatrachus reigi* is a large-sized frog (Fig. 3) that shares with the type species of the genus, *N. degiustoi*, not only its morphology and general proportions but also the presence of a parasphenoid with a trifid cultriform process, a long maxilla with a dorsally directed pars palatina, amphicoelous presacral vertebrae, free ribs associated with robust transverse processes, cleithrum medially expanded, radioulna lacking a well-developed olecranon process, a discrete intermedium in the carpus, and unfused tibiale and fibulare. However, a maxilla with a distinct pterygoid process and lacking teeth at least along the posterior two-thirds of its length) and a complete maxillary arch distinguish this species from *N. degiustoi*.

Living toads and frogs conform a well-corroborated monophyletic assemblage named Anura (Frost *et al.* 2006). *Notobatrachus* posses many but not all of the derived features that characterize this assemblage, thus, although its relationships have been discussed, it has been always considered one of the most basal members of the anuran lineage (Stipanicic and Reig 1957, Casamiquela 1961, Hecht 1962, Griffiths 1963, Estes and Reig 1973, Báez and Basso 1996, Rocek 2000, Gao and Wang 2001, Gao and Chen 2004). In the last years, the inclusion of *Notobatrachus* in several phylogenetic analyses has corroborated its basal position, which is even basal to the common ancestor of all extant species (Báez and Basso 1996, Gao and Wang 2001, Gao and Chen 2004). Consequently, this Jurassic frog is not contained in Anura but in Salientia, the more inclusive taxon that encloses Anura and all amphibians more closely related to anurans than to salamanders.

It is interesting to note that, even when the Triassic and Jurassic fossil record of salientians is scarce and fragmentary, *Notobatrachus* is especially well preserved. The type species, *Notobatrachus degiustoi* is superbly preserved as numerous, fine impressions of disarticulated and partially articulated skeletons, even at different ontogenetic stages (Estes and Reig 1973, Báez and Basso 1996, Báez and Nicoli 2004). All the specimens of *N. degiustoi* have been recorded in many outcrops of the La Matilde Formation of the Deseado Massif area in the Santa Cruz province. Notoriously, the single other species known from pre-Cretaceous sequences in South America until now, *Vieraella herbsti*, also comes from southern Patagonia, particularly the Early Jurassic Roca Blanca Formation of Santa Cruz. This species, however, is represented by only one specimen, preserved as incomplete, partially articulated ventral and dorsal impressions (Reig 1961, Estes and Reig 1973, Báez and Basso 1996). Few other remains, either ascribed to the crown-group Anura or considered as outside the anuran node, have been described from Triassic and Jurassic rocks outside South America. Only two species, considered the most basal known salientian (Ford and Cannatella 1993, Báez and Basso 1996, Gao and Wang 2001) have been recovered from Triassic sediments: *Triadobatrachus massinoti*, represented by a single, incomplete, partially articulated specimen from the Lower Triassic of Madagascar (Piveteau 1937, Estes and Reig 1973, Rage and Rocek 1989, Rocek and Rage 2000), and *Czatkobatrachus polonicus*, known from disarticulated bones of the Early Triassic fissure deposits at the Czatkowice locality in Poland (Evans and Borsuk-Bialynicka 1998, Borsuk-Bialynicka and Evans 2002). The Jurassic fossil frogs collected outside South America are not significantly more abundant: *Rhadinosteous parvus* from Late Jurassic Morrison Formation of Utah (Henrici 1998) and *Prosalirus bitis* from the Early Jurassic Kayenta Formation of Arizona (Shubin and Jenkins 1995, Jenkins and Shubin 1998), both only known by fragmentary, disarticulated material, and *Eodiscoglossus santojae*, from the Late Bathonian of Spain, represented by several specimens partially articulated (Hecht 1970, Estes and Reig 1973, Evans *et al.* 1990, Sanchiz 1998). Most of these Mesozoic species already posses the derived, particular anatomy that characterize anuran and, thus, they do not contribute significantly to our understanding of the sequence of acquisitions that conduce to that particular Bauplan or of the processes that underlie its evolution. In summary, although recent studies based on DNA sequences of living amphibian have suggested that the origin of Anura should have occurred in the Triassic (Roelants and Bossuyt 2005, Roelant *et al.* 2007), or even earlier (San Mauro *et al.* 2005), the fossil record of this lineage is still deficient. In this context, the presence of a relatively well-preserved basal salientia in the Cañadón Asfalto Formation not only contributes to our knowledge of the early evolutionary history of the anuran, but also invites us to continue working in this sequence considering the potentiality of its content of fossil frogs.

Turtles: Turtle remains, represented by cranial and postcranial elements have been found in Queso Rallado locality (Fig. 4). These remains were identified as a new species named *Condorchelys antiqua* by Sterli (2008). The peculiar mixture of plesiomorphic (such as the presence of an open interpterygoid vacuity, a primitive basicranium, broad vertebral scutes in the carapace, among others) and derived characters (such as the morphology of the tympanic cavity, the absence of teeth, among others) found in this turtle suggests that *C. antiqua* does not belong to any of the modern turtle groups, but it represents an earlier stage in turtle evolution (Sterli 2008). This result agrees with the hypothesis proposed by Joyce (2007) about turtle evolution where some fossil turtles had differentiated before the split of modern turtles into the two main extant groups (Cryptodira and Pleurodira).

The new data brought by this new species from Cerro Cóndor, together with the results obtained by Joyce (2007) and Sterli and Joyce (2007), shed new evidence to understand the early history of this clade and, consequently, the origin of modern turtle groups. The oldest almost complete turtle remains were found in the Upper Triassic of Germany and Argentina, however isolated fragments of turtles were found in other localities in Thailand and Greenland (Baur 1887, Fraas 1913, Broin 1985, Jenkins *et al.* 1994, Rougier *et al.* 1995). All these discoveries around the world during the Upper Triassic show that turtles were well-spread by that time and that they should have originated before. During the Lower Jurassic the fossil turtle record is sparse and only three species were described. The most complete of these findings is *Kayentachelys aprix* (North America) represented by cranial and postcranial remains (Gaffney *et al.* 1987). The other two Lower Jurassic turtles are not so complete: one is represented only by an isolated skull that was assigned to *Australochelys africanus* (South Africa) and the other finding is represented only by a carapace and a plastron assigned to *Indochelys spatu-*

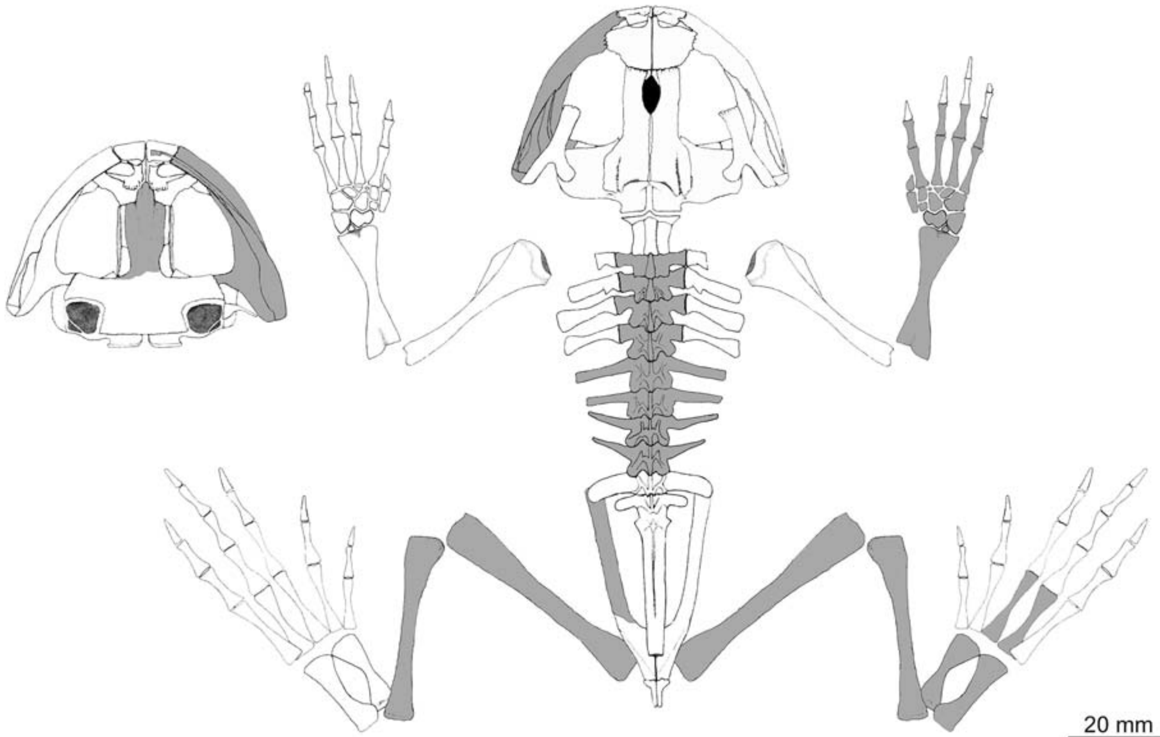

Figure 3: Skeletal reconstruction of *Notobatrachus reigi* from the Cañadón Asfalto Formation at Cerro Cóndor, based on the reconstruction of *N. degiustoi* (Báez and Nicoli, 2004). a) Skeleton in dorsal aspect, pectoral girdle and hyobranchial skeleton not shown. b) Skull in ventral aspect. References: in grey, bones attributed to *N. reigi* (catalogued as MPEF-PV 3006, 3045, 3051, and 3181), in white, unknown elements.

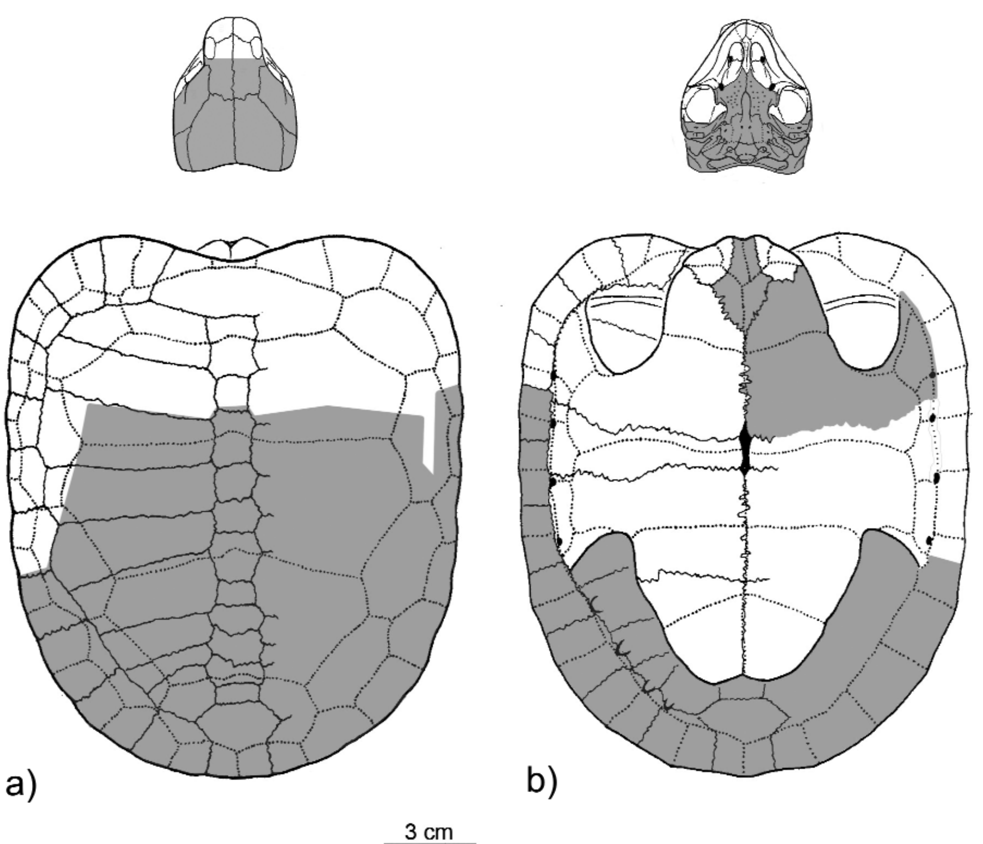

Figure 4: Turtle remains found in the Cañadón Asfalto Formation at Cerro Cóndor (Queso Rallado locality) and shown in the reconstruction of the closely related turtle *Kayentachelys aprix* from the Lower Jurassic of Kayenta Formation, USA (modified from Gaffney *et al.* 1987). a) Dorsal view of the skull and carapace. b) Ventral view of the skull and carapace. References: in grey, turtle remains found in Queso Rallado Locality (based on MPEF-PV 1152 -holotype-, MPEF-PV 1783A, B and C, MPEF-PV 3131, MPEF-PV 3132, MPEF-PV 3134, MPEF-PV 3136, MPEF-PV 3147, and MPEF-PV 3160), in white, unknown elements.

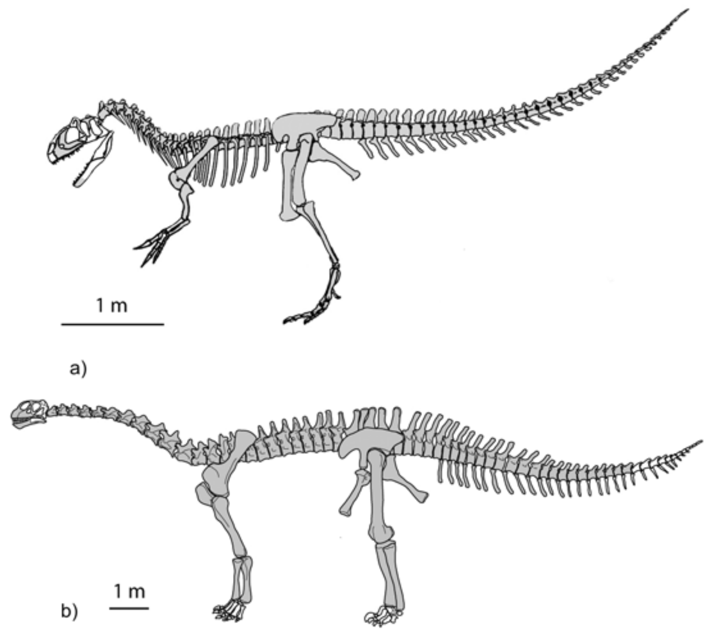

Figure 5:. Skeletal reconstructions: a) *Piatnitzkysaurus floresi* (based on PVL 4073 and MACN-PV CH895) and b) *Patagoasurus fariasi* (based on PVL 4170, PVL 4076, MACN-PV CH932, MACN-PV CH933, MACN-PV CH935, MACN-PV CH936) from the Cañadón Asfalto Formation the Cañadón Asfalto Formation at Cerro Cóndor. References: in grey, elements known from the holotype or referred specimens, in white, unknown elements.

lata (India) (Gaffney and Kitching 1994, Datta *et al.* 2000). During the Middle Jurassic the turtle record continues being scarce and fragmentary and only few species from Russia, Thailand, China and Mongolia were described (Tong *et al.* 2002, Matzke *et al.* 2004, Sukhanov 2006). Fortunately, from the Upper Jurassic to the present, the fossil turtle record is more abundant, and it shows that during the Upper Jurassic turtles spread over other environments like lagoons and open seas. *Condorchelys antiqua* represents the oldest continental turtle from the Jurassic of South America. Regarding the tempo and mode in the diversification of living turtle groups, there are two main hypotheses. Some authors believe that all living and fossil turtles (with the exception of some fossil turtles) belong to some of the two clades of living turtles, Pleurodira or Cryptodira (Gaffney *et al.* 2007). On the contrary, other authors pointed out that many fossil turtles do not belong to any of the living turtle clades, instead of that, they would have originated previously to the differentiation of the crown-group turtles (Joyce 2007). Following the first hypothesis, the crown-group turtles should have originated as soon as the oldest known turtle appeared during the Upper Triassic. However, following the second hypothesis, the turtle crown should have appeared during the Middle to Late Jurassic. As both hypotheses differ in a time span of 60 million years approximately (between Upper Triassic and Middle Jurassic), all the findings belonging to that period of time are very important to understand basal turtle relationships and the origin and diversification of living turtles. It is in this context where *Condorcheys antiqua* from the Middle to Upper Jurassic Cañadón Asfalto Formation becomes an important fossil in turtle evolution.

Mammals: Several mammalian specimens (Mammalia *sensu* Luo *et al.* 2002), which represent at least three species of two different mammalian groups, have been recovered from the Queso Rallado Locality (Rauhut *et al.* 2002, Rougier *et al.* 2007a, b). Among them, the recently erected *Argentoconodon fariasorum* (Rougier *et al* 2007 b) is only known, until now, from an isolated molariform that possesses a combination of plesiomorphic and derived features. This molar is characterized by a distinctly crown dominated by a longitudinal series of three major cups, a morphology traditionally described as a triconodont molariform. Triconodont teeth are common during the Jurassic in the Laurasian landmasses and occur in several mammalian groups (*e.g.* Morganucodontidae, Amphilestidae, Triconodontidae, etc.), having apparently appeared independently in each lineage, and, thus, its presence is not useful to establish phylogenetic relationships and taxonomic assignments (Rougier *et al.* 2007b). This, together with the fragmentary condition of *Argentoconodon* only allowed Rougier *et al.* (2007b) to attribute this species to the Theriimorpha clade.

The other two recently discovered and described mammalian species of Cañadón Asfalto Formation are *Asfaltomylos patagonicus* (Rauhut *et al.* 2002, Martin and Rauhut 2005) and *Henosferus molus* (Rougier *et al.* 2007a). Both share a derived tribosphenic molar pattern associated with plesiomorphic mandibular features (like the presence of a mandibular trough that could be related with the presence of postdentary bones partially attached to the lower jaw). These taxa have been interpreted as sister taxa, integrating the family Henosferidae (Rougier *et al.* 2007 a). Henosferidae represents a basal member of Australosphenida, an assemblage of Gondwanan mammals that probably also includes Monotremata (Luo *et al.* 2002, Rauhut *et al.* 2002, Martin and Rauhut 2005, Rougier *et al.* 2007a). The presence of a tribosphenic molar pattern in this group suggests that this pattern had evolved independently in two distinct mammal lineages, the Gondwanan Australosphenida and the Laurasian assemblage named Boreosphenida (Luo *et al.* 2002). It is interesting to note that the other single Jurassic Australosphenida and also the oldest known representative of the group, *Ambondro mahbo*, has been recovered from Bathonian sediments of the Mahajanga Basin of Madagascar (Flynn *et al.* 1999), suggesting an extensive spread of this group in Gondwana during Middle Jurassic times (Rauhut *et al.* 2002).

The similarities of *Argentoconodon fariasorum* with other taxa distributed in Laurasia, in addition to the combination of plesiomorphic and derived features found in this taxon and also in *Asfaltomylos patagonicus* and *Henosferus molus*, allowed Rougier *et al.* (2007b) to consider them as early representatives of an endemic Gondwanan mammal fauna not yet fully differentiated from the Laurasian forms during the Middle to Upper Jurassic. In summary, these findings, considering their age and putative phylogenetic relationships, have provided invaluable new evidence about the early evolution of mammals.

Dinosaurs: Two major groups of dinosaurs have been so far described from the Cañadón Asfalto Formation: Sauropoda and Theropoda.

Sauropod dinosaurs constituted the major component of the herbivorous fauna given their abundance in this formation, as also occur in most Jurassic and Cretaceous faunal assemblages of the Southern Hemisphere. The sauropod fossil record of the Cañadón Asfalto Formation is particularly important for understanding the evolution of this group. The diversification of the major sauropods lineages occurred in the Jurassic, including the appearance of forms with body sizes exceeding those of any other terrestrial organism (an evolutionary trend that continued during the Cretaceous). Two sauropod taxa have been described by Bonaparte (1979), *Volkheimeria chubutensis* and *Patagosaurus fariasi* (Fig. 5b), although Rauhut (2003) noted the possible presence of a third sauropod taxon among the specimens referred to *Patagosaurus*. The former is only known from a series of presacral vertebrae, pelvic, and hindlimb remains. The dorsal vertebrae show a series of plesiomorphic (primitive) characters (Bonaparte 1999), some of which resemble the condition of *Lapparentosaurus*, another fragmentary taxon known from the Middle Jurassic of Madagascar (Bonaparte 1999). Although more remains of this form are needed, *Volkheimeria* seems to represent a very early stage in the evolution of Sauropoda. *Patagosaurus*, instead, is known from a large number of remains (Bonaparte 1986, see also Coria 1994 and Rauhut 2003) and constitutes the best known basal eusauropod form the Southern Hemisphere. Basal eusauropods dominated the herbivorous fauna in the Middle Jurassic assemblages of other regions (*e.g.* Europe, Russia, China) and form the ancestral stock that gave origin to Neosauropoda (the group the later diversified and dominated the sauropod fossil record from the Late Jurassic to the Late Cretaceous). *Patagosaurus fariasi* has been traditionally compared with other Jurassic taxa from India (*Barapasaurus*), China (*Shunosaurus, Omeisaurus*), all of which form the set of basal eusauropods in recent phylogenetic analyses (Upchurch 1998, Wilson 2002). These forms, however, do not form a natural taxonomic group but rather represent a set of different stages of the early evolutionary history of Eusauropoda. The worldwide distribution of all these primitive forms shows that, so far, there is no evidence of regional differences during the radiation of eusauropod dinosaurs during the Middle Jurassic.

Theropods are the only carnivorous group of Dinosauria and have a broad fossil record from the Late Triassic. Two taxa are known from the Cañadón Asfalto Formation: *Piatnitzkysaurus floresi* (Bonaparte 1979) (Fig. 5a) and *Condorraptor currumili* (Rauhut 2005). As in the case of the above mentioned sauropods, these taxa also form part of a primitive stock of theropods known as basal Tentanurans. Although *Piatnitzkysaurus* and *Condorraptor* may have been very closely related forms (Smith *et al.* 2007), they form along with other basal tetanuran theropods a worldwide distributed assemblage of taxa in recent phylogenetic analyses (Smith *et al.* 2007), which reinforces the hypothesis of a Middle Jurassic dinosaur fauna of pangeic distribution.

CONCLUSIONS

The fossil record of Cañadón Asfalto Formation represents the most complete taxonomic sampling of the continental Middle Late Jurassic of Gondwana, and one of the most complete at global level. In addition to the classic dinosaur biota described in the 70`s, new taxonomic groups are now represented as a result of ten years of field works in Cerro Cóndor area. New represented taxa include equisetaleans, ferns and conifers among plants and amphibians, turtles, dinosaurs, and mammals, among tetrapods.

The known tetrapod taxa from the Cañadón Asfalto Formation include members of groups with a worldwide distribution, denoting the lack of faunal differentiation between the southern and northern hemisphere by the Middle-Late Jurassic. The only exception to this pattern is the presence of australosphenids, a clade of small mammals only known from the Southern Hemisphere. The faunal assemblage from the Cañadón Asfalto Formation is relevant not only from a biogeographical point of view but also because they represent early members of the major Mesozoic radiation of their respective groups (*e.g.* sauropods, theropods, turtles, anurans). These taxa thus shed light on several evolutionary problems that were classically based on evidence from the Northern Hemisphere.

An interdisciplinary approach to these forms, as well as the analysis of the paleobiogeographic and biostratigraphic significance of these records, will provide an integrative and supported reconstruction of this Patagonian environment and its worldwide significance for un-derstanding the evolution of the Jurassic continental biota.

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