# JURASSIC PALEOCLIMATES IN ARGENTINA, A REVIEW

### Wolfgang VOLKHEIMER<sup>1</sup>, Oliver W. M. RAUHUT<sup>2</sup>, Mirta E. QUATTROCCHIO<sup>3</sup> and Marcelo A. MARTINEZ<sup>3</sup>

<sup>1</sup> Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA), CCT - CONICET - Mendoza, Argentina. E-mail: volkheim@lab.cricyt.edu.ar

<sup>2</sup> Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany. E-mail: o.rauhut@lrz.uni-muenchen.de

<sup>3</sup> INGEOSUR (Instituto Geológico del Sur)-CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas). Universidad

Nacional del Sur, Departamento de Geología, Bahía Blanca, Argentina. E-mail: mquattro@criba.edu.ar; martinez@criba.edu.ar

### ABSTRACT

New paleoclimatic evidence from palynologic and vertebrate proxies provides more detailed data on climatic change during the Jurassic in Argentina. Comparison with paleomagnetic data shows that the Neuquén basin shifted from the highest paleolatitudes (50°S), by the end of the Triassic until the end of the Sinemurian. During the Pliensbachian-Toarcian it moved northward, reaching the lowermost paleolatitudes (25°S), and subsequently (Middle to Late Jurassic) the area moved again and attained eventually a position similar to its present-day position (30°S). These movements are reflected in the Jurassic palyno-floras. The high frequency of the pollen genus *Classopollis* (Cheirolepidiacean gymnosperms) is of special paleoclimatic importance in the Argentinian Jurassic, as it is indicative of seasonal aridity or semiarid conditions during large intervals of this Period. During the shift of the South American continent to the northernmost position, the arrival of an important group of Araucariaceae, represented by *Callialasporites* spp., in the Toarcian could indicate an amelioration related to more humid conditions. Jurassic dinocyst assemblages studied in the Neuquén basin have proved to be useful paleoclimatic and paleobiogeographic proxies. Abundant remains of marine crocodiles in the Mid- and Late Jurassic of the Neuquén basin indicate warm water temperatures for this basin, probably in excess of 20° C. The occurrence of abundant turtles and other ectothermic vertebrates in the Middle Jurassic Cañadón Asfalto Formation of Chubut is in general accordance with the warm climate indicated for this unit by geologic evidence.

Keywords: Paleoclimate, Jurassic, Argentina, Vertebrate evidence, Palynology.

**RESUMEN:** *Paleoclimas jurásicos en la Argentina, una revisión.* Nuevas evidencias de indicadores paleoclimáticos (palinológicos y de vertebrados) suministran datos detallados sobre los cambios climáticos en el Jurásico de la Argentina. La comparación con datos paleomagnéticos muestra como, desde fines del Triásico hasta el Sinemuriano Tardío, la cuenca Neuquina derivó ocupando las posiciones más australes (50°S). Durante el Pliensbaquiano-Toarciano se movilizó hacia el norte, alcanzando las más bajas latitudes (25°S), para luego ocupar, durante el Jurásico Medio y Tardío, posiciones similares a las actuales (30°S). Estos movimientos se reflejan en las palinofloras jurásicas. La alta frecuencia de polen del género *Classopollis* (Cheirolepidiaceae, gimnospermas) es de especial importancia paleoclimatológica, ya que indica aridez estacional o condiciones semiáridas durante largos intervalos de este Período. Durante la deriva del continente sudamericano a su posición más septentrional en el Toarciano, la llegada de un importante grupo de araucariáceas, representado por *Callialasporites* spp., indicaría el comienzo de condiciones climáticos y la evaluación paleobiogeográfica de las asociaciones de quistes de dinoflagelados en la cuenca Neuquina. Frecuentes restos de cocodrilos marinos en el Jurásico Medio y Tardío de la cuenca Neuquina indican temperaturas de aguas cálidas para esta cuenca, de probablemente más de 20°C. La presencia de abundantes tortugas y otros vertebrados exotérmicos en el Jurásico Medio de la Formación Cañadón Asfalto de Chubut está de acuerdo con las condiciones de clima cálido generalizadas, indicadas para esta formación por la evidencia geológica.

Palabras clave: Paleoclima, Jurásico, Argentina, Paleovertebrados, Palinología.

## INTRODUCTION

This brief essay mainly intents to be a critical revision of earlier contributions on Jurassic paleoclimates of southwestern Gondwana, especially through evaluation of new data in vertebrate paleontology and continental and marine paly-

#### nology.

From a palynological viewpoint, the uniformity of Jurassic and earliest Cretaceous floras appears to be more apparent than real (Batten 1984). A modern review of the knowledge on distribution, diversity, and paleogeographic and paleoenvironmental significance of Jurassic floras and palynofloras of Argentina is given by Quattrocchio *et al.* (2007).

The paleoclimatic situation of Argentina during the Jurassic Period was conditioned by its geographic position in midpaleolatitudes of southwestern Gondwana. Gondwana became part of the supercontinent Pangaea in the Permian. The disintegration of Pangaea/Gondwana during the Mesozoic is important for the climatic evolution during the Jurassic, when drying occurred in Gondwana, which was interpreted as indicative of the breakdown of the Pangean Megamonsoon (Parrish 1993).

# PALEOCLIMATIC INDICATORS

### a) Sporomorphs

Large numbers of Classopollis pollen in Mesozoic deposits are generally thought to reflect an abundance of representatives of Cheirolepidiacean gymnosperms of lowland vegetation, when the climate was at least seasonally dry or semiarid (Batten 1975). Alvin (1982) suggests that some species of cheirolepids undoubtedly were adapted to coastal environments and may have formed extensive coastal forests as the main components of a halophytic, salt-marsh community. Cheirolepidiaceae occupied a wide range of warm and semiarid habitats, and some groups were probably associated with freshwater environments (both lakes and rivers), or even inhabited freshwater stream banks or low-lying areas dissected by braided streams that may have dried out seasonally or irregularly (Alvin 1983). Other Cheirolepidiaceae may have been characteristic for higher, better drained soils. Maximal abundances of Classopollis have been correlated with evidence of warmth and aridity (Vakhrameev 1981, 1987).

### b) Dinoflagellate cysts

The Liassic until Bajocian Jurassic dinocyst assemblages of the Neuquén basin (Fig. 1) are characterized by low specific diversity and predominance of acavate proximate cysts. Chorate/acavate ratios increase during the Callovian and the Tithonian and specific diversity increases during the Jurassic. Chorate species are getting common in the Callovian and increase during the Late Jurassic (Fig. 2). The same tendency is registered offshore eastern Canada, at 25-30° northern paleolatitude, possibly reflecting warming trends in the Late Jurassic.

### c) Vertebrates

Vertebrates, especially ectothermic terrestrial forms, have proved to be useful as climate proxies in palaeoclimatic studies of mainly Cenozoic environments (e.g. Markovick 1998, Böhme 2003), and they might be helpful to interpret Mesozoic climates as well (e.g. Vandermark et al. 2007), though additional caution is needed when dealing with extinct groups (see Ostrom 1970). The record of Jurassic vertebrates from Argentina is still rather patchy, though a variety of dinosaurs, marine crocodiles, and a few other groups have been reported.

Although dinosaurs were sometimes used as climate proxies, allegedly indicating warm climates (e.g. Romer 1961, Colbert 1964), they seem to be poorly suited for these purposes, due to uncertainties regarding their physiology (Ostrom 1970). Indeed, recent finds of even sauropod dinosaurs at high latitudes (see Smith and Pol 2007) indicate that dinosaurs cannot reliably be used to interpret paleoclimates. The same applies to other groups, such as the pterosaurs, and caution is even needed when interpreting climates on the basis of larger taxonomic units that have living representatives, but are represented in the fossil localities under study solely by lineages that lie outside the radiation of the recent forms, such as crocodiles (Ostrom 1970, Markovick 1998). Keeping these restrictions in mind, some observations on possible climatic implications of the Jurassic vertebrates from Argentina will be offered.

Marine crocodiles, mainly of the family Metriorhynchidae, have been reported from both the Middle and the Late Jurassic of Argentina, principally from marine sediments of the Neuquén basin (Gasparini 1985, 1992, Gasparini *et al.* 2005, Pol and Gasparini 2007). Although the cautions noted above certainly apply for these extinct thalattosuchians, it might be noted that recent amphibious crocodiles seem to prefer water temperatures in excess of 24° C (Markovick 1998). Furthermore, longer spells of temperatures below 18° C may lead to organ malfunction in recent alligators, and feeding is already restricted at temperatures below 22° C (Markovick 1998). If similar restrictions applied to metriorhynchids, water temperature in the Neuquén basin did probably not drop below 20° C for longer periods of time in the late Middle and Late Jurassic environments in which these animals lived. The limits of a coldest month mean temperature of 5.5° C and a mean annual temperature of 14.2° C found by Markovick (1998) for recent amphibious crocodiles are probably not applicable to the fully marine thalattosuchians. Temperatures in excess of 20° C for the Neuquén basin are also in accordance with data from oxygen isotopes, which indicate temperatures between 24 and 27° C (Gasparini et al. 2002).

The Cañadón Asfalto Formation has yielded one of the most important vertebrate faunas from the Middle Jurassic of Gondwana (see Bonaparte 1979, Rauhut et al. 2001). Vertebrates recorded include a diverse dinosaur fauna (Bonaparte 1979, 1986, Rauhut 2002, 2005) and a variety of other groups, such as anuran amphibians (Báez and Nicoli 2008), turtles (Sterli 2008), and mammals (Rauhut et al. 2002, Rougier et al. 2007a, b). Interestingly, no crocodile remains have been confidently identified from this formation so far. However, this might be due to ecological reasons other than climate, since geological evidence indicates a rather warm climate for this formation (see above). It cannot be ruled out, though, that very high temperatures, in combination with at least seasonal aridity, might have been a limiting factor for crocodilians in the Cañadón Asfalto Formation (see Colbert et al. 1946). The abundant turtles found in the Cañadón Asfalto Formation (see Sterli 2008) are consistent with rather warm climates; in recent

turtles, even cold-adapted species do not occur in areas with warm month mean temperatures below 17.5° C (Tarduno *et al.* 1998).

# d) Paleolatitudes and paleomagnetic data

Comparison of paleoclimatic conclusions with data on paleolatitudes from paleomagnetic studies shows a good correspondence of paleoclimatic data and paleomagnetic latitudes. A paleomagnetic study in four ammonite-bearing marine sedimentary sections (Iglesia Llanos et al. 2006) shows that during the Middle and Late Jurassic, the South American continent eventually attained a position similar to its present-day position (Fig. 3). But that during the Hettangian-Sinemurian the 50° S-latitude was crossing the Neuquén basin, suggesting a cold climate in this basin during the earliest Early Jurassic (Spalletti et al. 1999, Gómez-Pérez 2003).

Based on the palynofloras this shift could be correlated with the distribution of some Jurassic floras. The Sinemurian - Early Toarcian microflora from the Los Patos Formation in the north of the basin (Volkheimer et al. 1978) and the Pliensbachian microflora of the Sierra de Chacaico Formation in the south (Volkheimer 1974, 1980) reflect the passage from a position of the Neuquén basin from 50° S to 25° S. The lower member of the Los Patos Formation (lowermost Pliensbachian - Sinemurian) exhibits a content of Classopollis not higher than 60 % on average (at 50° S), while the Upper Member (Late Pliensbachian - Early Toarcian) and Sierra de Chacaico Formation show the highest percentages of Classopollis (91 and up to 99 %).

During the shift of the South American continent to the northernmost position, another important microfloral change can be registered: The first appearance of the *Callialasporites* "complex" (*Araucariaceae*) is documented in the earliest Late Toarcian associated with Araucariacites *australis* and *A. pergranulatus*, for example



Figure 1: Location map showing the position of the localities and regions mentioned (Río Limay region of northern Patagonia, Neuquén basin, Sierra de Chacai Co, Mendoza region, Cañadón Asfalto basin).



Figure 2: Number of species in various encystment modes and total specific diversity in the Jurassic and earliest Cretaceous of the Neuquén basin (adapted from Quattrocchio 1986). For methodology see Quattrocchio (1984).

in arroyo Lapa, Neuquén (Volkheimer 1971). The arrival of the new group of Araucariaceae, represented by *Callialasporites* spp., in the Toarcian (Volkheimer and Quattrocchio 1981) could indicate an amelioration related to more humid conditions. This conclusion could be extended to Australia, where the same pattern of *Classopollis* and the *Callialasporites* "complex" is observed (Monteil 2006). During the Late Jurassic (and Early Cretaceous) a broad arid belt, whose most conspicuous feature was the Botucatú desert, (studied by Bigarella and Salamuni 1964), extended from approximately 15° to 30° of southern paleolatitude. Evaporites of considerable thickness and distribution along the Pacific margin complete the picture of this warmarid region. Only in southern Patagonia prevailed moist conditions, as indicated by arborescent ferns and products of ancient weathering (Volkheimer 1969, 1970a, b).

The Jurassic magmatic paroxysm was the immediate predecessor of a large scale Gondwanaland disintegration (Uliana and Biddle 1988). Those basins close to the western margin of South America continued to accumulate marine deposits during the Neocomian. Large areas of the southern South American interior became depositional sites for non-marine clastic material.

The Late Jurassic to Neocomian sequence records active crustal stretching in areas along the present margins of the South Atlantic. By 130 Ma the first oceanic floor was formed in the South Atlantic (Rabinowitz and LaBrecque 1979, Gerrard and Smith 1982).

# SUMMARY OF JURASSIC PALEOCLIMATES

### a) Early Jurassic paleoclimates

Neuquén basin: The Sinemurian - Early Toarcian palynoflora from the Los Patos Formation in the north of the basin and the Pliensbachian microflora of the Sierra de Chacaico Formation in the south of the same basin reflect the passage from a position of the Neuquén basin at 50° S to 25° S, taking into account the cheirolepidiacean pollen content, which rises from 41.5 % in the lower member to 91 % of Classopollis in the upper member (Volkheimer et al. 1978), indicating increasing warmth and aridity during the deposition of the Los Patos Formation. The relative abundance of the thermophilic Classopollis (reaching 25 % as the maximum of the total spectrum of palynomorphs) in the Late Toarcian Nestares Formation of the Río Limay region of northern Patagonia probably reflects the local environments. The presence of warm (-temperate) and humid conditions (at least temporarily) is also compatible with the composition of associated palynomorph assemblages consisting mainly



**Figure 3:** By the end of the Triassic until the end of the Sinemurian, the studied region (Neuquén basin) was at its southernmost position (c. 50° S). From then on, it moved northward at about 20 cm yr-1 and reached its northernmost location (c. 25° S) in the Pliensbachian. Subsequently, the area moved again to the south at 10 cm yr-1 and eventually attained c. 30° S by the end of the Jurassic, which is similar to its present-day position (from Iglesia Llanos *et al.* 2006).

of hygrophile elements: bryophyte/pteridophyte spores, associated with comparatively smaller amounts of conifer pollen (Zavattieri *et al.* 2008).

A fundamental feature of the climatic evolution of the Jurassic in the southern Andean region is the gradually increasing aridity during this Period. A cool climate is inferred for the Neuquén basin for the earliest Early Jurassic, based on the general absence of carbonate deposits and a high siliciclastic input into the basin (Spalletti *et al.* 1999, Gómez-Pérez 2003). The Middle and Late Liassic of the andean and pre-andean regions of Neuquén and Mendoza were characterized by moist climatic conditions, as shown by the frequency of coal and well preserved fossil floras.

### b) Middle Jurassic paleoclimates

*Central Patagonia: Cañadón Asfalto basin:* In central Extra-Andean Patagonia the continental volcano-sedimentary sequence of mainly siliciclastic lacustrine strata of the Cañadón Asfalto Formation is of special value for paleoclimatic considerations. The abundant mega- and microfloral evidence (Volkheimer *et al.* 2001) suggest warm climatic conditions during the Middle Jurassic of this region. The Cheirolepidiaceae dominated the spectrum, associated with Araucariaceae. Warm and relatively humid climatic conditions are indicated by high percentages of the thermophilic Cheirolepidiaceae, associated with Araucariaceae, which need relatively humid conditions.

Lacustrine carbonates (marls and algal limestones) are frequent in this formation. They are good climatic indicators, "because they are restricted to generally dry climates where the ground waters are not unduly acid" (Fairbridge 1967). However, thin coal seams found in parts of the Cañadón Asfalto sequence also indicate short periods of more humid conditions at least in the basal parts of the formation. The conchostracans from this formation are occurring in banded shales. As an example, fifteen or more successive sea-

sons are represented in a thickness of 19 cm of sediment. This points to a seasonal sedimentation rate of 1 mm or less. Other evidence, as growth bands, points to wet-dry cycles in the water bodies inhabited by the conchostracans studied by Tasch (in: Tasch and Volkheimer 1970). Cabaleri et al. (2005) studied a saline paleolake of the Cañadón Asfalto Formation near the village of Cerro Condor, middle valley of the Chubut River. Within a lacustrine facies association they observed an extensive biohermal belt (500 m long and 39 m thick), showing three growthstages of microbial communities: a core facies with discontinuous stromatolite laminae, formed by green filamentous algae, interbedded with mudstone; a flank facies (up to 22 m thick), made up by stratiform stromatolites with intercalations of Magadi-type chert laminae and a top facies assemblage, consisting of thick hemispheroidal stromatolites, interbedded with Magadi-type chert and affected by desiccation processes, presenting crack systems and caliche covers, indicating arid conditions and a gradual transition from eulittoral to supralittoral environments (Cabaleri and Armella 2005). The biohermal belt favoured the formation of the pan lake of Cañadón Carrizal. Cycles present a sedimentation pattern that responds to climatic variations. The paleoenvironmental history of the lake is defined by a succession of five cycles that lead to the progressive reduction of the water body, each cycle being shallower than the previous one and ending with evaporites.

The same authors emphasize that the mentioned succession of different cycles of expansion-contraction during the evolution of the lake is a consequence of the tectonic history of the basin, which was interpreted as a pull-apart structure (Silva Nieto *et al.* 2002), characterized by differential movements of small blocks that delimit horsts and grabens.

Neuquén basin: During late Bajocian times, in a context of marine regression and drying out of the basin, widespread sulphatic rocks (the gypsum of the Tábanos Formation) were deposited. During the Callovian a return to moister conditions occurred, probably related to a marine ingression. In the southern part of the Neuquén basin thin coal seams are widely distributed, bearing an abundant palynoflora with many representatives of the hygrophile ferns (Volkheimer 1972). A hypothetic scenario for the Middle Jurassic in the southern part of the Neuquén basin was proposed by Quattrocchio et al. (2001), on the basis of sedimentary facies and palynological data obtained from the study of eight stratigraphic sections. The analysis of the terrestrial palynological assemblages (102 species of sporomorphs) shows that certain plant groups dominated the scenario, in particular the Cheirolepidiaceae, Araucariaceae and Podocarpaceae and to a lesser degree Cyatheaceae, Osmundaceae, Marattiaceae, Dipteridaceae, Lycopodiaceae, Schizaeaceae, Anthocerotaceae, Ricciaceae, Cycadales/Bennettitales, Caytoniaceae and Gnetales. In addition to the conventional approach using percentage values, principal component analysis (Martínez et al. 1996) proved to be an excellent and complementary tool, because it reduced the data set into definite groups of representative taxa.

Quattrocchio et al. (2001) used modern analogues, the Chilean-Argentinian forest and the Planalto of southern Brazil, to explain the paleoclimatic and paleoenvironmental conditions during the Middle Jurassic. In the Planalto (about 1000 m above sea level) the Araucariaceae and Podocarpaceae grow together, but the latter disappear with an increase of temperature and humidity farther north in Brazil. The influence of acid effusives of the Serra Geral Formation conditions the low pH of the soils. In the Neuquén basin, rhyolites of the Choiyoi Group (Permian-Triassic) and other acid rocks of the basement could have been the substratum of the ancient Araucariaceae. According to the above mentioned assessment, they proposed a plateaus scenario with warm to temperate conditions and variable precipitation rates through the



Figure 4: The South American arid belt during the Late Jurassic (adapted from Volkheimer, 1969). Paleolatitudinal position of the continent during the Late Jurassic is from Iglesia Llanos *et al.* (2006).

### Middle Jurassic.

The sedimentary facies and the palynologic assemblages of the Middle Jurassic depositional sequences (García et al. 1994) at Sierra de Chacaico are considered, taking into account the Classopollis content. This genus is dominant in all the assemblages, with increasing frequencies from the offshore-prodelta deposits, to a maximum in the stream mouth bar. This genus is here considered as a coastal proxy related to extraordinary flooding of the delta plain. In this scenario Classopollis acts as a clastic component, sensitive to increments of the sedimentary input. Classopollis reaches up to 90 %, associated with bars of the prodelta deposits.

### c) Late Jurassic paleoclimates

During Kimmeridgian times, approximately 150 to 155 My ago, as a consequence of the Araucanian Movements, the paleogeography and climate of South America underwent fundamental changes. A series of marginal basins began to subside near the eastern border of the continent.

Neuquén basin and related areas: The world-

wide marine transgression was reflected by the important marine ingression of the Tithonian sea in the Neuquén basin. The Tithonian Berriasian microfloras of the Neuquén basin are very similar and correspond to the Equisetosporites -Trisaccites Assemblage (Volkheimer and Pöthe de Baldis 1982). The only difference between Tithonian - Berriasian microfloras is the lower diversity of the later (Volkheimer 1980, Quattrocchio et al. 2003). The sporomorph assemblages show marked change only at the Berriasian/Valanginian boundary, by the appearance of the conspicuous and abundant Cyclusphaera psilata (Riccardi et al. 1990).

A large region of southern South America was subject to extremely arid conditions during the Late Jurassic (Fig. 4) and parts of the Early Cretaceous. In the Chaco-Paraná basin a large paleodesert, documented by eolian sandstones, extended from Minas Gerais (Brazil) to Uruguay (Bigarella and Salamuni 1964) and central Argentina (Padula and Mingramm 1968, Volkheimer 1967). The paleoclimatic scenario of an extremely arid region was complemented by thick gypsum and anhydrite deposits of Late Oxfordian age, which extended from Zapala (Neuquén Province, Auquinco Formation) to Mendoza and San Juan provinces and continued to southern Perú. Again marine regression (increasing continentality) was accompanied by an increase of aridity.

Biohermal limestones of Middle Oxfordian age (La Manga Formation, Neuquén basin) indicate warm and shallow oceanic waters in large areas of this basin.

# CONCLUSIONS

1) The use of vertebrates as paleoclimatic proxies in the Jurassic of Argentina is currently severely restricted. One reason for this is the very patchy Jurassic record of especially terrestrial vertebrates in Argentina, with the only good fauna being that of the Mid-Jurassic Cañadón Asfalto Formation of Chubut. The other problem in using Jurassic vertebrates as climate proxies in general concerns the fact that all groups represented belong to extinct lineages with no close living relatives, and, thus, their climatic preferences and necessities remain speculative (see Ostrom 1970). This is especially true for groups such as ichthyosaurs or plesiosaurs, which do not have any living relatives, and for the dinosaurs, the living representatives of which (the birds) are highly specialized physiologically. Although also not unproblematic, other groups that have more similar living relatives, such as anurans, turtles, and crocodiles might help to interpret general aspects of Jurassic climates, although caution is advisable in interpreting their implications. Thus, abundant marine crocodiles in the Middle and Late Jurassic of the Neuquén basin indicate warm water temperatures in this basin, and the presence of turtles and other ectothermic vertebrates, such as frogs, in the Cañadón Asfalto Formation of Chubut also indicate a rather warm climate for this unit. In both cases, these interpretations are in agreement with other lines of evidence, both geologic and palaeontologic, so that the vertebrates seem to reliably reflect the climatic conditions.

2) Beside the thermophilic character previously postulated for the Cheirolepidiaceae, dominant in almost all the palynological assemblages through the Jurassic, it is important to analyze the facies in which these pollen grains occur. For example, in marine deposits of the Middle Jurassic (Neuquén basin) they show increasing frequencies from the offshore-prodelta deposits, to a maximum in the stream mouth bar. Principally they are considered as a coastal proxy related to extraordinary flooding of the delta plain. In this case Classopollis acts as a clastic component, sensitive to increments of the sedimentary input. Classopollis reaches up to 90 % associated with bars of the prodelta deposits.

For paleoclimatic inferences it is important to consider also the relationships between palynomorph concentrations and vegetation types. For example the income of a new group of the Araucariaceae in the Toarcian is postulated to have been associated with moist conditions.

There is also an increasing need to understand the taphonomic processes that act upon the palynomorphs, in order to obtain accurate paleoclimatic and paleoenvironmental interpretations.

### ACKNOWLEDGEMENTS

We wish to acknowledge the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) for economic support (PIP 5222 and PIP 5297); IANI-GLA-CCT-CONICET-Mendoza for laboratory facilities, to the Secretaría General de Ciencia y Tecnología de la Universidad Nacional del Sur (SEGCyT), Bahía Blanca, for economic support, to Drs. E. Schrank and Z. Gasparini for many useful comments and corrections and to Lic. Paula Narváez for correction of the manuscript.

### WORKS CITED IN THE TEXT

- Alvin, K.L. 1982. Cheirolepidaceae: biology, structure and paleoecology. Review of Palaeobotany and Palynology 37: 71-98.
- Alvin, K.L. 1983. Reconstruction of a Lower Cretaceous conifer. Botanical Journal of the Linnaean Society 86: 169-176.
- Báez, A.M. and Nicoli, L. 2008. A new species of *Notobatrachus* (Amphibia, Salienta) from the Middle Jurassic of northwestern Patagonia. Journal of Paleontology 82 (2): 372-376.
- Batten, D.J. 1975. Wealden palaeoecology from the distribution of plant fossils. Proceedings of Geologists' Association 85 (for 1974): 433-458.
- Batten, D.J. 1984. Palynology, climate and the development of Late Cretaceous floral provinces in the Northern Hemisphere; a review. Fossils and Climate: 127-163.
- Bigarella, J.J. and Salamuni, R. 1964. Paleowind Patterns in the Botucatú Sandstone (Triassic-Jurassic) of Brazil and Uruguay. In Nairn, A.E.M. (ed.) Problems in Palaeoclimatology, Interscience Publishers, John Wiley & Sons Ltd., 406-409, London.

- Böhme, M. 2003. The Miocene climatic optimum: evidence from ectothermic vertebrates of central Europe. Palaeogeography, Palaeoclimatology, Palaeoecology 195: 389-401.
- Bonaparte, J.F. 1979. Dinosaurs: a Jurassic assemblage from Patagonia. Science 205: 1377-1379.
- Bonaparte, J.F. 1986. Les dinosaures (Carnosaures, Allosauridés, Sauropodes, Cetiosauridés) du Jurassique Moyen de Cerro Condor (Chubut, Argentine). Annales de Paléontologie (Vertebr.-Invertebr.), 72 Fascicule 3: 247-289, and Fascicule 4: 325-386, Masson, Paris.
- Cabaleri, N.G. and Armella, C. 2005. Influence of a biohermal belt on the lacustrine sedimentation of the Cañadón Asfalto Formation (Upper Jurassic, Chubut province, Southern Argentina. Geologica Acta 3(2): 205-214.
- Cabaleri, N.G., Armella, C. and Silva Nieto, D.G. 2005. Saline lakes of Cañadón Asfalto Formation (Middle-Upper Jurassic), Cerro Condor, Chubut Province (Patagonia), Argentina. FACIES, International Journal of Paleontology, Sedimentology and Geology 10.1007/s 10347-004-0042-5, Springer Verlag, Heidelberg.
- Colbert, E.H. 1964. Climatic zonation and terrestrial faunas. In Nairn, A.E.M. (ed.) Problems in paleoclimatology, Interscience: 617-639, London.
- Colbert, E.H., Cowles, R.B. and Bogert, C.M. 1946. Temperature tolerances in the American alligator and their bearing on the habits, evolution and extinction of the dinosaurs. Bulletin of the American Museum of Natural History 86(7): 327-374.
- Fairbridge, R.W. 1967. Carbonate rocks and paleoclimatology in the biochemical history of the Planet. In Chilingar, G.V., Bissell, H.J. and Fairbridge, R.W. (eds) Carbonate Rocks. Developments in Sedimentology 9 A, PAGI-NAS, Elsevier, Amsterdam.
- García, V.M., Zavala, C.A. and Quattrocchio, M.E. 1994. Relación entre análisis palinológico y análisis de facies. Aplicación al Grupo Cuyo (Jurásico Medio) en la Cuenca Neuquina. Revista de la Asociación Geológica Argentina 49(1-2): 184-195.
- Gasparini, Z. 1985. Los reptiles marinos Jurásicos de América del Sur. Ameghiniana 22(1-2): 23-34.
- Gasparini, Z. 1992. Marine reptiles of the cir-

cum-Pacific region. In: Westerman, G.E.G. (ed.): The Jurassic of the Circum-Pacific. Cambridge University Press 361-365, Cambridge.

- Gasparini, Z., Cichowolski, M. and Lazo, D.G. 2005. First record of *Metriorhynchus* (Reptilia: Crocodyliformes) int eh Bathonian (Middle Jurassic) of the eastern Pacific. Journal of Paleontology 79(4): 801-805.
- Gasparini, Z., Spalletti, L., Matheos, S. and Fernández, M. 2002. Reptiles marinos y paleoambiente del Jurásico superior-Cretácico inferior en la yesera del Tromen (Neuquén, Argentina): un caso de estudio. 15º Congreso Geológico Argentino (El Calafate), Actas 1: 473-478.
- Gerrard, I. and Smith, G.C. 1982. Post-Paleozoic succession and structures of the Southwestern African margin. In Watkins, J.S. and Drake, C.L. (eds.) Studies in Continental Margin Geology, American Association of Petroleum Geologists, Memoir 34: 49-74.
- Gómez-Pérez, I. 2003. An Early Jurassic deepwater stromatolitic bioherm related to possible methane seepage (Los Molles Formation, Neuquén, Argentina). Palaeogeography, Palaeoclimatology, Palaeoecology 201: 21-49.
- Iglesia Llanos, M.P., Riccardi, A.C. and Singer, S.E. 2006. Palaeomagnetic study of Lower Jurassic marine strata from the Neuquén Basin, Argentina: A new Jurassic apparent polar wander path for South America. Earth and Planetary Science Letters 252: 379-397.
- Markovick, P.J. 1998. Fossil crocodilians as indicators of Late Cretaceous and Cenozoic climates: implications for using palaeontological data in reconstructing palaeoclimate. Palaeogeography, Palaeoclimatology, Palaeoecology 137: 205-271.
- Martínez, M., García, V. and Quattrocchio, M. 1996. Análisis de componentes principales aplicado al estudio palinológico del Jurásico medio de Cuenca Neuquina, Argentina. 12° Congreso Geológico Argentino y 3° Congreso de Exploración de Hidrocarburos, Actas 5: 171-179.
- Monteil, E. 2006. Australian Mesozoic and Cenozoic Palynology Zonations - updated to the 2004. Geologic Time Scale. Geoscience Australia, Record 2006/23.
- Ostrom, J.H. 1970. Terrestrial vertebrates as indicators of Mesozoic climates. In Yochelson,

E.L. (ed.) Proceedings of the North American Paleontological Convention, Allen Press, 347-376, Lawrence.

- Padula, E.L. and Mingramm, A. 1968. Estratigrafía, distribución y cuadro geotectónicosedimentario del "Triásico" en el subsuelo de la llanura Chaco-Paranense. 3º Jornadas Geológicas Argentinas (Comodoro Rivadavia, 1966), Actas 1: 291-331.
- Parrish, J. 1993. Climate of the Supercontinent Pangea. Journal of Geology 101: 215-233.
- Pol, D. and Gasparini, Z. 2007. Crocodyliformes. In Gasparini, Z., Salgado, L. and Coria, R.A. (eds.) Patagonian Mesozoic reptiles, Indiana University Press, 116-142, Bloomington and Indianapolis.
- Quattrocchio, M.E. 1984. Sobre el posible significado paleoclimático de los quistes de dinoflagelados en el Jurásico y Cretácico inferior de la Cuenca Neuquina. 3º Congreso Argentino de Paleontología y Bioestratigrafía (Corrientes), Actas: 107-113.
- Quattrocchio, M.E. 1986. Paleolatitude indicated by encystment mode and species diversity of Jurassic dinoflagellates in the Neuquén Basin, Argentina. In Westermann, G.E.G. (ed.) Topic C: Ocean Currents and Climate, Project 171-IGCP, Circum-Pacific Jurassic Group: 17-19, Hamilton.
- Quattrocchio, M.E., Martínez, M.A. and Volkheimer, W. 2007. Las floras jurásicas de la Argentina. Asociación Paleontológica Argentina. Ameghiniana 50° Aniversario, Publicación Especial 11: 87-100.
- Quattrocchio, M.E., García, V., Martínez, M. and Zavala, C. 2001. A hypothetic scenario for the Middle Jurassic in the southern part of the Neuquén Basin, Argentina. 7° International Symposium on Mesozoic Terrestrial Ecosystems, Asociación Paleontológica Argentina. Publicación Especial 7: 163-166.
- Quattrocchio, M.E., Martínez, M.A., García, V. M. and Zavala, C.A. 2003. Palinoestratigrafía del Tithoniano-Hauteriviano del centro-oeste de la Cuenca Neuquina, Argentina. Revista Española de Micropaleontología 35: 51-74.
- Rabinowitz, P.D. and La Brecque, J. 1979. The Mesozoic South Atlantic Ocean and evolution of its continental margin. Journal of Geophysical Research 84: 5973-6002.
- Rauhut, O.W.M. 2002. Los dinosaurios de la Formación Cañadón Asfalto: diversidad, filogenía

y biogeografía. Ameghiniana 39 (4, Suplemento): 15R-16R.

- Rauhut, O.W.M. 2005. Osteology and relationships of a new theropod dinosaur from the Middle Jurassic of Patagonia. Palaeontology 48(1): 87-110.
- Rauhut, O.W.M., López-Arbarello, A., Puerta, P. and Martin, T. 2001. Jurassic vertebrates from Patagonia. Journal of Vertebrate Paleontology 21 (suppl. to 3): 91A.
- Rauhut, O.W.M., Martin, T., Ortíz Jaureguizar, E. and Puerta, P. 2002. A Jurassic mammal from South America. Nature 416: 165-168.
- Riccardi, A.C., Damborenea, S.E. and Manceñido, O. 1990. 3. South America and Antarctica Peninsula. 3.1 Lower Jurassic of South America and Antarctic Peninsula. Newsletters in Stratigraphy 21 (2): 75-103.
- Romer, A.S. 1961. Palaeozoological evidence of climate: vertebrates. In Nairn, A.E.M. (ed.) Descriptive palaeoclimatology. Interscience 183-226, New York.
- Rougier, G.W., Garrido, A., Gaetano, L., Puerta, P., Corbitt, C. and Novacek, M.J. 2007a. First Jurassic triconodont from South America. American Museum Novitates 3580: 1-20.
- Rougier, G.W., Martinelli, A.G., Forasiepi, A.M. and Novacek, M.J. 2007b. New Jurassic mammals from Patagonia, Argentina: a reappraisal of australosphenidan morphology and interrelationships. American Museum Novitates 3566: 1-54.
- Silva Nieto, D., Cabaleri, N., Salani, F. and Coluccia, A. 2002. Cañadón Asfalto, una cuenca de tipo "pull apart" en el área de Cerro Condor, Provincia del Chubut. 15° Congreso Geológico Argentino, Actas 1: 238-243.
- Smith, N.D. and Pol, D. 2007. Anatomy of a basal sauropodomorph dinosaur from the Early Jurassic Hanson Formation of Antarctica. Acta Palaeontologica Polonica 52(4): 657-674.
- Spalletti, L.A., Franzese, J.R., MacDonald, D. and Gómez-Pérez, I. 1999. Palaeogeographic evolution of southern South America during the Cretaceous. 5° Simposio sobre o Cretáceo do Brasil, Actas 87-95, Serra Negra.
- Sterli, J. 2008. A new, nearly complete stem turtle from the Jurassic of South America with implications for turtle evolution. Biology Letters 43(3): 286-289.
- Tarduno, J.A., Brinkman, D.B., Renne, P.R., Cottrell, R.D., Scher, H. and Castillo, P. 1998. Evi-

dence for extreme climatic warmth from Late Cretaceous Arctic vertebrates. Science 282: 2241-2244.

- Tasch, P. and Volkheimer, W. 1970. Jurassic conchostracans from Patagonia. The University of Kansas Paleontological Contributions, Paper 50: 1-23, Kansas.
- Uliana, M.A. and Biddle, K.T. 1988. Mesozoic Cenozoic paleogeographic and geodynamic evolution of southern South America. Revista Brasileira de Geociências 18(2): 172-190.
- Vakhrameev, V.A. 1981. Pollen *Classopollis*: indicator of Jurassic and Cretaceous climates. The Palaeobotanist 28-29: 301-307.
- Vakhrameev, V.A. 1987. Climates and the distribution of some gymnosperms in Asia during the Jurassic and Cretaceous. Review of Palaeobotany and Palynology 51: 205-212.
- Vandermark, D., Tarduno, J.A. and Brinkman, D.B. 2007. A fossil champsosaur population from the high Arctic: implications for Late Cretaceous palaeotemperatures. Palaeogeography, Palaeoclimatology, Palaeoecology 248: 49-59.
- Volkheimer, W. 1967. La paleoclimatología y los climas del Mesozoico argentino. Sociedad Argentina de Minería y Geología, Revista Minera, Geología y Mineralogía 28(3): 41-48, Buenos Aires.
- Volkheimer, W. 1969. Palaeoclimatic Evolution in Argentina and Relations with other Regions of Gondwana. In Gondwana Stratigraphy, Earth Sciences 2, IUGS-UNESCO Symposium (Buenos Aires, 1967), Actas 551-587, Paris.
- Volkheimer, W. 1970a. Jurassic microfloras and paleoclimates in Argentina. Second Gondwana Symposium (South Africa), Proceedings and Papers: 543-549, Pretoria.
- Volkheimer, W. 1970b. Neuere Ergebnisse der Anden-Stratigraphie von Süd-Mendoza (Argentinien) und benachbarter Gebiete und Bemerkungen zur Klimageschichte des südlichen Andenraums. Geologische Rundschau 59 (3): 1088-1124, Stuttgart.
- Volkheimer, W. 1971. Algunos adelantos en la microbioestratigrafía del Jurásico en la Argentina y comparación con otras regiones del hemisferio austral. Ameghiniana 8(3-4): 341-355.
- Volkheimer, W. 1972. Estudio palinológico de un carbón Caloviano de Neuquén y consideraciones sobre los paleoclimas jurásicos de la

Argentina. Revista del Museo de La Plata (nueva serie) 6 (Paleontología 4): 101-157.

- Volkheimer, W. 1974. Palinología estratigráfica del Jurásico de la Sierra de Chacai Co y adyacencias (Cuenca Neuquina, República Argentina). II. Descripción de los palinomorfos del Jurásico inferior y Aaleniense (Formaciones Sierra Chacai Co y Los Molles). Ameghiniana 11: 135-172.
- Volkheimer, W. 1980. Liassic microfloras of the Neuquén Basin (Argentina): relations with other Gondwanic areas. 4° International Palynological Conference (Lucknow 1976-1977) 2: 269-280.
- Volkheimer, W. and Pöthe de Baldis, D. 1982. Significado estratigráfico de microfloras paleozoicas y mesozoicas de la Argentina. 5° Congreso Latinoamericano de Geología, Actas 403 424, Buenos Aires.
- Volkheimer, W. and Quattrocchio, M.E. 1981. Distribución estratigráfica de los palinomorfos jurásicos y cretácicos en la faja andina y áreas adyacentes de América del Sur Austral con especial consideración de la Cuenca Neuquina. En Volkheimer, W. y Musacchio, E.A. (eds.) Cuencas sedimentarias del Jurásico y Cretácico de América del Sur, Comité Sudamericano del Jurásico y Cretácico 2: 407-444.
- Volkheimer, W., Manceñido, M. and Damborenea, S. 1978. Zur Biostratigraphie des Lias in der Hochkordillere von San Juan, Argentinien. Münstersche Forschungen für Geologie und Paläontologie 44/45: 205-235, Münster.
- Volkheimer, W., Quattrocchio, M.E. and Cabaleri, N.G. 2001. Palynology and paleoenvironment of the lacustrine Cañadón Asfalto Formation, Jurassic of Central Patagonia, Argentina. 34th Annual Meeting of the American Association of Stratigraphic Palynologists, Abstract Volume: 43, San Antonio.
- Zavattieri, A.M., Rosenfeld, U. and Volkheimer, W. 2008. Palynofacies analysis and sedimentary environments of Early Jurassic coastal sediments at the southern border of the Neuquén Basin, Argentina. Journal of South American Earth Sciences 25: 227-245.

Recibido: 5 de junio, 2008 Aceptado: 15 de agosto, 2008