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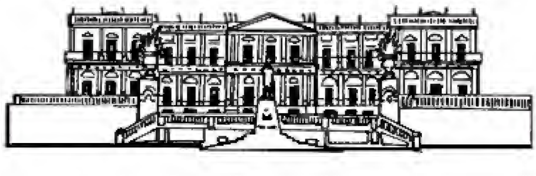
ARQUIVOS
DO
MUSEU NACIONAL

Nunquam aliud natura, aliud sapienta dicit
Juvenal, 14, 321
In silvis academi quoerere rerum,
Quamquam Socraticis madet sermonibus
Ladisl. Netto, *ex Hor*

VOL.LXV
N.4



RIO DE JANEIRO
Outubro/Dezembro
2007

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II LATIN-AMERICAN CONGRESS OF VERTEBRATE PALEONTOLOGY

In the last decades there was a notable expansion in vertebrate paleontology as a result of the commitment and efforts made by several paleontologists around the world. In Latin America this growth was particularly expressive, with several new discoveries done in the last years, some quite spectacular. This knowledge was diffused not only to the international scientific community, but also to the general public in which the media played a major role. The scientists dedicated to the study of vertebrate paleontology in Latin America felt the necessity to gather the professionals of the field to discuss the new information and ideas that were being brought to light.

For that purpose the Latin-American Congress of Vertebrate Paleontology was established bringing together researchers active in this field. The first one (I Congreso Latinoamericano de Paleontología de Vertebrados – I CLPV), organized by the Sociedad Paleontologica de Chile (SPACH), was held in Santiago, Chile, from October 29th to November 1st, 2002.

The extremely positive result of the Santiago meeting showed that this kind of convention should be expanded and be made on a more regular basis. Therefore, after deliberation of those present in the I CLPV, the Museu Nacional/UFRJ in Rio de Janeiro was chosen to host the second meeting from August 10th to 12th, 2005.

The scientific sessions were held at the Rio Othon Palace Hotel, located in Copacabana, one of the nicest neighborhoods of Rio de Janeiro. Over three hundred people attended the meeting, among scientists, students and others interested in fossils.

The Organizing Committee was composed essentially of professors, technicians and students of the Museu Nacional. We chose not to include a company specialized in organizing congresses since most of them are not prepared to deal with the particularities of a paleontological meeting. Furthermore when such a company is involved, the registration fee tends to be higher for the participants.

The Scientific Committee that was responsible for evaluating the contributions (over two hundred) consisted of several researchers covering all aspects of vertebrate paleontology.

The timing of the II CLPV was very special since 2005 was the centennial commemoration of Llewellyn Ivor Price's anniversary. Price was one of the most active paleontologists of Brazil and is worldwide known for his scientific contributions. The homage of the II CLPV to this paleontologist was organized by Dr. Diogenes de Almeida Campos at the Companhia de Pesquisa de Recursos Minerais (CPRM).

Still regarding exhibitions, a temporary exhibit of vertebrate paleontology was opened at the Museu Nacional with several fossils and replicas, such as the volant non-avian dinosaur *Microraptor gui* from China.

Several workshops and symposia were held during the meeting. The workshop FUTURE OF VERTEBRATE PALEONTOLOGY IN LATIN AMERICA: THE STUDENT PERSPECTIVE was particularly special being the first of this kind in South America, allowing students to change valuable information with guest professionals. Also, for the first time in Brazil, several South-American paleoartists had the opportunity to present and discuss their work.

The outcome of the meeting was much higher than expected not only by the presence of paleontologists from Latin America but also from several other parts of the world. The Organizing Committee still receives nice comments from the participants. We will take this opportunity and thank them for their support.

The II CLPV also made it possible that complete papers be published in the Arquivos do Museu Nacional, the most traditional scientific publication of Brazil. As one might imagine due to the success of this event, a much higher number of manuscripts than expected were turned in, impeding the publication of those contributions in one sole volume. Here we present the first volume; the second will be published in the first issue of this journal in 2008.

We would like to thank all the referees that have contributed reviewing the manuscripts submitted to the II CLPV. A complete list will be presented in the next volume.

Thank to all that have made this meeting a success.

Alexander W. A. Kellner
Deise D. R. Henriques
Editors of this volume

II CONGRESSO LATINO-AMERICANO DE PALEONTOLOGIA DE VERTEBRADOS - VOLUME 1

A expansão do conhecimento sobre os vertebrados fósseis, observada nas últimas décadas, reflete o esforço e a dedicação de paleontólogos de todo o mundo. Em especial, na América Latina este crescimento foi bastante expressivo. Nos últimos anos a franca ascensão da paleontologia de vertebrados foi retratada pelas diversas descobertas realizadas, algumas delas espetaculares. A difusão dos conhecimentos obtidos atingiu a comunidade científica internacional e o papel da imprensa foi crucial permitindo que a população como um todo tomasse ciência dos achados.

A comunidade paleontológica dedicada aos estudos dos vertebrados fósseis na América Latina sentiu, então, a necessidade de reunir os profissionais da área para discutir as novas informações e idéias que estavam surgindo. Assim, com o objetivo de congregar e aproximar os pesquisadores da área foi criado o Congresso Latino-americano de Paleontologia de Vertebrados. A primeira versão deste encontro (I Congreso Latinoamericano de Paleontología de Vertebrados – I CLPV) ocorreu entre 29 de outubro e 01 de novembro de 2002, em Santiago, no Chile e foi organizada pela Sociedad Paleontologica de Chile (SPACH).

O resultado positivo do encontro de Santiago provou que este tipo de evento deveria se expandir e se tornar regular. Desta forma, após uma deliberação dos presentes ao I CLPV, o Museu Nacional/UFRJ do Rio de Janeiro foi escolhido como organizador da segunda edição deste Congresso, que se realizou no período de 10 a 12 de agosto de 2005. As sessões científicas foram realizadas no Rio Othon Palace Hotel, localizado em Copacabana, um aprazível bairro do Rio de Janeiro onde se encontra uma das mais belas praias do estado. O encontro reuniu cerca de trezentas pessoas entre pesquisadores, estudantes e interessados em fósseis.

A Comissão Organizadora do evento foi composta basicamente por professores, técnicos e estudantes do Museu Nacional. Optou-se por não envolver uma empresa de eventos uma vez que esta nem sempre consegue se adequar à especificidade de um encontro de pesquisadores na área de paleontologia, além de resultar em um alto custo para o congressista. A Comissão Científica responsável pela revisão das contribuições recebidas (mais de duzentas) foi bastante ampla, procurando retratar a diversidade de assuntos encontrados dentro da pesquisa de vertebrados fósseis. A data do evento foi especial já que no ano de 2005 se comemorou o centenário de Llewellyn Ivor Price, falecido em 1980, que foi um dos mais ativos paleontólogos do país e é mundialmente conhecido por suas contribuições em ciências paleontológicas. A homenagem prestada pelo II CLPV a este pesquisador, coordenada pelo Dr. Diogenes de Almeida Campos, se realizou nas dependências da Companhia de Pesquisa de Recursos Minerais (CPRM) e emocionou a todos que tiveram o prazer de ter tido convivido com L.I. Price.

Ainda no âmbito de exposições foi inaugurada, nas dependências do Museu Nacional, uma mostra temporária de paleontologia de vertebrados, na qual foram apresentadas réplicas e reconstituições em vida de alguns fósseis como, por exemplo, o dinossauro alado *Microraptor gui* encontrado na China.

Vários workshops e simpósios foram realizados. Entre estes destacamos o workshop FUTURE OF VERTEBRATE PALEONTOLOGY IN LATIN AMERICA: THE STUDENT PERSPECTIVE, o primeiro do gênero na América do Sul, que teve o propósito de possibilitar a troca de informações sobre diversos aspectos profissionais entre estudantes. Ainda, o evento possibilitou reunir pela primeira vez no Brasil diversos paleoartistas sul-americanos que expuseram suas obras e discutiram as mesmas com os pesquisadores presentes.

O resultado superou as expectativas e contou com a presença não só de profissionais da América Latina como também de outros países do mundo. Ainda hoje a Comissão Organizadora recebe mensagens desses colegas expressando contentamento em terem participado do evento, ao que queremos nesta oportunidade agradecer.

Como última fase do II CLPV, houve a possibilidade de que trabalhos completos fossem submetidos para publicação nos Arquivos do Museu Nacional, a mais tradicional revista científica do Brasil. Como preço do sucesso, o número de contribuições foi mais alto do que se supunha. Desta forma, não houve possibilidade de englobar todos os trabalhos em um volume único. Este é o primeiro. O segundo será publicado no primeiro volume do ano de 2008.

Queremos aqui agradecer aos revisores que contribuíram com suas sugestões e correções dos manuscritos submetidos. Uma lista completa será apresentada no próximo volume.

A todos que contribuíram para o sucesso deste evento o nosso muito obrigado.

Alexander W. A. Kellner
Deise D. R. Henriques
Editores

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NEW FISH RECORDS FROM THE TURONIAN OF THE SERGIPE BASIN, NORTHEASTERN BRAZIL [1]

(With 7 figures)

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HILDA MARIA ANDRADE DA SILVA [2]
EDILMA DE JESUS ANDRADE [4]

ABSTRACT: Recent fieldwork carried out in two quarries from the Cotinguiba Formation, Sergipe Basin, has yielded three new fish specimens. The Sergipe Basin is located in the coastal offshore portion of the State of Sergipe, northeastern Brazil. The basin contains one of the most extensive upper Mesozoic rock successions among the northern South Atlantic basins, mainly the well-represented Cretaceous carbonate succession. It includes the Cotinguiba Formation, which ranges from Cenomanian to Coniacian. In this paper, we reported new occurrences of fishes represented by an indeterminate teleostean from the lower Turonian and an amiid and a dercetid from the middle Turonian. These new records widen the paleogeographical distribution of the Amiidae and Dercetidae in the Turonian.

Key words: Amiidae. Dercetidae. Teleostei *incertae sedis*. Turonian. Sergipe Basin.

RESUMO: Novos registros de peixes do Turoniano da Bacia de Sergipe, nordeste do Brasil.

Recentes trabalhos de campo realizados em dois afloramentos da Formação Cotinguiba, Bacia de Sergipe, renderam três novos espécimes de peixes. A Bacia de Sergipe está localizada na costa do Estado de Sergipe, nordeste do Brasil. A bacia contém uma das mais extensas sucessões rochosas do Mesozóico Superior dentre as bacias do norte do Atlântico Sul, principalmente, a bem representada sucessão carbonática do Cretáceo. Ela inclui a Formação Cotinguiba, que se estende do Cenomaniano ao Coniaciano. Neste trabalho, nós registramos novas ocorrências de peixes representadas por um teleósteo indeterminado do Turoniano Inferior e um amiídeo e um dercetídeo do Turoniano Médio. Esses novos registros ampliam a distribuição paleogeográfica dos Amiidae e Dercetidae no Turoniano.

Palavras-chave: Amiidae. Dercetidae. Teleostei *incertae sedis*. Turoniano. Bacia de Sergipe.

INTRODUCTION

The marine Cretaceous rocks exposed in the Sergipe Basin contain a rich macroinvertebrate fauna dominated by molluscs. Ammonites and bivalves (*e.g.*, HESSEL, 1988; BENGTSON, 1996; ANDRADE *et al.*, 2004) are generally the most common and diverse groups. Fish records are relatively rare and represented by ptychodontids (CARVALHO & GALLO, 2002), pycnodonts (*e.g.*, COPE, 1886; WOODWARD, 1907; SILVA SANTOS & FIGUEIREDO, 1988; HOOKS *et al.*, 1999; MACHADO, 2005), and enchodontids (*e.g.*, SCHAEFFER, 1947; SILVA SANTOS & SALGADO, 1969; COELHO, 2004; GALLO & COELHO, 2005). Here we describe three new fish specimens from the Turonian (Upper Cretaceous) of the Sergipe Basin, northeastern Brazil. We recognized a probable amiid, a dercetid, and an indetermined teleostean, which are reported for the first time from the Cotinguiba Formation.

GEOGRAPHICAL AND GEOLOGICAL SETTING

The Sergipe Basin is located in the coastal and contiguous offshore part of the State of Sergipe in northeastern Brazil (Fig.1). The onshore portion of the basin occupies a narrow coastal strip, approximately 15 to 50km wide and 200km long. The offshore portion extends to water depths greater than 2,000m. The paleogeographical setting of the Sergipe Basin during the late Early and Late

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Cretaceous is a direct consequence of the strong tectonic activity that affected the area since the beginning of the rifting between South America and Africa in the Early Cretaceous. Structurally the basin consists of a series of half-grabens with a regional dip averaging 10-15° to the southeast, resulting from NE-SW-trending normal faults (Koutsoukos *et al.*, 1993).

The basin contains one of the most extensive upper Mesozoic rock successions among the northern South Atlantic basins, a fact that is further enhanced by the existence of numerous outcrops. In particular, it contains the well-represented Cretaceous carbonate succession, spanning the Aptian to Coniacian interval (Souza-Lima *et al.*, 2002). The geological evolution and the development of the marine Cretaceous of the Sergipe Basin have been discussed by several authors. More detailed information can be found in Ojeda & Fugita (1976), Ojeda (1982), Bengtson (1983), Chang *et al.* (1988), Lana (1990), Feijó (1994), and Souza-Lima *et al.* (2002), among others. The marine Cretaceous succession consists of the carbonate Riachuelo (Aptian-Albian) and Cotinguiba (Cenomanian-Coniacian) formations and the clastic Calumbi and Marituba formations. The material described herein derives from the Cotinguiba Formation, which was deposited in neritic to upper bathyal environments of a carbonate ramp.

MATERIAL AND METHODS

The material for this study was collected in the marine limestones from two localities (Fig.2) of the Cotinguiba Formation, in the Sergipe Basin, northeastern Brazil. It comprises three specimens: an indetermined teleostean was found in the lower Turonian of the locality Retiro 26; an amiid came from the middle Turonian of the locality Retiro 26 and a dercetid was collected from the middle Turonian of the locality Muçuca 5. The locality Muçuca 5 was described by Bengtson (1983, Appendix 1) and Retiro 26 by Hessel (1988) and Andrade (2005).

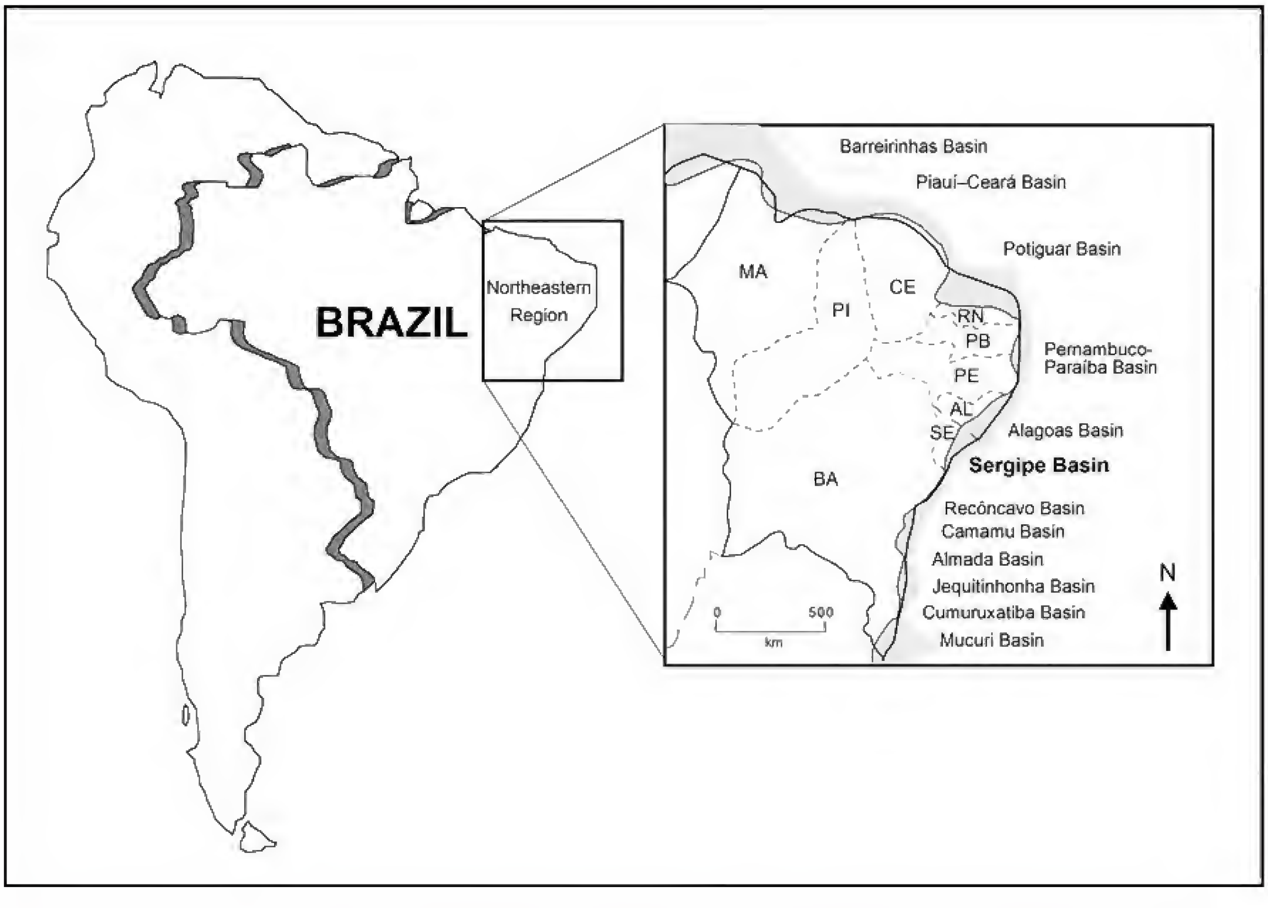

Fig.1- Location map of the Sergipe Basin and others continental margin basins (dotted) of northeastern Brazil. Abbreviations of state names: (AL) Alagoas, (BA) Bahia, (CE) Ceará, (MA) Maranhão, (PB) Paraíba, (PE) Pernambuco, (PI) Piauí, (RN) Rio Grande do Norte, (SE) Sergipe.

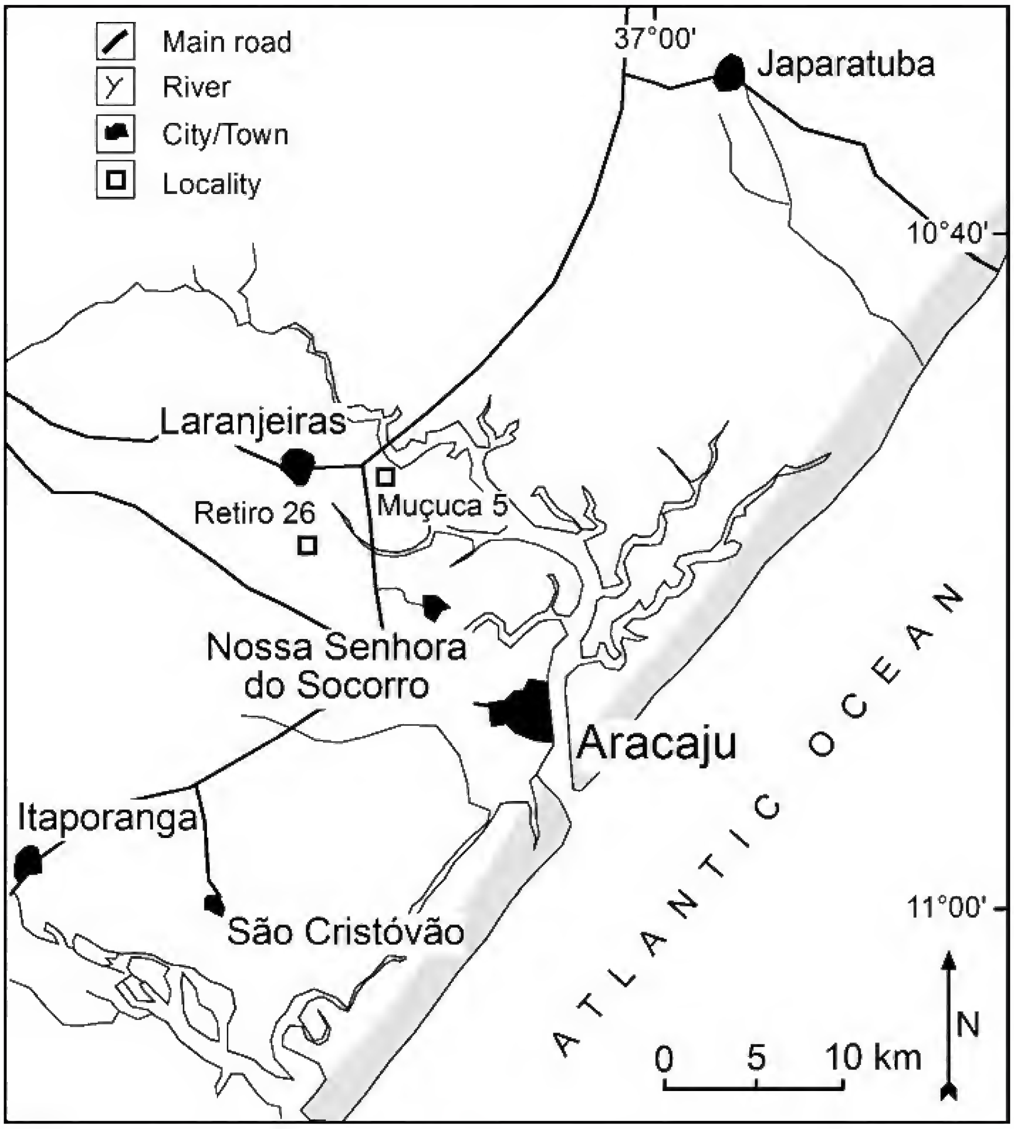

Fig.2- Simplified map of the onshore area of the Sergipe Basin, with localities Retiro 26 and Muçuca 5 (modified after Seeling & Bengtson, 2003).

The specimens are housed at the paleontological collection of the Museu Nacional, Rio de Janeiro, Brazil, under the registration numbers MN 7028-V, MN 7029-V, and MN 7030-V.

The specimens are only mechanically prepared with the aid of steel and carbide needles. Methacrylate resin (Paraloid B-67) was used to consolidate and to protect the bones. Ethyl acetate was dropped to emphasize anatomical details during the observation under a Leica Zoom 2000 stereomicroscope.

RESULTS

Paleoichthyofauna

1) Actinopterygii
Neopterygii
Amiiformes
Amiidae

The specimen MN 7028-V is represented by part of the vertebral column showing the boundary between abdominal and caudal regions. The preservation does not allow a clear observation of diplospondyly. The centra are large, as long as deep, smooth-sided, and show a slight lateral depression. The pleural ribs are long and well-ossified bones that are abruptly truncated at their distal ends. They articulate directly on the side of the centra. Parapophyses are not verified. The neural spines are very large but not very elongate.

The haemal spines are elongate and stout; the haemal arches are fused to their respective centra. Intermuscular bones are lacking as it does with all amiids (Fig.3A).

Due to the incompleteness of the specimen, it can be only tentatively assigned to the Amiidae, possibly to Vidalamiini (*sensu* Grande & Bemis, 1998) (Fig.3B).

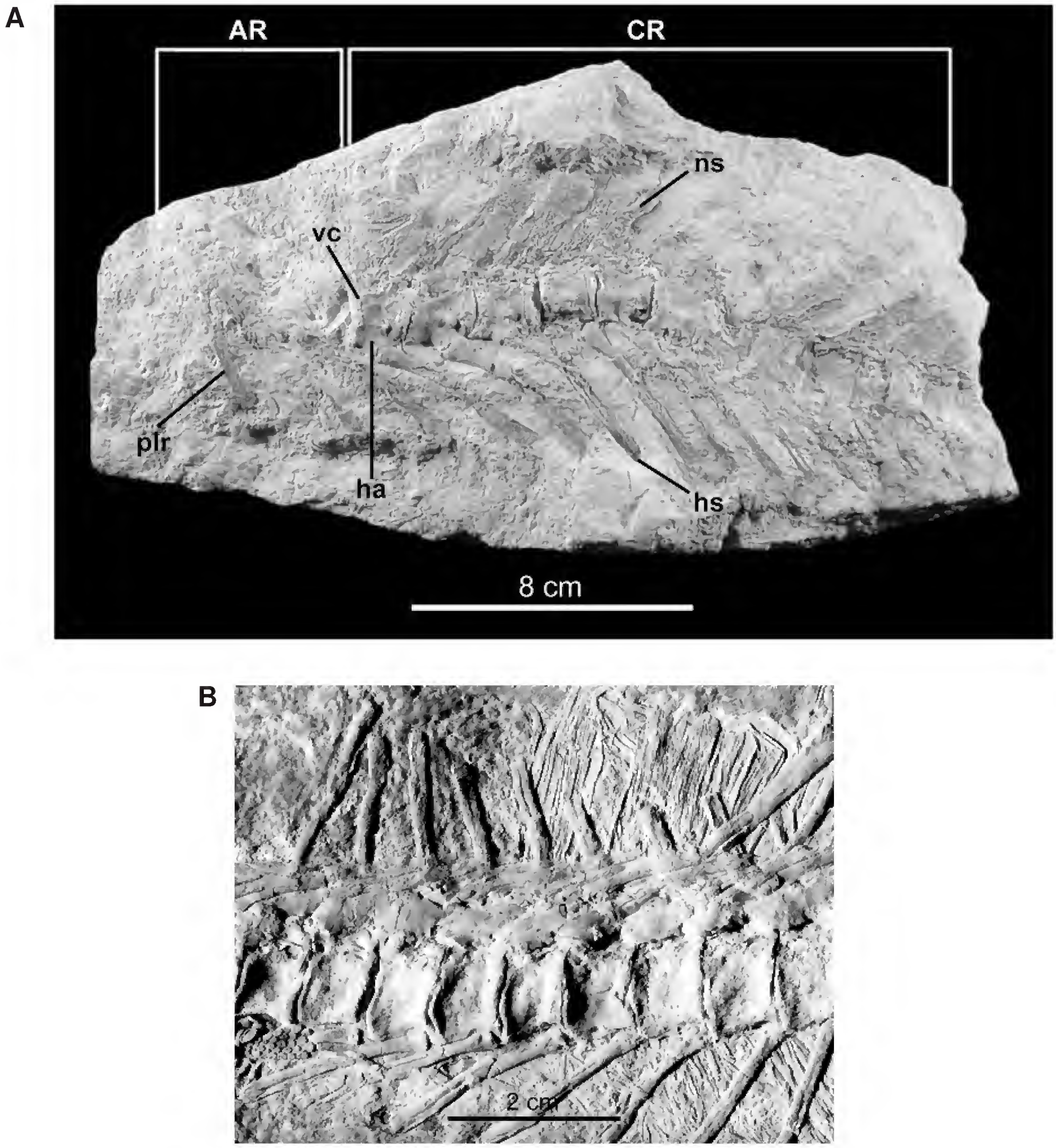

Fig.3- Portion of the vertebral column of Vidalamiini: (A) specimen from the Cotinguiba Formation (MN 7028-V), in left lateral view; (B) the Vidalamiini *Pachyamia mexicana*, in right lateral view (modified after Grande & Bemis, 1998). Anatomical abbreviations: (AR) abdominal region; (CR) caudal region; (ha) haemal arch; (hs) haemal spine; (ns) neural spine; (plr) pleural rib; (vc) vertebral centrum.

2) Teleostei
Neoteleostei
Aulopiformes
Dercetidae

The material MN 7029-V consists of a set of 11 vertebrae from the abdominal and caudal regions. The precaudal vertebrae are strong, longer than deep, medially constricted, with neural arch markedly curved. They bear two pairs of transverse processes per centrum. The anterior processes incline slightly forwards, whereas the posterior ones incline slightly toward the posterior region (Fig.4). The caudal vertebrae are deeper than long and medially constricted. The entire length of the dorsal surface of all centra is occupied by an elongated neural arch; the neural spine is short and inclined; the haemal spine is long and posteriorly projected (Figs.5-6).

Similar vertebrae are found in certain Dercetidae, such as *Rhynchodercetis gortanii* (see Goody, 1969).

3) Teleostei indetermined

The material (MN 7030-V) is represented by part of the opercle and cleithrum and a large part of the trunk. The caudal fin is not preserved. The body is covered by thin cycloid scales, apparently cordiform, strongly imbricated. Several concentric circuli are observed on their surface but radii seem to be absent. The scales of the lateral line are easily discernible by bearing tubes of the sensory canal (Fig.7).

The specimen is provisorily identified as a Teleostei *incertae sedis*.

DISCUSSION

Considering the amiid, the specimen was compared with literature data (*e.g.*, Chalifa & Tchernov, 1982; Grande & Bemis, 1998), which allow to tentatively assign it to the Vidalamiini. The similar features are (Fig.3): presence of smooth centra and short and well-ossified ribs abruptly truncated at their distal ends and the pattern of attachment of the haemal spines (autogenous). According to Grande & Bemis (1998), the peculiar truncation of the ribs is a diagnostic character of Vidalamiini (*Vidalamia* + *Pachyamia*). So far as known, the genus *Vidalamia* occurs from the Berriasian to the Hauterivian of Spain (Wenz & Poyato-Ariza, 1994; Grande & Bemis, 1998). Hitherto, *Pachyamia* was found in the marine Cenomanian of Israel (Chalifa & Tchernov, 1982) and ?late Albian of Mexico (Grande & Bemis, 1998).

The specimen MN 7029-V (Figs.5A-6A) shows a very reduced neural spine, which is proposed as a synapomorphy of the family Dercetidae by Gallo *et al.* (2005). Representatives of this family are found in the Cenomanian to the Danian deposits of Tethyan Europe, Asia, Africa, Central and South America.

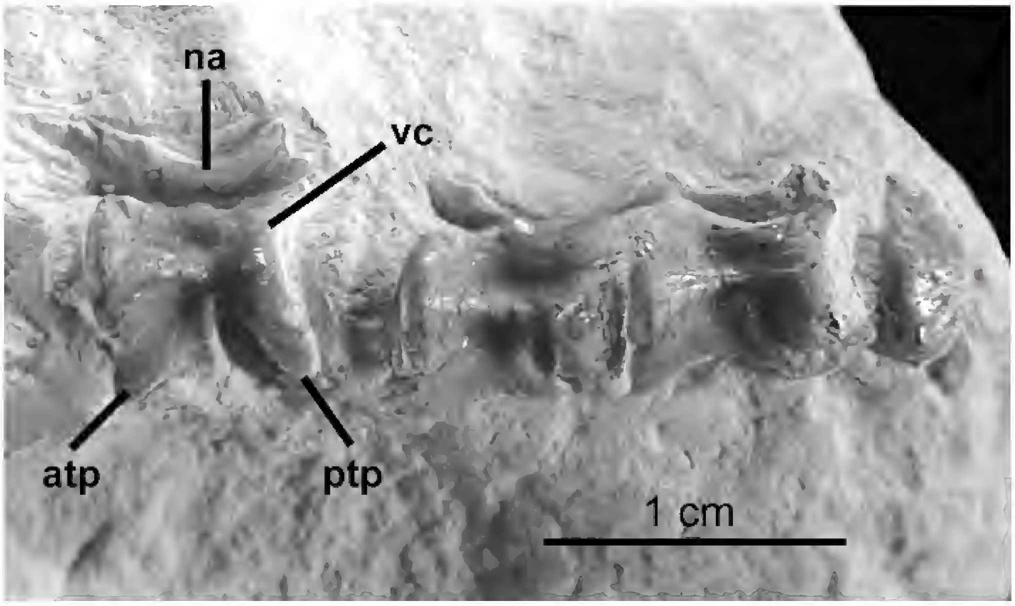

Fig.4- Precaudal vertebrae of the Dercetidae from the Cotinguiba Formation (MN 7029-V), in left lateral view. Anatomical abbreviations: (atp) anterior transverse process; (na) neural arch; (ptp) posterior transverse process; (vc) vertebral centrum.

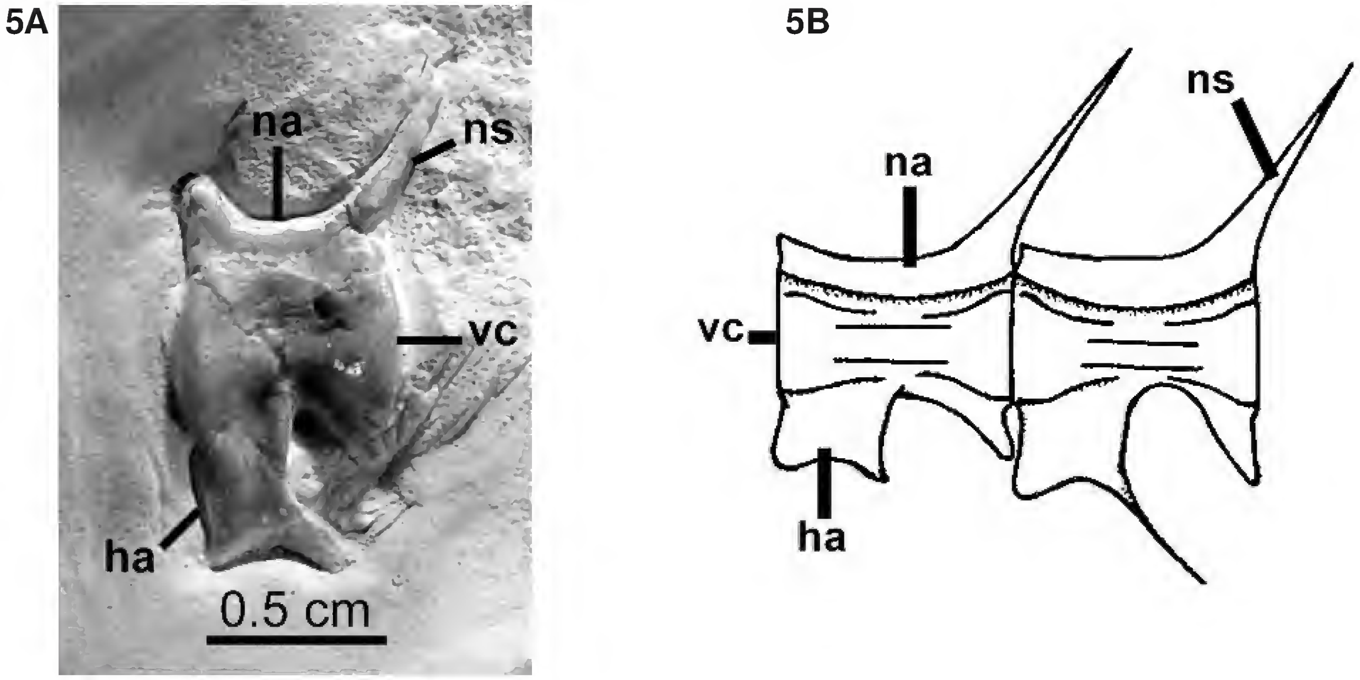

Fig.5- Anteriormost caudal vertebra of the Dercetidae, in left lateral view: (A) specimen from the Cotinguiba Formation (MN 7029-V); (B) first and second caudal vertebrae of *Rhynchodercetis gortanii* (modified after Goody, 1969). Original drawing without scale. Anatomical abbreviations: (ha) haemal arch; (na) neural arch; (ns) neural spine; (vc) vertebral centrum.

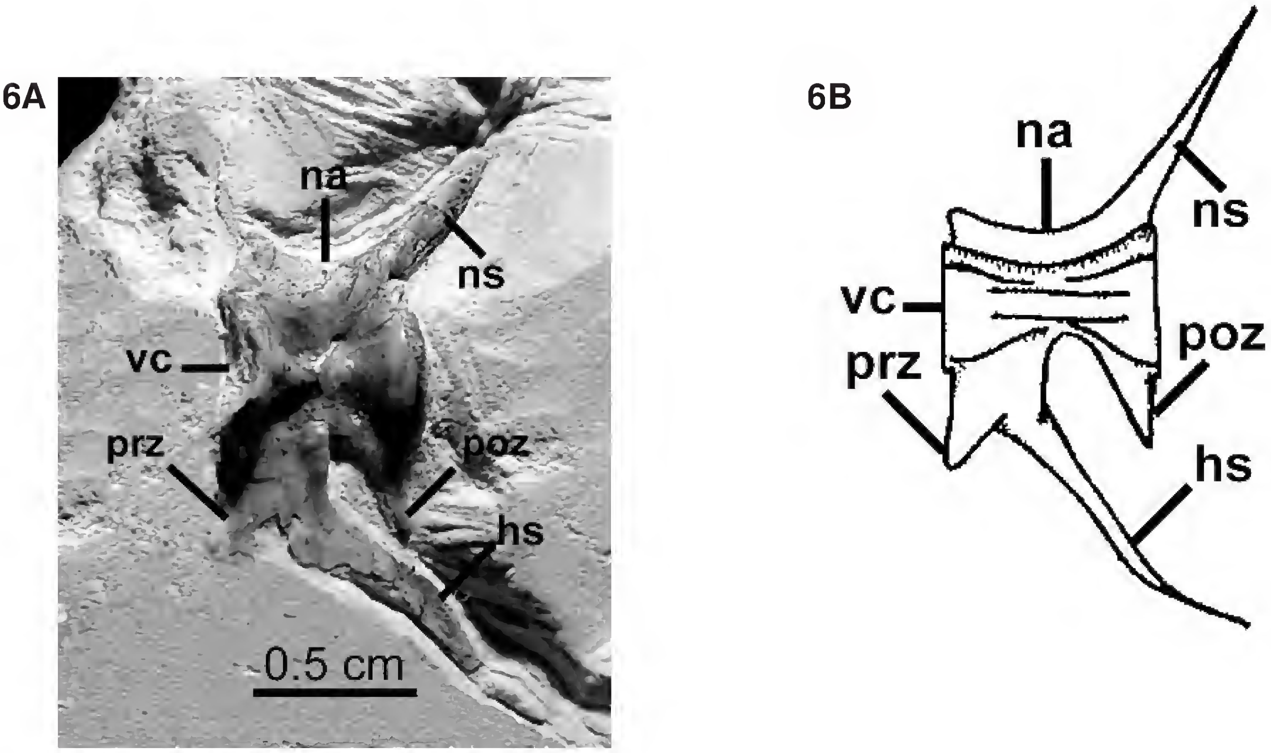

Fig.6- Caudal vertebra of the Dercetidae, in left lateral view: (A) specimen from the Cotinguiba Formation (MN 7029-V); (B) fifteenth caudal vertebra of *Rhynchodercetis gortanii* (modified after Goody, 1969). Original drawing without scale. Anatomical abbreviations: (hs) haemal spine; (na) neural arch; (ns) neural spine; (poz) postzygapophysis; (prz) prezygapophysis; (vc) vertebral centrum.

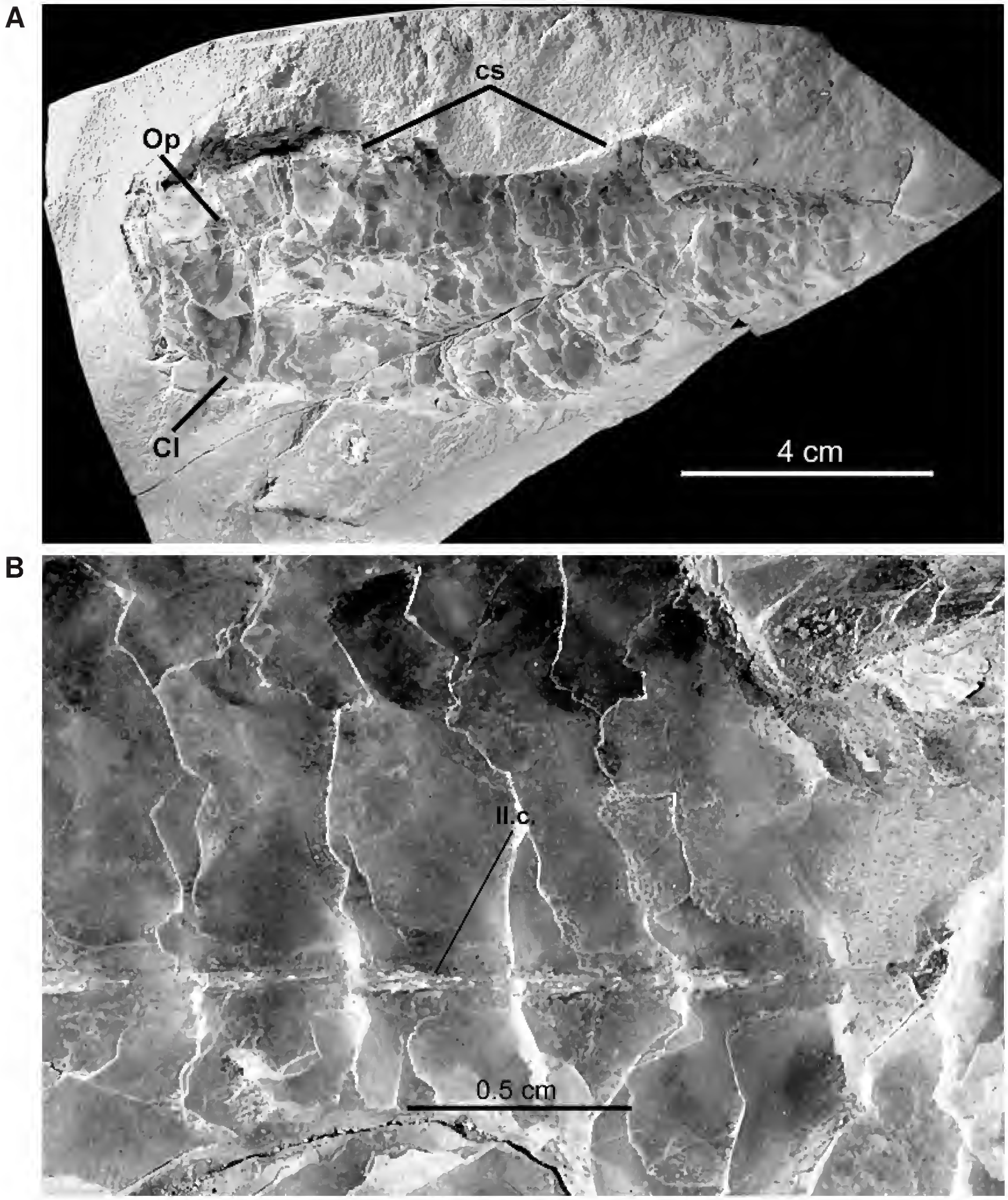

Fig.7- Teleostei *incertae sedis* from the Cotinguiba Formation (MN 7030-V): (A) articulated cycloid scales; (B) detail of the scales of the lateral line. Anatomical abbreviations: (Cl) cleithrum; (cs) cycloid scales; (ll.c.) lateral line canal; (Op) opercle.

This latter record comes from the early Turonian of the Pelotas Basin (southern Brazil) and occurs together with chondrichthyan and osteichthyan. This association shows remarkable taxonomic correspondence with members from the Turonian assemblages of northeastern Brazil, Morocco, and Mexico, suggesting a biogeographical hypothesis which was investigated (Gallo *et al.*, 2007).

Regarding the specimen MN 7030-V (Fig.7), the scales represent most of the preserved material. These structures are very generalized, which make difficult a more inclusive classification within Teleostei.

The age of the fishes above described is established using the biostratigraphical zonation for the Turonian of the Sergipe Basin by ANDRADE *et al.* (2003, 2005) and ANDRADE (2005), which is based on inoceramids and ammonites. The amiid and the dercetid fishes occur in the middle Turonian in the *Mytiloides hercynicus* Zone. The Teleostei *incertae sedis* comes from the lower Turonian in the *Mytiloides labiatus* and *Mammites nodosoides-Kamerunoceras turoniense* zones.

These new records of Amiidae and Dercetidae in the Cotinguiba Formation widen their paleogeographical distribution during Turonian.

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MORPHOMETRIC ANALYSIS OF THE UPPER CRETACEOUS BRAZILIAN SIDE-NECKED TURTLE *BAURUEMYS ELEGANS* (SUÁREZ, 1969) (PLEURODIRA, PODOCNEMIDIDAE) [1]

(With 3 figures)

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ABSTRACT: The Upper Cretaceous Brazilian side-necked turtle *Bauruemys elegans* is a basal branch of Podocnemididae. Several well preserved topotypes of *B. elegans* were collected during field work in the last decade and a quantitative study of its morphologic variation is, therefore, feasible. Forty characters that represent distances of two landmarks (*e.g.* intersections between bone plates) were analyzed. The investigation was performed through multivariate exploration via Principal Component Analysis (PCA). Neural series measurements have shown little variation, whereas vertebral scute series were more variable. Only a single specimen was out of 95% ellipse of PC2 and PC3 of comprised measurements of the plastron and this out plot was interpreted as due to ontogenetic difference. No other specimen showed significant difference to the medial values, corroborating the null hypothesis that the sample represents a unique population of *B. elegans* and the observed variation would be explained by different age stages.

Key words: *Bauruemys elegans*. Principal Components Analysis. Pirapozinho site. Testudines.

RESUMO: Análise morfométrica da tartaruga do Cretáceo Superior brasileiro *Bauruemys elegans* (Suárez, 1969) (Pleurodira, Podocnemididae).

A tartaruga Pleurodira do Cretáceo Superior brasileiro *Bauruemys elegans* é um ramo basal de Podocnemididae. Diversos topótipos bem preservados de *B. elegans* foram coletados durante trabalhos de de campo realizados nas últimas décadas e um estudo sobre sua variação morfológica é, portanto, viável. Quarenta caracteres (medidas) representando distâncias entre dois marcos anatômicos (*e.g.* interseções entre placas ósseas) foram analisados. A investigação foi realizada através de exploração multivariada via Análise de Componentes Principais (PCA). As medidas da série neural apresentaram pequena variação em relação às da série vertebral, que se mostraram mais variáveis. Somente um único exemplar ficou fora da elipse de 95% para os PC2 e PC3 das medidas do plastrão e este desvio foi interpretado como devido a diferenças ontogenéticas. Nenhum outro espécime apresentou diferenças significativas dos valores médios, corroborando a hipótese nula de que a amostra é representativa de uma única população de *B. elegans* e de que a variação observada pode ser explicada como devida a diferenças etárias.

Palavras-chave: *Bauruemys elegans*. Análise de Componentes Principais. Sítio de Pirapozinho. Testudines.

INTRODUCTION

The site of Pirapozinho, informally called “Tartaruguito”, was discovered during the construction of Sorocabana railroad in 1950’s (Suárez, 1969a,b,c; 2002). Situated in the municipality of Pirapozinho (west of São Paulo State, 22°13’08"S; 51°25’59"W, Fig.1) this is the type-locality of *Bauruemys elegans* (Suárez, 1969), a basal branch of Podocnemididae (Kischlat, 1996; Romano & Azevedo, 2006), that corresponds to the single fossil turtle from Bauru Basin which is represented by cranial and post-cranial materials. Yet, four other nominal Testudines taxa have been proposed to Bauru Basin, namely: *Roxochelys harrisi* (Pacheco, 1913), *Bauruemys brasiliensis* (Staeche, 1937), *Roxochelys wanderleyi* Price, 1953, and *Cambaremys langertoni* França & Langer, 2005. In most recent revisions, *R. harrisi* was considered a *nomen dubium* and *B. brasiliensis* was only tentatively allocated in *Bauruemys* (Kischlat, 1994; Kischlat *et al.*, 1994),

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corresponding to an *incertae sedis* (Oliveira & Romano, 2007). Nevertheless, França & Langer (2005) assumed that *Cambaremys langertoni* might represent a juvenile form of *Bauruemys brasiliensis* and that this uncertainty could not be dismissed until more complete specimens are recovered.

Several well-preserved specimens attributed to *B. elegans* were collected at "Tartaruguito" site during field work performed in the last ten years and a quantitative approach is feasible. Classical morphometric studies have been carried out with living pleurodiran turtles in order to determine population structure and sex ratio, mainly in species of *Podocnemis* (*e.g.*: Kuchling, 1988; Valenzuela *et al.*, 1997; Escalona & Fa, 1998; Valenzuela, 2001; Fachín-Terán *et al.*, 2003; Fachín-Terán & Vogt, 2004). However, this kind of approach is rare in paleontological studies (*e.g.*: Forster, 1996; Christiansen, 1999).

Preliminary taphonomic studies (Henriques *et al.*, 2002, 2005) suggest that a single population of *B. elegans* is represented in the sample collected at "Tartaruguito". We analyzed some specimens collected at this locality to investigate if significant variation could be determined. The quantitative information was explored using bivariate and multivariate morphometric shape analysis, in order to test the null hypothesis suggested by taphonomic analyses.

MATERIAL AND METHODS

A total of 18 topotypes of *Bauruemys elegans* (MN 4327-V, MN 6674-V, MN 6761-V, MN 6762-V, MN 6771-V, MN 6772-V, MN 6782-V, MN 6789-V, MN 6790-V, MN 6791-V, MN 6795-V, MN6796-V, MN 6797-V, MN 6798-V, MN 6800-V, MN 6807-V, MN 7015-V, MN 7016-V) from the collection of the Departamento de Geologia e Paleontologia, Museu Nacional, Universidade Federal do Rio de Janeiro (DGP/MN/UFRJ) were examined in this study. All specimens were prepared with traditional techniques (May *et al.*, 1994).

We employed 24 carapace and 16 plastron characters which were separated into three sorts of quantitative data matrix (covariance matrix): (1) total lengths and width, (2) comprised measurements of the carapace, and (3) comprised measurements of the plastron. The turtle shell provides numerous landmarks for depicting morphological variation in a objective way, and it is easy to identify homology between the elements of the shell and determinate quantitative characters. All characters represent distances of two landmarks (*e.g.* intersections between bone plates; see Fig.2) and measurements of the neural plates were preferred since it is the most variable elements of the turtle shell (Pritchard, 1988). Measurements of all characters are in mm and were made by Pedro Romano using Mitutoyo micrometer (Stainess-Hordened) of 150 and 1000mm.

All statistic analyses were conducted using the software PAST version 1.15 (Hammer *et al.*, 2003). Descriptive statistics (including arithmetic means, standard deviation, median, maximum and minimums values) of all 40 characters were calculated in order to express the variation of each one. Multivariate analyses were performed using exploration via Principal Component Analysis (PCA). The PCA is one of the simplest of the multivariate methods and the objective of this analysis is to take some variables and find combinations of these to produce indices (the variance or eigenvalues of the PC) that are uncorrelated, which means that the indices are measuring different dimensions in the data (Manly, 1986). If the original variables are highly correlated, positively or negatively, mean that the variables are adequately represented by two or three principal components and that there is a good deal of redundancy in the data if there is very high correlation (Manly, 1986).

Since all characters analyzed represent linear measurements, we aim to investigate if the variation between the specimens is significant and/or if there is a pattern of distribution in the sample. Therefore, each specimen was scattered in order to seek for difference among specimens, and each character was loaded in order to show what degree the original variables are different of principal components. However, our analyses do not consider the possibility of polimorfism and sexual dimorphism as eventual explanations for the variability observed since those explanations need *a priori* assumptions undetectable on the sample (*i.e.*: discrete categories of characters, as tail length, which might be used to determine sexual dimorphism).

Abbreviations: (TLC) Total Length of Carapace; (TWC) Total Width of Carapace; (LN) Length of Nuchal; (LN1) Length of first Neural; (LN1) Length of first Neural; (LN2) Length of second Neural; (LN3) Length of third Neural; (LN4) Length of fourth Neural; (LN5)

Length of fifth Neural; (LN6) Length of sixth Neural; (WN) Width of Nuchal; (WN1) Width of first Neural; (WN2) Width of second Neural; (WN3) Width of third Neural; (WN4) Width of fourth Neural; (WN5) Width of fifth Neural; (WN6) Width of sixth Neural; (LS1) Length of first Scute; (LS2)- Length of second Scute; (LS3) Length of third Scute; (LS4) Length of fourth Scute; (WS1) Width of first Scute; (WS2) Width of second Scute; (WS3) Width of third Scute; (WS4) Width of fourth Scute; (TLP) Total Length of Plastron; (TWP) Total Width of Plastron; (LEP) Length between Epiplastra; (LEN) Length of Endoplastron; (LHY) Length of Hyoplastra; (LHP) Length of Hypoplastra; (LXI) Length of Xiphiplastra; (WEN) Width of Endoplastron; (WHH) Width between Hyo-Hypoplastron; (WHX) Width between Hypo-Xiphiplastron; (LGU) Length of Inter-gular Scute; (LHU) Length of Inter-humeral Scute; (LPE) Length of Inter-pectoral Scute; (LAB) Length of Inter-abdominal Scute; (LFE) Length of Inter-femoral Scute; (LAN) Length of Inter-anal Scute.

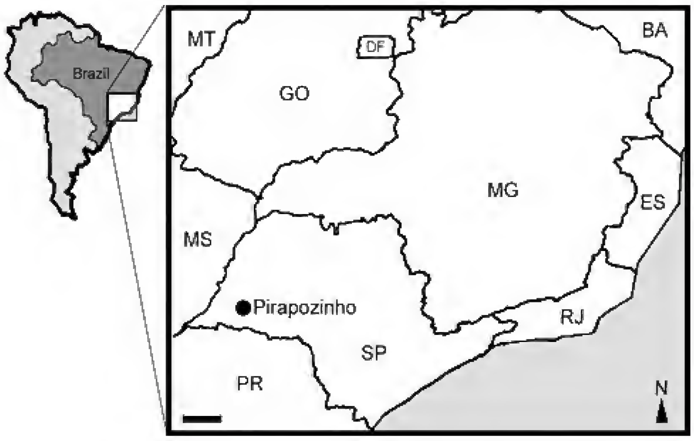

Fig.1- Map of southwester Brazil . Dot indicates location of Pirapozinho site from which the specimens were collected (22° 13' 08'' S; 51° 25' 59'' W). Scale bar: 100 Km. Acronyms: BA (Bahia State), DF (Distrito Federal), ES (Espirito Santo State), GO (Goiais State), MG (Minas Gerais State), MS (Mato Grosso do Sul State), MT (Mato Grosso State), PR (Paraná State), RJ (Rio de Janeiro State), SP (São Paulo State).

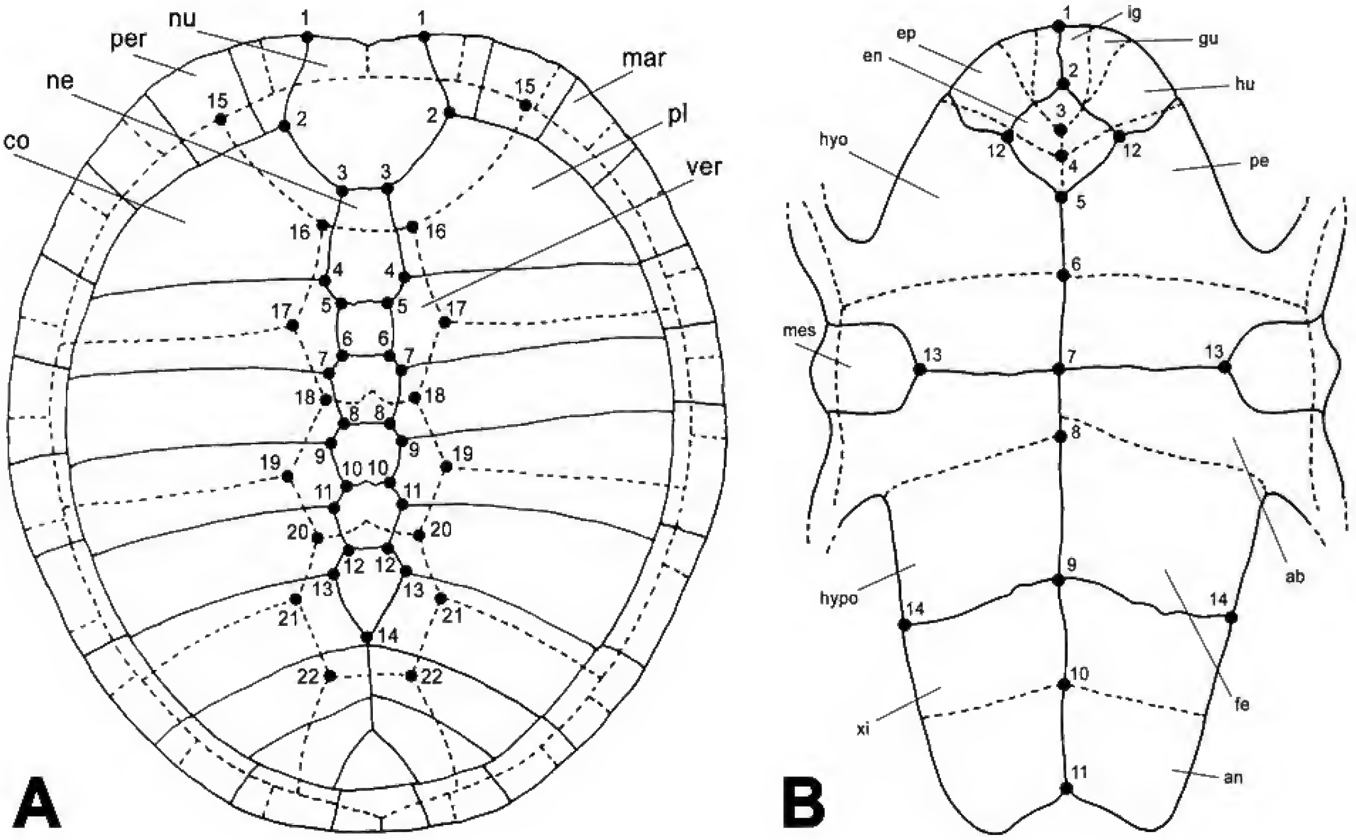

Fig.2- Landmarks of carapace (A) and plastron (B) used to trace linear measurements. The 14 quantitative characters (linear vectors) are indicated at tables 1 and 2. Figure based on specimens MN 6674-V; MN 6762-V and MN 6772-V. Abbreviations: (ab) abdominal scute, (an) anal scute, (co) costal bones, (en) endoplastron, (ep) epiplastron, (fe) femoral scute, (gu) gular, (hu) humeral scute, (hypo) hypoplastron, (hyo) hyoplastron, (ig) intergular, (mar) marginal scute, (mes) mesoplastron, (ne) neural plates, (nu) nuchal bone, (pe) pectoral scute, (per) peripheral bones, (pl) pleural scutes, (ver) vertebral scutes, (xi) xiphiplastron.

RESULTS

The descriptive statistics of all characters are sumarized in Table 1. As expected, the total length and width characters (TLP, TWP, TLC, TWC) have shown the biggest variation amplitude. Neural series measurements (LN, LN1, LN2, LN3, LN4, LN5, LN6, WN, WN1, WN2, WN3, WN4, WN5, WN6) have shown little variation whereas vertebral scute series (LS1, LS2, LS3, LS4, WS1, WS2, WS3, WS4) were more variable. Plastron characters (LEP, LEN, LHY, LHP, LXI, WEN, WHH, WHX, LGU, LHU, LPE, LAB, LFE, LAN) have shown equivalent variation.

PCA were performed to three classes of characters from three distinct covariance matrix (Fig.3). The first three principal components obtained from a covariance matrix of total lengths and width respond for 88.298% of the total variation (PC1 = 60.704%, PC2 = 26.057 e PC3 = 1.537%). The first three principal components obtained from a covariance matrix of comprised measurements of the carapace respond for 80,213% of the total variation (PC1 = 49,532%, PC2 = 21,497% e PC3 = 9,184%).

TABLE 1. Descriptive statistics of the three sorts of characters analyzed (total length and width, comprised measurements taken from the carapace, and comprised measurements taken from the plastron) including mean values (Mean), standard deviation (SD), median values (Median), number of entries (N), and smallest and largest values (Max and Min).

	Characters	Vector*	Mean	SD	Median	N	Max and Min
Total length and width	TLC	---	275.4	35.7	279.4	8	348.0 – 225.0
	TWC	---	230.8	42.2	220.0	7	317.5 – 185.0
	TLP	---	236.5	41.7	218.05	6	299.4 – 189.0
	TWP	---	182.2	33.9	165.5	7	242.5 – 149.0
Comprised measurements taken from the carapace	LN	1-2	37.4	10.6	33.0	8	60.2 – 26.0
	LN1	3-4	36.9	4.4	37.5	9	44.6 – 27.4
	LN2	5-6	19.6	3.2	19.2	10	27.6 – 15.0
	LN3	6-8	25.4	3.8	24.6	9	33.1 – 20.5
	LN4	8-10	22.6	3.5	22.0	10	30.7 – 18.3
	LN5	10-12	23.0	4.6	22.7	12	34.0 – 18.2
	LN6	12-14	25.1	7.6	23.8	11	45.5 – 16.1
	WN	2-2	47.9	8.3	45.6	6	64.6 – 38.7
	WN1	4-4	24.4	3.9	24.1	10	33.4 – 18.0
	WN2	5-5	16.9	1.8	17.0	10	21.4 – 14.0
	WN3	7-7	23.9	3.7	24.0	10	33.5 – 20.0
	WN4	9-9	23.8	3.8	23.6	10	33.6 – 19.0
	WN5	11-11	25.6	6.1	23.8	12	43.0 – 20.3
	WN6	13-13	24.1	6.3	23.0	11	40.6 – 16.4
	LS1	15-16	42.3	6.8	41.8	9	56.3 – 31.4
	LS2	16-18	55.6	7.2	56.1	11	68.5 – 43.0
	LS3	18-20	49.9	10.7	46.8	12	79.0 – 38.6
	LS4	20-22	46.9	10.7	44.1	11	76.0 – 35.3
	WS1	15-15	70.1	8.0	68.9	7	84.0 – 58.4
	WS2	17-17	62.5	6.5	61.8	9	76.2 – 54.0
	WS3	19-19	60.3	7.7	60.5	10	79.0 – 51.0
	WS4	21-21	56.6	12.8	51.7	11	89.4 – 45.0
Comprised measurements taken from the plastron	LEP	1-2	20.7	3.6	20.65	8	25.4 – 14.3
	LEN	2-5	43.8	10.1	39.6	9	60.1 – 33.5
	LHY	5-7	67.5	20.4	62.5	12	130.0 – 50.5
	LHP	7-9	45.7	9.4	41.6	13	62.5 – 35.6
	LXI	9-11	63.4	8.0	63.2	13	80.5 – 53.2
	WEN	12-12	44.2	9.9	40.15	10	60.4 – 32.2
	WHH	7-13	59.4	12.7	56.9	13	89.4 – 46.0
	WHX	9-14	48.2	6.7	48.1	13	61.3 – 40.5
	LGU	1-3	43.3	9.7	39.1	8	62.0 – 33.4
	LHU	3-4	10.1	3.3	9.4	11	19.6 – 7.1
	LPE	4-6	41.6	9.9	41.35	12	60.4 – 25.7
	LAB	6-8	50.6	10.0	46.8	13	70.1 – 38.4
	LFE	8-10	57.8	9.5	55.8	12	80.0 – 42.9
	LAN	10-11	33.8	4.7	33.2	13	44.3 – 27.7

Measurements of all characters are in mm; (*) landmarks used to trace linear measurements. See figure 2.

The first three principal components obtained from a covariance matrix of comprised measurements of the plastron respond for 92,507% of the total variation (PC1 = 48,403%, PC2 = 23,944 e PC3 = 20,160%). In Table 2 are summarized the loadings values of all 40 characters for the first three principal components. Twenty nine characters are positively correlated with respective first principal component. Two total lengths and width characters (TLP, TWP), six carapace characters (LN5, LN6, WN5, WN6, LS5, LS4) and three plastron characters (LEP, LEN, LGU) are negatively correlated.

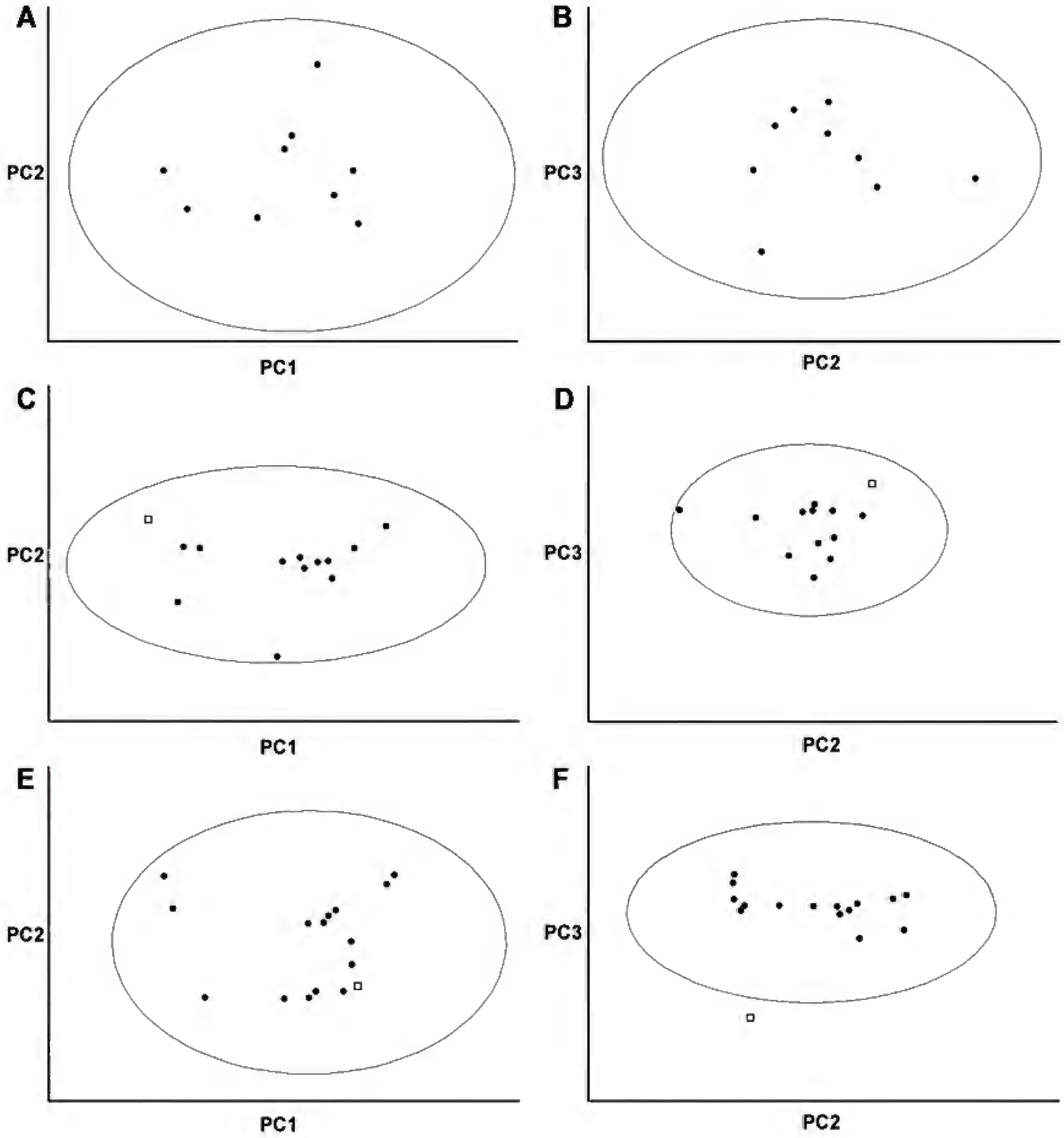

Fig.3- Bi-plot of Principal Components. (A) PC1 vs PC2 of total lengths and width measurements, (B) PC2 vs. PC3 of total lengths and width measurements (C) PC1 vs. PC2 of comprised measurements of the carapace, (D) PC2 vs. PC3 of comprised measurements of the carapace, (E) PC1 vs. PC2 of comprised measurements of the plastron, and (F) PC2 vs. PC3 of comprised measurements of the plastron. The circles indicate the 95% ellipse of normal distribution. Only the specimen MN 6782-V (white square) was out of this ellipse for PC2 vs. PC3 bi-plot of comprised measurements of the plastron.

Twenty four characters are positively correlated with respective second principal component. Nine carapace characters (LN1, LN2, WN, WN1, WN2, WN3, LS1, LS2, WS2) and seven plastron characters (LHY, LHP, LXI, WHH, WHX, LAB, LAN) are negatively correlated. Only 19 characters are positively correlated with respective third principal component. Despite that, all loadings values (positives and negatives) are relatively low.

DISCUSSION

The habitat of some extant Podocnemididae is similar to that inferred to "Tartaruguito" site based on geological studies and taphonomic data, which indicates a seazonal semi-arid climate to the region with waterlessness regions during dry station (Langer & Bertini, 1995; Henriques *et al.*, 2002, 2005). Based on this scenario, it is possible that the sample represents a single population of *Bauruemys elegans* which individuals agglomerated and died around a drying-up water body. Since a single population consists on a conjunct of semaforontes, the present morphometric study do not exclude the scenario proposed by Henriques (2006), on which at least ten distinct events of

TABLE 2. The first three Principal Components (PC) loadings of the three sorts of characters analyzed (total length and width, comprised measurements taken from the carapace, and comprised measurements taken from the plastron).

	Characters	Vector*	PC1	PC2	PC3
Total length and width	TLC	---	+ 0.6005	+ 0.2909	− 0.5014
	TWC	---	+ 0.5640	+ 0.4566	+ 0.2265
	TLP	---	− 0.5338	+ 0.5984	− 0.5496
	TWP	---	− 0.1909	+ 0.5906	+ 0.6287
Comprised measurements taken from the carapace	LN	1-2	+ 0.2869	+ 0.0105	+ 0.1791
	LN1	3-4	+ 0.2634	− 0.0519	− 0.0301
	LN2	5-6	+ 0.0847	− 0.0999	− 0.0311
	LN3	6-8	+ 0.0998	+ 0.0637	+ 0.0701
	LN4	8-10	+ 0.0596	+ 0.0748	+ 0.1698
	LN5	10-12	− 0.0091	+ 0.1715	− 0.0002
	LN6	12-14	− 0.0576	+ 0.2296	− 0.1786
	WN	2-2	+ 0.2846	− 0.0608	− 0.5441
	WN1	4-4	+ 0.1445	− 0.0083	+ 0.0922
	WN2	5-5	+ 0.0980	− 0.0158	+ 0.0624
	WN3	7-7	+ 0.1375	− 0.0166	+ 0.0388
	WN4	9-9	+ 0.0629	+ 0.0863	+ 0.1738
	WN5	11-11	− 0.0275	+ 0.2003	− 0.0455
	WN6	13-13	− 0.0511	+ 0.2098	− 0.1511
	LS1	15-16	+ 0.3187	− 0.0626	− 0.0479
	LS2	16-18	+ 0.2479	− 0.1272	+ 0.2101
	LS3	18-20	− 0.0400	+ 0.3741	− 0.0455
	LS4	20-22	− 0.0823	+ 0.3926	− 0.2741
	WS1	15-15	+ 0.5052	+ 0.2343	− 0.1103
	WS2	17-17	+ 0.4475	− 0.1143	− 0.0399
	WS3	19-19	+ 0.2434	+ 0.3420	+ 0.6279
	WS4	21-21	+ 0.0107	+ 0.5481	− 0.0595
Comprised measurements taken from the plastron	LEP	1-2	− 0.0120	+ 0.2498	+ 0.0091
	LEN	2-5	− 0.0028	+ 0.5564	+ 0.0351
	LHY	5-7	+ 0.5026	− 0.0028	− 0.4568
	LHP	7-9	+ 0.3343	− 0.0228	− 0.0727
	LXI	9-11	+ 0.2714	− 0.0495	+ 0.5388
	WEN	12-12	+ 0.0280	+ 0.5344	+ 0.0491
	WHH	7-13	+ 0.4267	− 0.0694	− 0.1460
	WHX	9-14	+ 0.2089	− 0.0353	+ 0.4131
	LGU	1-3	− 0.0272	+ 0.5367	+ 0.0192
	LHU	3-4	+ 0.0094	+ 0.0700	− 0.1106
	LPE	4-6	+ 0.2385	+ 0.1848	− 0.2274
	LAB	6-8	+ 0.3577	− 0.0099	− 0.1017
	LFE	8-10	+ 0.3625	+ 0.0735	+ 0.3726
	LAN	10-11	+ 0.1350	− 0.0301	+ 0.2939

(*) Landmarks used to trace linear measurements. See figure 1.

agglomeration of turtles might have occurred in this locality. The PCAs plotted a single specimen (MN 6782-V) out of 95% ellipse of normal distribution, that corresponds to PC2 and PC3 of comprised measurements of the plastron (see Fig2F). MN 6782-V is the biggest specimen analyzed, but it is represented only by the posterior portion of the carapace and medial portion of the plastron, and does not present any distinctive character in relation to *B. elegans*. Therefore, this out plot was interpreted as due to ontogeny.

Neural series is the most inter-specific variable element of the turtle shell (PRITCHARD, 1988). In the present sample, the measurements of neurals have shown little variation confirming the null hypothesis of having a single population of *Bauruemys elegans* in the sample. Interestingly, the length and width values of neural 5 and 6 showed negative loadings for PC1 and PC3. As pointed by PRITCHARD (1988), neurals might become fused in adults in several Testudines taxa, including extant Podocnemididae genus *Erymnochelys*. In *Podocnemis* and *Peltocephalus*, the number of neurals is usually seven. In *Erymnochelys*, the seven neurals are present in young specimens, but the last two neurals are liable to fuse in old animals (PRITCHARD, 1988). This trend might explain the negative loading values of neurals 5 and 6 as a tendency of reduction of size of those elements in the adult of *Bauruemys elegans*.

The observed morphometric difference among analyzed specimens supports the null hypothesis provided by taphonomic data, *i.e.*: that the sample represents a single population of *B. elegans*. Since no significant variation was observed, the explanation for this variation is assumed to be ontogenetic.

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PAST AND PRESENT DISTRIBUTION OF IGUANID LIZARDS [1]

(With 10 figures)

MARC AUGÉ [2]

ABSTRACT: The systematic diversity of the European iguanids is briefly reviewed. A new species, *Geiseltaliellus pradiguensis* sp.nov., is described from the Middle Eocene. The past distribution of iguanid lizards during the late Cretaceous and the Paleogene is examined and contrasted with their present distribution. These observations suggest that Iguanidae had a broad distribution during the late Mesozoic/ early Cenozoic and that, afterwards, iguanid lizards have withdrawn from Eurasia. Competition with other groups may have contributed to the extinction of Old World iguanid lizards. The fossil record shows that agamids did not play a central role in the extinction of iguanids. Mechanisms that affected the history of iguanids in Europe and Asia might be competitive interactions with lacertid lizards. Arguments for and against this hypothesis are examined. A test is carried out on the relative abundance of the iguanids and lacertids in Europe during the Eocene in order to reveal the potential role of competition.

Key words: Squamata. Iguanidae. Middle Eocene. France.

RESUMO: Distribuição passada e presente de lagartos iguanídeos.

A diversidade sistemática dos iguanídeos europeus é brevemente revisada. Uma nova espécie, *Geiseltaliellus pradiguensis* sp.nov., é descrita para o Eoceno Médio. A distribuição dos lagartos iguanídeos durante o Cretáceo e o Paleógeno é aqui examinada e contrastada com sua recente distribuição. As observações feitas sugerem que os Iguanidae tiveram uma ampla distribuição durante o Mesozóico Superior/Cenozóico Inferior e que, ulteriormente, os lagartos iguanídeos desapareceram da Eurásia. A competição com outros grupos pode ter contribuído para a extinção desses lagartos do Velho Mundo. O registro fóssil demonstra que os agamídeos não foram os responsáveis pela extinção dos iguanídeos. As interações competitivas com os lagartos lacertídeos devem ter sido os mecanismos que afetaram a história dos iguanídeos na Europa e na Ásia. Argumentos a favor e contra esta hipótese são examinados. É feito um teste sobre a abundância relativa dos iguanídeos e lacertídeos na Europa durante o Eoceno de forma a revelar o papel potencial da competição.

Palavras-chave: Squamata. Iguanidae. Eoceno Médio. França

INTRODUCTION

Today, iguanid lizards occur mainly in the Western Hemisphere but a few critical exceptions are registered in Madagascar and remote Pacific islands (Fiji and Tonga). The family has a wide ecological range in both tropical and temperate areas from extreme deserts to tropical rainforest interiors. Their fossil record is not very abundant but shows that the family has been in existence in Asia, North and South America, and possibly in Europe as early as the Cretaceous.

Generally, in the Old World, "iguanid niches" are occupied by agamid lizards (family Agamidae). The classic view (Darlington, 1957) is that the iguanids have been replaced by the more advanced agamids on the Old World continents, notably in Africa. The recent discovery of fossil iguanids in Asia and Europe reinforce this suggestion. However, Blanc (1982) casts doubt on this hypothesis and he wrote: "we have difficulty explaining how the poorly diversified African agamids could have succeeded in totally supplanting the eventual iguanids. Their currently allopatric distributions appear to be more the result of general historical consequences than of competition."

Kuhn (1944) named the first unquestionable european iguanid lizard, *Geiseltaliellus longicaudus*, together with the species *Capitolacerta dubia*. Estes (1983) synonymized *Capitolacerta dubia* with *Geiseltaliellus longicaudus*. A comprehensive taxonomic revision of these lizards was published by Hoffstetter (1955), who rejected their assignment to the Iguanidae. However, Estes (1983) demonstrated that the

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specimens cannot be placed in any other family.

The time scale used for faunal analysis is that defined in SCHMIDT-KITTLER (1987) and BIOCHROM'97 (1997) (Tab.1).

Institutional Abbreviations: MNHN: Muséum national d'Histoire naturelle, Paris; USTL: Université des Sciences et Techniques du Languedoc.

SYSTEMATIC PALEONTOLOGY

EOCENE IGUANIDS

Four iguanid species are known in the European Eocene. The last European iguanids are recorded in the locality of Escamps (MP19), just before the "Grande Coupure", *i.e.*, the Eocene/Oligocene boundary. The traditional definition of the Iguanidea is retained here (= non-acrodont iguanian), keeping in mind that the family could be paraphyletic (FROST & ETHERIDGE, 1989). In other words, the family is considered a metataxon, and neither monophyly nor paraphyly can be evidenced.

Order Squamata Oppel, 1811
Infraorder Iguania Cuvier, 1807
Family IGUANIDAE Gray, 1827

Geiseltaliellus Kuhn, 1944

Type-species – *Geiseltaliellus longicaudus* Kuhn, 1944

Known distribution – Early Eocene (MP7, Dormaal) to late Eocene (MP19, Escamps). Germany, France, Belgium, ?Portugal.

TABLE 1. Stratigraphic positions of lacertilian localities in Europe. Subdivision of the European continental Eocene and Oligocene, based on mammalian standard levels for the Paleogene (MP), as proposed by SCHMIDT-KITTLER (1987) and BIOCHROM' 1997. These biostratigraphic intervals are correlated with the absolute scale (Ma) according to LEGENDRE & LÉVÊQUE (1997).

EPOCH	AGE - MARINE STAGES	MP	STANDARD-LEVELS	LOCALITIES
			France	Europe
EOCENE	-34	20		
		19	Rosières	Mormont-Entreroches
			Escamps	(Swiss)
	PRIABONIAN	18	Gousnat, Ste-Néboule	Osborne beds (England)
			La Débruge	
	-37	17	Perrière, Malpérié	
			Les Pradigues, Fons 1-7	Hordle Bed (England)
		16	Grisolles, Chéry-Chartreuve	
			Lavergne, Le Bretou, Robiac	
	-41	15		
	BARTONIAN			
		14	Lissieu	
		12-13	Saint-Maximin	Geiseltal oMK
	LUTETIAN			Geiseltal Umk (Germany)
		11		Geiseltal UK
	-49			Messel (Germany)
		10	Prémontré, Cuis	
			Grauves, Mas de Gimel	
	YPRESIAN	8-9	Sézanne, Condé-en-Brie	
			Avenay, Mutigny	
		7		Silveirinha (Portugal)
				Dormaal (Belgium)
PALEOC.		6	Berru, Cernay	
	THANETIAN			
		1-5	?Menat	Hainin (Belgium)
				Walbeck (Germany)
	-65			

Geiseltaliellus longicaudus Kuhn, 1944

Capitolacerta dubia Kuhn, 1944: 364, Taf. 20.
Geiseltaliellus louisi Augé, 1990: 114, fig.1.

Holotype – GM 4043, complete specimen, fig.1a-c, pl.19 *in* Kuhn (1944).

Known distribution – Early Eocene (MP7) to Middle Eocene (MP16).
Germany, France, Belgium, ?Portugal.

Comments – *Geiseltaliellus longicaudus* (Figs.1-2) is characterized by having a long tail, three times the length of the body, and the parietal bears a sagittal crest. The teeth are slender, moderately heterodont: the first ten teeth are unicuspid and the following teeth are clearly triconodont, dentary tooth number is 20-25. Medially, the dentary shows a slender subdental shelf which has no sulcus dentalis. The ventral and dorsal borders of the dentary that define the narrow Meckelian canal are nearly contiguous anteriorly.

All records referred to the Iguanidae in Europe were rejected by Hoffstetter (1942, 1955). Nevertheless, the specimens cannot be placed in any other family: *Geiseltaliellus* has a heterodont dentition, its dentaries shows an interesting combination of high-crowned, tricuspid and highly pleurodont teeth, while lacking a sulcus dentalis (dental gutter). This combination of character states indicates that *Geiseltaliellus* is referrable to the family Iguanidae. The tricuspid condition in the Iguanidae is commonly characterized by having a large apical cusp and smaller anterior and posterior cusps. Tricuspid teeth are common in Teiidae, and also occur in some genera of Xantusiidae and Lacertidae. However, in the tricuspid teeth of teiids, the base of the tooth is often swollen and embedded in an important deposit of cementum. The tricuspid condition in the two genera of Xantusiidae is obviously different from that of iguanids: in xantusiids, the two side cusps are more lingually located than the central cusp. The majority of lacertid lizards bear bicuspid teeth, some have tricuspid dentition (*i.e.*, *Plesiolacerta lydekkeri*, from the French middle and late Eocene), but all lacertid lizards show a marked *sulcus dentalis* near the base of the teeth.

The fully preserved skeletons of *Geiseltaliellus* from Messel (MP11) near Darmstadt and the Geiseltal (MP12) pit near Halle (both in Germany), share a large number of morphological similarities with several species formerly (and erroneously) attributed to the Cordylidae.

Geiseltaliellus lamandini (Filhol, 1877)

Lacerta lamandini Filhol, 1877: 489, 490, fig.421.
Pseudolacerta lamandini Hoffstetter, 1942: 239.

Holotype – incomplete right mandible, Old collections of the Phosphorites du Quercy, MNHN, QU 17739, fig.421 *in* Filhol (1877).

Known distribution – End of the Middle Eocene (MP17, Malpérié) to the late Eocene (MP19, Escamps), France, Phosphorites du Quercy.

Comments – The teeth of *G. lamandini* are in general similar to those of *G. longicaudus,* differing in being more stoutly built. Medially, *G. lamandini* bears a clearly defined subdental shelf on the dentary, no definite *sulcus dentalis* can be recognized. The Meckelian canal is narrow, limited anteriorly by the nearly contiguous ventral and dorsal borders, as in *G. longicaudus.*

Hoffstetter (1942) described *Pseudolacerta lamandini* and *Pseudolacerta mucronata*, two Lacertilia from the Eocene of the Phosphorite du Quercy (France), as members of the family Cordylidae, opinion subsequently confirmed by Augé (1987). However, this assignment cannot be maintained, owing to the morphology of the posterior part of the dentary and absence of a *sulcus dentalis* near the base of the teeth. In the holotype of *Pseudolacerta lamandini*, the posterior part of the dentary extends well under the coronoid, a position common to all iguanians, and very different from the morphology exposed in the Scincoidea (Scincidae + Cordylidae). Within the Scincoidea, the posterior part of the dentary does not reach the level of the middle point of the coronoid. Moreover, the posterior part of the dentary is deeply incised by the supraangular notch. Obviously, these features are absent from both *Pseudolacerta* and *Geiseltaliellus*. On these grounds, I have transferred the species *Pseudolacerta lamandini* to the genus *Geiseltaliellus*.

Geiseltaliellus pradiguensis sp.nov.

Holotype – Posterior part of a right maxilla having 14 well-preserved teeth, USTL, PRA 1221 (Fig.3).
Type-locality and range – Les Pradigues, Phosphorites du Quercy, France, end of the Middle Eocene (MP17).

Etymology – From the locality of Les Pradigues, France.

Material – Holotype (Fig.3); anterior part of a right maxilla, USTL, MAL 608, Malpérié (Fig.4) (Phosphorites du Quercy, France).

Known distribution – End of the Middle Eocene

(MP17), Phosphorites du Quercy, France.

Diagnosis – *Geiseltaliellus pradiguensis* sp.nov. is a middle Eocene iguanid distinguished from all other iguanid lizards by its teeth tricuspid, very slender, and tall. Only one-fifth of the tooth height projects beyond the level of the lateral parapet of the maxilla.

Description – The holotype consists of an incomplete right maxilla. The anterior part and the dorsal process of the maxilla are broken. Medially, above the tooth row, a deep, elongated notch (jugal groove) cuts into the posterior part of the supradental shelf. A large maxillary foramen opens in the supradental shelf, above the level of the fifteenth tooth (from the rear of the tooth row). The lateral surface of the jaw is smooth and bears a large lateral foramen.

The maxillary teeth are pleurodont, with the major part of each tooth attached to the lateral parapet of the jaw. The teeth are slender and very tall, slightly compressed under the crown. The tooth shafts are strongly compressed anteroposteriorly. Teeth are closely spaced. No *sulcus* separates the tooth row from the supradental parapet.

The tooth bases are attached close to the lingual border of the supradental shelf and they are not swollen; instead, several teeth have developed a median basal excavation for tooth replacement. The tooth crowns are markedly tricuspid, with a triangular central cusp flanked by two small lateral cusps.

A combination of characters of these maxillae strongly indicates their affiliation within iguanid lizards: tricuspid teeth, absence of a *sulcus* that separates the tooth bases from the supradental shelf; presence of an elongated jugal groove on the dorsal surface of the supradental shelf.

The two specimens are lumped together as *Geiseltaliellus pradiguensis* sp.nov. on the basis of their general resemblances in having tricuspid teeth, with only 20% of their height projecting beyond the parapet of the jaw. These two maxillae are referrable to *Geiseltaliellus* on the basis of their slender and high tooth shafts, their tooth crowns parallel-sided (*i.e.*, not flared) with a triangular central cusp and the deep, elongated notch on the dorsal surface of the supradental shelf. However, *G. pradiguensis* sp.nov. is clearly different from other species of *Geiseltaliellus,* primarily in having slender and high crowned teeth projecting only one/fifth of their height beyond the level of the lateral parapet of the jaw (as opposed to one/third in other species).

Geiseltaliellus sp.

Known distribution – Early Eocene (MP7), to the late Eocene (MP19).

Another, unnamed species is present at Grisolles (MP16) (Figs.5-6), northern France, and the last record of *Geiseltaliellus* is in the late Eocene of Escamps (MP19).

Pseudolacerta De Stefano, 1903

Type-species – *Pseudolacerta mucronata* (Filhol, 1877).

Pseudolacerta mucronata (Filhol, 1877)

Lacerta mucronata Filhol, 1877: 489, fig.424. Zittel, 1893: 600.
Pseudolacerta mucronata Hoffstetter, 1942: 240.

Holotype – Dentary, certainly lost, MNHN, fig.424 *in* Filhol (1877).

Known distribution – Middle Eocene (MP16) to the late Eocene (MP19). France, Phosphorites du Quercy.

Comments – Teeth strongly heterodont; the first teeth are unicuspid, posteriorly recurved with an slightly inflated base and a pointed apex. The following teeth are slender, tricuspid, and similar to the posterior teeth of *Geiseltaliellus*. The *sulcus dentalis* is lacking and the Meckelian canal is limited by curved borders. A combination of characters of the dentary indicates its affiliation within iguanid lizards: tricuspid teeth, absence of a *sulcus* that separates the tooth bases from the subdental shelf, absence of a dorsal ridge on the subdental shelf.

Pseudolacerta sp.

Known distribution – Middle and late Eocene (MP16-MP19), Phosphorites du Quercy, France.

Comments – A second species (still unamed) is known in the genus *Pseudolacerta.* Its dentary teeth are very similar to those of *P. mucronata*. *Pseudolacerta* sp. differs from *P. mucronata* by its narrow Meckelian canal limited by straight borders and its smaller size.

Cadurciguana Augé, 1987

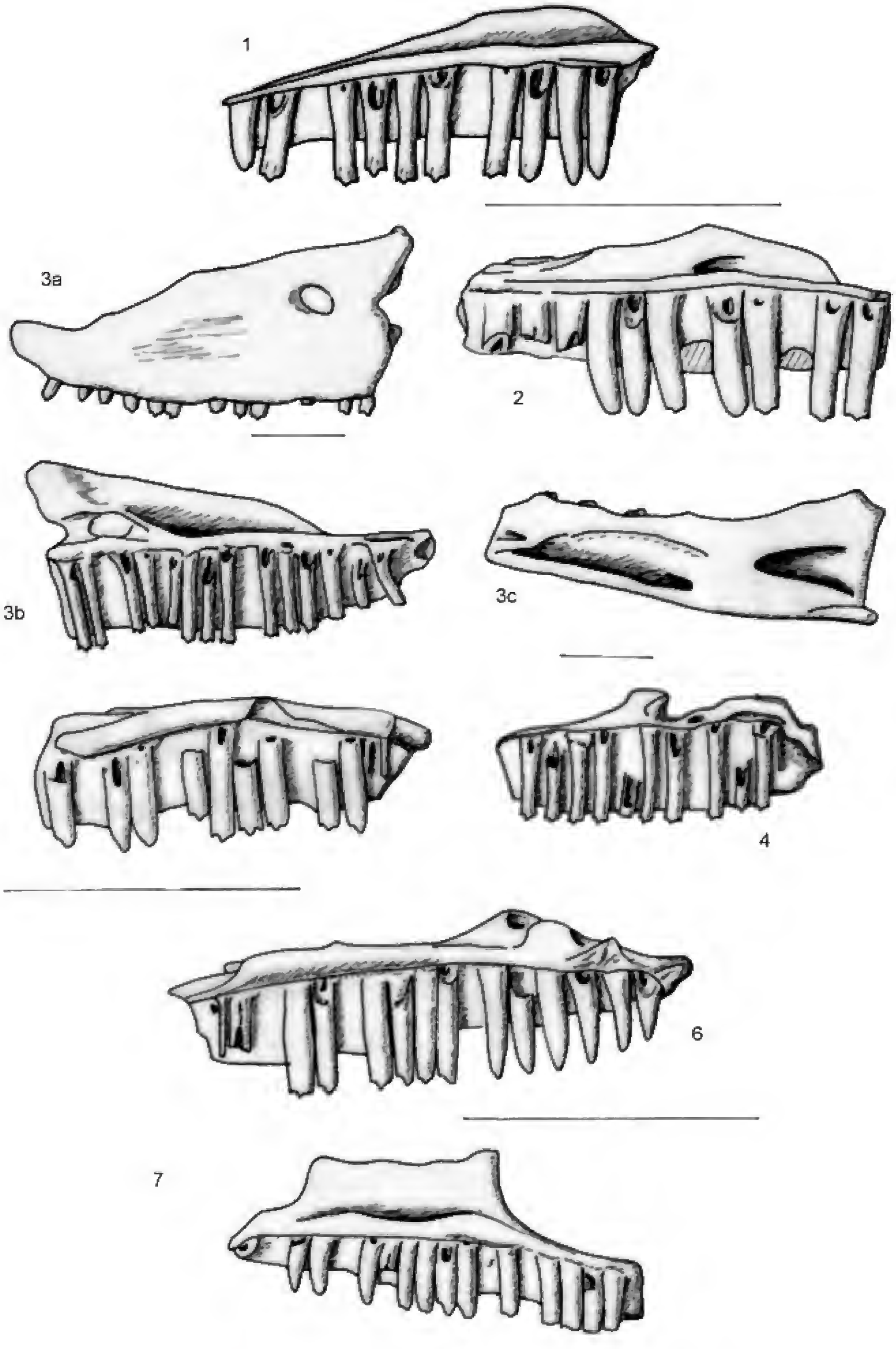
Type-species (and only species known in the genus) – *Cadurciguana hoffstetteri* Augé, 1987

Cadurciguana hoffstetteri Augé, 1987

Holotype – Left dentary, USTL, ECC 2502, figs.1-3 *in* Augé (1987).

Known distribution – Middle Eocene (MP16) to the end of the Late Eocene (MP19), France, Phosphorites du Quercy.

Comments – *Cadurciguana hoffstetteri* (Fig.7) shows strong evidence of iguanid affinities: total loss of the *sulcus dentalis*, faintly tricuspid teeth on the dentary, and greatly reduced splenial. Moreover, the frontals are fused and hourglass shaped, with the scar of the parietal foramen on the fronto-parietal border.



Geiseltaliellus longicaudus - fig.1- incomplete left maxilla, Prémontré, early Eocene (MP10), MNHN, medial view; fig.2- incomplete right maxilla, Dormaal, early Eocene (MP7), coll. E.Wille, medial view. *Geiseltaliellus pradiguensis* sp.nov. - fig.3- holotype, incomplete right maxilla, USTL, PRA 1221, Les Pradigues, middle Eocene (MP17); (a) labial view, (b) medial view, (c) dorsal view; fig.4- incomplete left maxilla, USTL, MAL 608, Malpérié, middle Eocene (MP17); medial view.; *Geiseltaliellus* sp. - fig.5- incomplete right maxilla, MNHN, Grisolles, middle Eocene (MP17); medial view; fig.6- incomplete left maxilla, MNHN, Grisolles, middle Eocene (MP17); medial view; fig.7- *Cadurciguana hoffstetteri*, incomplete right maxilla, MNHN, Le Bretou, middle Eocene (MP16); medial view. Scale bars: (1-2, 5-7) = 5mm, (3-4) = 2mm.

CRETACEOUS IGUANIDS

The discovery of late Cretaceous iguanids from Spain and France documents the earliest record for the Iguanidae in Europe. Two Campanian localities have yielded indeterminate iguanid lizards: Laño, in Spain (Basque Country) (RAGE, 1999), and Champ-Garimond in Southern France (SIGÉ *et al.*, 1997). The material is fragmentary but the maxilla and dentary bear pleurodont, flared, tricuspid teeth, strongly compressed labio-lingually. The resorption pits, when present, open at the medial side of the tooth base. Such teeth may belong to iguanid lizards, however, because of the fragmentary nature of the material, this assignment cannot be definitively ascertained.

These two early iguanids from the Upper Cretaceous of Europe provide fossil evidence supporting the interpretation of ETHERIDGE & DE QUEIROZ (1988) who regarded the tricuspid crown pattern as a primitive condition within iguanids.

DISTRIBUTION OF IGUANIDAE

Iguanids are a primarily American group of lizards but their distribution is clearly disjunct. Two iguanid genera exist in Madagascar and Grand Comore Island, *Chalarodon* and *Oplurus*. An iguanid (*Brachylophus*) has reached Fiji and Tonga in the Pacific, on which islands the genus is endemic. Fiji and Tonga also have giant extinct iguanids (PREGILL & DYE, 1989; WORTHY *et al.*, 1999). Such a puzzling distribution has been known as a "biogeographic enigma" or an "irritating problem" (BLANC, 1982).

Discoveries of late Cretaceous fossils of the group from Europe and the Gobi Desert (BORSUK- BIALYNICKA & ALIFANOV, 1991; GAO & HOU, 1995a, b; 1996) demonstrate the presence of iguanids in Europe and East Asia. The present pattern of distribution of iguanid lizards shows that they have withdrawn from Eurasia.

CARLQUIST's (1974) statement on the subject seems especially relevant here: "the best explanation seems to be that iguanas are a very ancient group of reptiles which have been extinguished on the Eurasian and African mainland". Two factors may have contributed to the extinction of Old World iguanid lizards: the Eocene-Oligocene climate deterioration and the competition with other groups. Here we examine the potential role of competition.

AGAMIDAE vs. IGUANIDAE

The development of better adapted families of lizards in the Old World could have caused the extinction of the Iguanidae in all areas where the families competed (AVERY & TANNER, 1971). Members of the family Agamidae are ecological equivalents for many iguanids and are widespread in the Old World. Agamidae have even been called "Old World counterparts of the New World iguanids" (*e.g.*, GOIN *et al.*, 1978). Some members of the two groups (Agamidae and Iguanidae) look alike and they do many similar things. Two of the most striking ecological equivalents are the Australian Thorny devil (*Moloch horridus*, Agamidae) and the North American horned lizard (*Phrynosoma platyrhinos*, Iguanidae), both of which exploit a diet of ants.

In the absence of direct information, the best evidence of competitive replacement between two groups of animals comes from their complementary distributions. Some 300 living species of agamids have an Old World distribution in southern Eurasia, Africa, and Australia. Nowhere in the world, except on Fiji, do iguanids and agamids live side by side, they have a complementary distribution. This complementary distribution is strongly suggestive of competitive interactions (DIAMOND, 1975). Hence, agamids may have caused the extinction of the Iguanidae where the two families overlapped.

The reality of competitive replacement should also be distinguishable in the fossil record: postulated competitors could have co-occurred in at least some part of their ranges (evidence for shared stratigraphic and geographic distributions) and the supposed better adapted group must replace or drive to extinction "inferior" group.

Agamid and iguanid lizards co-occurred in Europe and North America during the Eocene.

In Europe, agamid lizards made their first appearance in the early Eocene (MP7, locality of Dormaal), in the form of a single genus and species, *Tinosaurus europeocaenus* Augé & Smith, 1997. *Tinosaurus* becomes progressively less abundant during the early Eocene and its last record in Europe appears to be in the middle Eocene (MP13, DUFFAUD & RAGE, 1997). Thus, during the Eocene, the extinction of agamid lizards predated the disappearance of iguanids in Europe.

Agamids managed to enter North America during the Eocene, as demonstrated by the presence of the species *Tinosaurus stenodon* in the Middle

Eocene of Wyoming, but they were unable to persist on that continent after the Upper Eocene. During that time, iguanid lizards were well established in North America.

In both cases, the fossil record shows the persistence of iguanids while agamids became extinct, thus the expected pattern of replacement is not supported. Moreover, Pianka (1986) and Cloudsley-Thompson (1999) stated that the differences between the ecologies of most iguanid and agamid lizards that they studied are much more striking than are the similarities.

LACERTIDAE vs. IGUANIDAE

The radiation of Lacertidae during the Paleogene could be linked to the decline of the Iguanidae. Apparently, during the Cretaceous, only iguanid existed. Lacertidae arose during the Paleogene in Europe and radiated throughout the Eocene and the Oligocene. The iguanid lizards disappeared from Europe across the Eocene/Oligocene boundary and from Asia after the Oligocene.

On an other hand, lacertid and iguanid lizards display a perfect complementary distribution: they are entirely separated from each other in their geographic distribution today. The extant species of lacertids have an Old World distribution in Eurasia and Africa and they are absent from Madagascar and North and South America.

It is clear that lacertid and iguanid lizards were sympatric during part of their evolution in Eurasia. They have co-occurred during the Eocene in Europe and both families are known in the Asian fossil record. Does the fossil record confirm the hypothesis of competitive replacement (Fig.8)?

North and South America: iguanid lizards have been well established in North and South America since the Cretaceous. There is a purported Mesozoic record of an iguanian from the Upper Cretaceous of Brasil (*Pristiguana* Estes & Price, 1973) (Estes & Price, 1973). Moreover Apesteguia *et al.* (2005) report an incomplete lizard frontal from the Cretaceous of Patagonia that could belong to an iguanid. Some iguanid taxa have been recovered from the late Cretaceous of Canada (*Cnephasaurus* and two unnamed genera, Gao & Fox, 1996). Extant lacertids are absent from the continent and no records of fossil lacertids are known.

Madagascar: lizards are the most speciose group of terrestrial vertebrates on the island of Madagascar, the extant lizard fauna includes chamaeleonids, iguanids, scincids, cordylids, and gekkonids. Typical mainland African forms (agamids, lacertids, varanids) are absent. Moreover, the lizard fossil record from Madagascar is nearly lacking (Krause *et al.*, 2003).

Africa: Scincomorph lizards have been discovered in the Upper Jurassic of Africa (Zils *et al.*, 1995; Broschinski, 1999), but true lacertids are not known in Africa before the Quaternary. Extant and fossil iguanids are apparently absent from Africa.

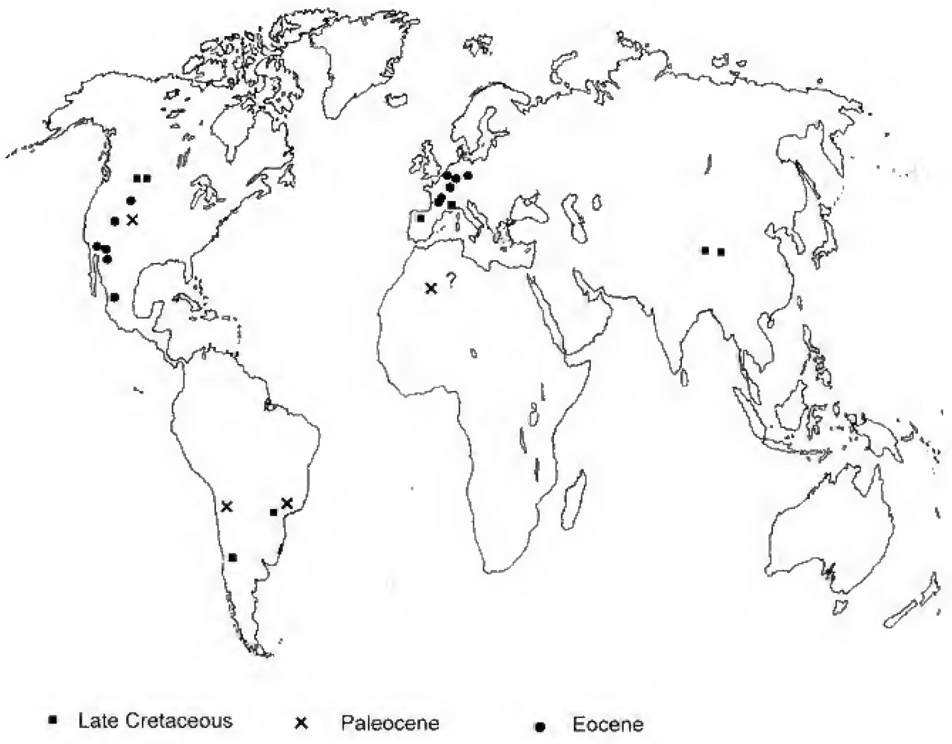


Fig.8- Distribution of fossil iguanid lizards.

However, some fragmentary dentaries from the Paleogene of Morocco have tricuspid teeth that suggest iguanids affinities. It must be added that the two specimens in hand are poorly preserved and their assignment is highly debatable.

Asia: the Mesozoic iguanid record of Asia has been recently improved. Early Cretaceous deposits in Central Asia and Mongolia have yielded indeterminate iguanians (GAO & NESSOV, 1998), while a diversity of iguanid taxa has been recovered from the Campanian and Maastrichtian of Mongolia and China (ALIFANOV, 1996; BORSUK-BIALYNICKA & ALIFANOV, 1991; GAO & HOU, 1995a, b, 1996; GAO & NORELL, 2000). Maybe iguanid lizards were still present in Asia during the Paleocene, their last occurrence on the continent appears to be from the Oligocene (CKHIKVADZE *et al.*, 1983; ALIFANOV, 1993).

ALIFANOV (1993) suggests a long “cryptic” history of the Lacertidae during the late Cretaceous in Asia. However, in a personal communication, V. R. Alifanov states “In 1993, I published the preliminary information about the Cretaceous lacertids, but now I think it was an error. In any case I do not regard true lacertids as an Asiatic group in origination.” Apparently, lacertid lizards made their first appearance in Asia during the late Paleogene (Oligocene?).

In Asia, the fossil record shows the persistence of lacertids while iguanids became extinct, supporting the expected pattern of replacement.

Europe: iguanid lizards are present during the entire Eocene in Europe. The last European iguanids are recorded in the locality of Escamps (MP19), just before the “Grande Coupure”, *i.e.*, the Eocene/Oligocene boundary.

The locality of Hainin (Paleocene, MP1-5) could contain a lacertid fossil (VAN DYCK, 1983). However, this record is not confirmed by FOLIE (2006). The first confirmed lacertid lizards has been yielded by the locality of Cernay (France), from the Upper Paleocene (AUGÉ, 2005). Lacertid lizards are well-represented in the fossil record during the Eocene and the Oligocene in Europe. Only one genus, *Dormaalisaurus*, is known in the early Eocene of Dormaal, Belgium, but three genera are recorded from the late Eocene (*Plesiolacerta* and two new genera). *Succinilacerta succinea* (BÖHME & WEITSCHAT, 1998; BORSUK-BIALYNICKA *et al.*, 1999) is another small genus preserved in the Baltic amber (certainly middle Eocene).

To sum up, in Europe and Asia, the fossil record shows the persistence of lacertids while iguanids became extinct, supporting the expected pattern of replacement. Moreover, apparently lacertids have never reached the areas where extant iguanids are distributed. They have never been sympatric in North and South America nor in Madagascar. They could have co-occurred in Africa but the fossil record is too sparse to establish this point.

Lacertids may have caused the extinction of the Iguanidae where the two families overlapped.

COMPETITIVE EXPLANATIONS AND THE FOSSIL RECORD

Competitive explanations have traditionally been used by palaeontologists to account for the replacement of one group by another. In all cases, these explanations have been questioned by a closer study of the fossil record (RAUP, 1982; BENTON, 1983, 1987, 1996; MILLER, 2000). For contrary opinions, see MILLER & SEPKOSKI (1988) and SEPKOSKI (1996).

Two taxa are said to be in competition if an increase in abundance by either one harms the other (MACARTHUR, 1972). Such competitive interactions are viewed as necessary correlates of evolution by natural selection, according to the idea clearly expressed by Darwin when he made an analogy between the number of species on the Earth and a surface entirely covered with “ten-thousand sharp wedges”. In this metaphor, he stated that the origination of a new taxon can occur only by the displacement of a preexisting one.

There are several ways in which clade A replaces clade B in the fossil record, but two broad patterns emerges: the first is the competitive pattern and it would be like a pair of matched wedge-shaped clades, one decreasing and the other increasing side by side, best known as the double-wedge pattern. The second pattern has been called the “mass-extinction” replacement and it would show one group coming to an end abruptly and the other increasing thereafter (BENTON, 1996).

The classic example of supposed long-term competitive interaction between brachiopods and bivalves was studied by GOULD & CALLOWAY (1980) and they find no evidence of competitive replacement. Instead, the data suggest a mass-extinction and opportunistic replacement pattern.

Three principles guide the analysis: first, postulated competitors should have met each other in at least some part of their ranges (evidence for shared stratigraphic and geographic distributions). We do know that lacertids and iguanids were sympatric in the European Eocene, more than fifteen localities have yielded both iguanid and lacertid remains. Second, it is necessary to show that they shared some major aspects of their modes of life (as a proxy for a more precise demonstration that they shared a limiting ressource or a common enemy). Third, the reality of competitive replacement should be distinguishable in the fossil record by assessing the relative abundances of the two groups in question through time: the "double wedge" pattern.

MODE OF LIFE

Diet

It has been suggested that there is a fairly tight correlation between diet and crown shape in lizards (Hotton, 1955; Montanucci, 1968). However, on a broad scale, there appears to be little diet-related variation in crown form and the vast majority of pleurodont squamates have numerous, relatively small, unicuspid to tricuspid teeth. These tooth forms are associated with a variety of invertebrate prey types of food (arthropod-insect eating lizards) as well as some percentage of plant food. Fossil iguanids and lacertids presented such dental shapes (uni-, bi- or tricuspid teeth for lacertids; uni-tricuspid teeth for iguanids) and they are both considered as generalized lizards or arthropod eaters.

Size

Competitive interactions between two groups imply that both taxa shared comparable body size. There are no body mass estimation techniques for fossil lizards. Here dentary size has been used as an estimate of size in fossil lizard taxa. The distribution of body size is right-skewed on untransformed axes (Fig.9). The tail of small numbers of large species is marked, and the smallest size class is not the most speciose. Recent examinations of the size distributions of mammals and birds support the notion that most species tend to be of intermediate size (Blackburn & Gaston, 1994; Fenchel, 1993). The right-skewed body size distribution of Eocene iguanid and lacertid lizards conforms to many vertebrate assembly studied, principally in North America (Brown & Nicoletto, 1991; Brown *et al.*, 1993; Maurer *et al.*, 1992; Gaston & Blackburn, 2000). Thus, this distribution is unlikely to be severely biased. The bar chart shows that Eocene iguanid and lacertid lizards shared comparable body size in Europe. A statistical test confirms this opinion. The Kolmogorov-Smirnov test (K-S) compares the complete shapes and positions of two distributions. The K-S test does not assume a normal distribution, and is then a suitable method for comparing the two samples (Hammer & Harper, 2006).

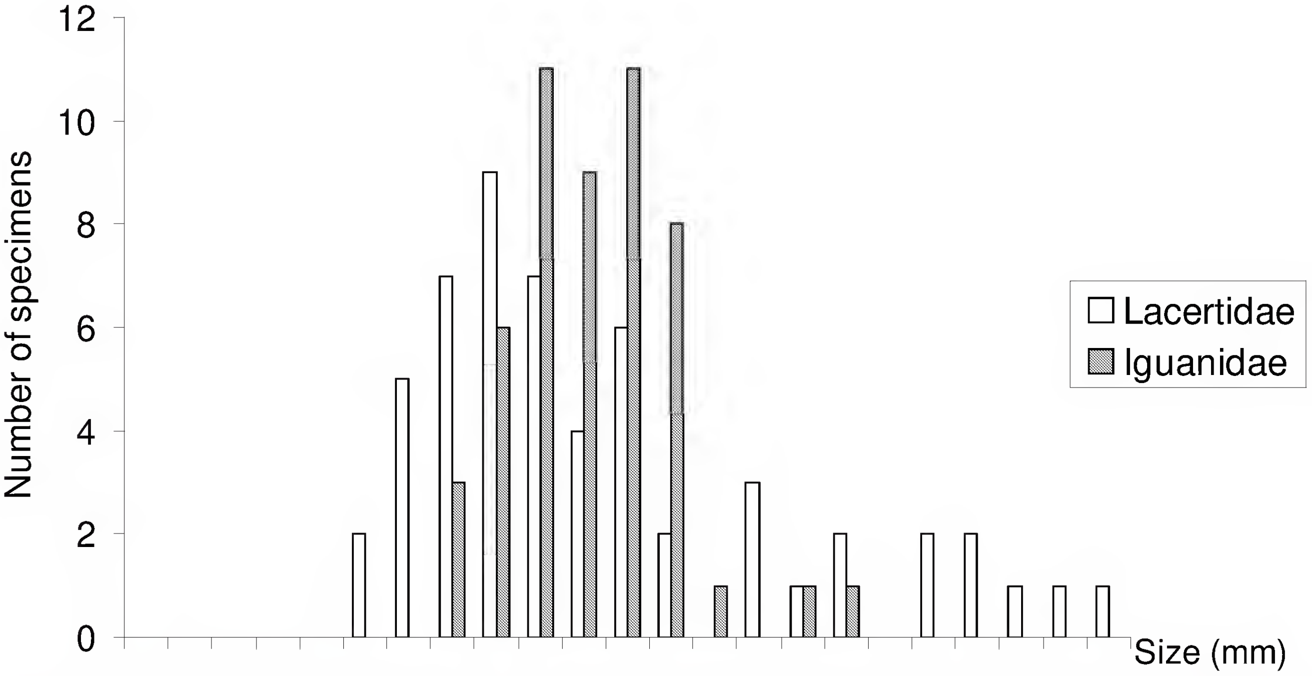


Fig.9- Size (measurements taken from the dentary) of the iguanid and lacertid lizards during the Eocene in Europe.

Using the K-S test, we arrive at the test statistic D = 0.24 and the probability of the equality of the two distributions is p = 0.076. Hence, the null hypothesis of equal distributions cannot be rejected.

Did lacertid lizards increase in diversity at the expense of iguanids?

Our raw data are the total number of iguanids and lacertids species and individuals living at any time during each of the mammalian standard level (MP) intervals in Europe.

Plots of number of species, or of individual animals, against time show that there is no evidence for double-wedge pattern in the fossil record (Fig.10). Instead, the general impression is one of positive association between iguanid and lacertid diversity, at least during the late Eocene.

The disappearance of iguanid lizards in Europe was associated with a single event: the Eocene-Oligocene extinction which deeply and permanently reduced the diversity of iguanids but only temporarily reduced the diversity of lacertids. The data suggest a mass-extinction replacement pattern.

In summary we find no evidence at all for the claim of negative interaction in diversity between iguanids and lacertids through time.

DISCUSSION AND CONCLUSION

A major turnover occurred in the european mammalian fauna near the Eocene-Oligocene (E-O) boundary (known as the Grande Coupure, see Stehlin, 1909). Together with mammals, the Quercy localities contain an important assemblage of lizards. Their study has revealed an important change among lizards (Rage, 1984; 1986; Rage & Augé, 1993; Augé, 1993, 2000; Milner *et al.*, 2000; Delfino *et al.*, 2001). In Europe, the Late Eocene-Early Oligocene epochs constituted the most critical turning point in the Cenozoic history of the lizards.

During the Late Eocene, the lizard faunas were abundant and diverse. Nine families and 17 species are present in the standard level MP19 (mammalian standard level of Escamps), before the Eocene-Oligocene transition. Unfortunately, no lizard remains are known from the last Eocene standard level (MP20).

At the family and species levels, the lizards were severely affected by the "Grande Coupure". A drop in diversity is protracted between the MP20 (latest Eocene) and the MP21 levels (earliest Oligocene) and a low in diversity appears in the level MP21 (five families, eight species). Four families or subfamilies encountered in the European Late Eocene became extinct between the MP19-20/MP21 standard levels interval (Iguanidae, Gekkonidae, Glyptosaurinae, and Helodermatidae).

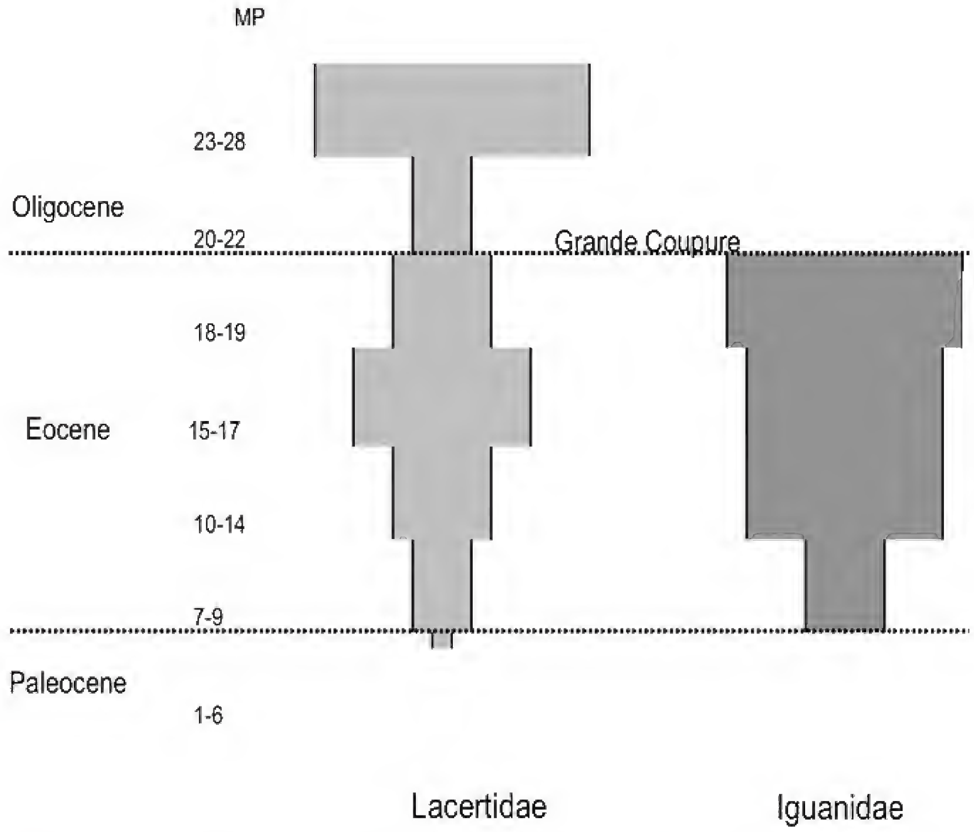


Fig.10- Relative diversity of iguanid and lacertid lizards through the Eocene and Oligocene in Europe. Time is standard level number, beginning in the early Eocene. The sole localities that have yielded both iguanid and lacertid lizards, are considered. *Eolacerta robusta* has not been included in the study, according to Müller (2001), the suggestion that *Eolacerta* belongs to the modern family Lacertidae cannot be corroborated.

At lower taxonomic levels, estimates of species level extinctions range as high as 80%. They include members of virtually all the families present in the late Eocene. Thus, the E-O event provides evidence of a high rate of extinction not matched with originations.

All of the iguanid species known in the Late Eocene became extinct across the Eocene-Oligocene boundary. Similarly, the diverse lacertid fauna became extinct in Europe near the E-O boundary. However, at the beginning of the Oligocene, several lacertid species appear, with *Lacerta filholi*, and the development of several amblyodont, *i.e.*, durophagous members of the family Lacertidae (*Mediolacerta, Pseudeumeces, Dracaenosaurus*). During that time, no iguanid lizard reappeared in Europe.

Hence, it seems that extinction rates were equal for iguanid and lacertid species across the Eocene-Oligocene boundary. Johst & Brandl (1997) assume that large environmental perturbations have similar effects on all species. However, some species are slower to recover while other have more opportunities for speciation and immigration. Net diversification rates seem to accelerate for lacertid lizards after the Eocene-Oligocene event. Views on biases in speciation and immigration during recovery intervals seem to be dominated by assumption and supposition, with empirical evidence being weak or absent (Jablonski, 2005). Maybe the Eocene-Oligocene faunal turnover create an opportunity to examine this mechanisms.

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THE FIRST "PROTOSUCHIAN" (ARCHOSAURIA: CROCODYLIFORMES) FROM THE CRETACEOUS (SANTONIAN) OF GONDWANA [1]

(With 16 figures)

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ABSTRACT: The remains of "protosuchians" from the Cretaceous come, to exception of "Las Hoyas crocodyliform" from the Lower Cretaceous of Spain, exclusively of Central Asia: *Zaraasuchus*, *Gobiosuchus*, *Zosuchus*, and *Artzosuchus* from the Upper Cretaceous of Mongolia; *Tagarosuchus* from Lower Cretaceous of Southern Siberia; *Edentosuchus*, *Sichuanosuchus*, and *Shantungosuchus* from Lower Cretaceous of China. We report a new basal crocodyliform taxon, *Neuquensuchus universitas* gen.nov., sp.nov., from Neuquén Province, Argentina, belonging to Bajo de la Carpa Formation, representing the first and only "protosuchian" from the Cretaceous of Gondwana. The articulated and fragmentary materials belonged to a willowy, slender species, with very long and thin extremities. As in *Shantungosuchus*, the cervical centers are lengthened, with prominent ventral keel and well developed anteroventral parapophyses. As in basal crocodylomorphs, it possesses two sacral vertebrae. Also, a much enlarged scapular blade, with well developed acromial ridge and the posterior edge similar to *Sichuanosuchus*. The pronounced deltopectoral crest in the complete humerus is equivalent to *Sichuanosuchus* and as this, a circular, elongated and thin shaft with the medial condyle longer than the lateral one. Also, the complete ulna and radius is similar in their proportions to *Sichuanosuchus*. As this, the pubis is lengthened, very thin in the half section and not very expanded distally. The femur, tibia and fibula are elongated and similar to other non-derivated crocodyliforms. Besides representing the first Cretaceous "protosuchian" of Gondwana, the occurrence of these outside of Asia and Europe during the Cretaceous offers new evidence of pre-Albian dispersion between Gondwana and Central Asia through Europe.

Key words: Crocodylomorpha. Protosuchian. *Neuquensuchus universitas* gen.nov., sp.nov. Cretaceous. Gondwana.

RESUMEN: El primer "protosuquio" (Archosauria: Crocodyliformes) del Cretácico (Santoniano) de Gondwana.

Los restos de "protosuquios" del Cretácico provienen, a excepción del "crocodyliforme de Las Hoyas" del Cretácico Inferior de España, exclusivamente de Asia Central: *Zaraasuchus*, *Gobiosuchus*, *Zosuchus* y *Artzosuchus* del Cretácico Superior de Mongolia; *Tagarosuchus* del Cretácico Inferior del sur de Siberia; *Edentosuchus*, *Sichuanosuchus* y *Shantungosuchus* del Cretácico Inferior de China. Aquí reportamos un nuevo taxón de crocodyliforme basal, *Neuquensuchus universitas* gen.nov., sp.nov., de la provincia de Neuquén, Argentina, correspondiente a la Formación Bajo de la Carpa, representando el primer y único "protosuquio" del Cretácico de Gondwana. Los materiales fragmentarios y articulados corresponden a una especie esbelta y delgada, con extremidades largas y delgadas. Al igual que en *Shantungosuchus*, los centros cervicales son alargados, con una quilla ventral prominente y parapófisis anteroventrales bien desarrolladas. Como en los crocodyliformes basales, *Neuquensuchus* posee dos vértebras sacras. Además, una hoja escapular muy expandida, con un puente acromial bien desarrollado y el borde posterior similar a *Sichuanosuchus*. La cresta deltopectoral pronunciada en el húmero es equivalente a la de *Sichuanosuchus* y al igual que este, la diáfisis es circular, alargada y delgada con el cóndilo medial mayor que el lateral. Asimismo, las proporciones del radio y la úlna son similares a *Sichuanosuchus*. Como este, el pubis es alargado, muy delgado en su sección media y poco expandido distalmente. El fémur, tibia y fíbula son alargados y similares a otros crocodyliformes no derivados. Además de representar el primer "protosuquio" cretácico de Gondwana, su presencia fuera de Asia y Europa durante el Cretácico ofrece nueva evidencia de un evento de dispersión pre-Albiano entre Gondwana y Asia Central a través de Europa.

Palabras clave: Crocodylomorpha. Protosuquio. *Neuquensuchus universitas* gen.nov., sp.nov. Cretácico. Gondwana.

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INTRODUCTION

Fossil remains of basal non-Metasuchia Crocodyliformes from Cretaceous come almost exclusively from the Asian continent, to exception of "Las Hoyas Crocodyliform" (Sanz *et al.*, 1988) (Fig.1) from the Lower Cretaceous of Las Hoyas, Spain (upper Barremian; Diéguez *et al.*, 1995). The Asian forms are represented by species coming from China, Mongolia and Russia. From China comes *Edentosuchus tienshanensis* (Young, 1973; Pol *et al.*, 2004), a Protosuchia from the Lower Cretaceous of Tugulu Group, Xinjiang; *Shantungosuchus hangjinensis* (Wu *et al.*, 1994) from the Luohandong Formation, Zhidan Group, Inner Mongolia and *Sichuanosuchus shuhanensis* (Wu *et al.*, 1997) from an uncertain locality of Sichuan. From Mongolia come forms belonging to the Campanian age. *Gobiosuchus kielanae* (Osmólska, 1972; Osmólska *et al.*, 1997) comes from the Bayan Zak locality; *Gobiosuchus* (?)*parvus* (Efimov, 1983), later considered conspecific of *G. kielenae* (Osmólska *et al.*, 1997), comes from Üüden Sair locality; *Zosuchus davidsoni* (Pol & Norell, 2004a) and *Zaraasuchus shepardi* (Pol & Norell, 2004b) come from Zos Canyon locality; *Artzosuchus brachicephalus* (Efimov, 1983), a very fragmentary form of uncertain filiation, comes from the same locality that *G.* (?)*parvus*. Lastly, *Tagarosuchus kulemzini* (Alifanov *et al.*, 1999), with practically complete skull, comes from the Lower Cretaceous of Shestakovo locality, South Siberia.

Here we present a new basal form of crocodyliform from the Upper Cretaceous of Northern Patagonia, Neuquén Province, Argentina. The remains come from the Bajo de la Carpa Formation, Neuquén Group (Fig.2), and represent the first "protosuchian" form for the Cretaceous of Gondwana. In this paper, we describe the anatomy of this new Crocodyliform together with a parsimony analysis of their phylogenetic relationships.

MATERIAL AND METHODS

The remains were found and gathered by Mr. Oscar de Ferrariis (at that time Director of the Museum of the National University of Comahue), together with J.O.C. The materials of this new basal crocodyliform were originally referred as *Notosuchus* (MUCPv-137) and were collected in 1987. The study of the museum collection allowed us to find one more specimen represented by fragmentary postcranial material but in good preservation (Fig.3).

Institutional abbreviations: GMPKU, Geological Museum, School of Earth and Space Sciences, Peking University, Beijing, People's Republic of China; IGM, Mongolian Institute of Geology, Ulaan Bataar, Mongolia; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, People's Republic of China; LACM, Natural History Museum of Los Angeles County, Los Angeles, California, USA; MACN, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MUCP, Museo de Geología y Paleontología, Universidad Nacional del Comahue, Neuquén, Argentina; UNC, Department of Geological Sciences, University of North Carolina at Chapel Hill; ZDM, Zigong Dinosaur Museum, Zigong, Sichuan, China; ZPAL, Instytut Paleobiologii PAN, Warszawa, Poland.

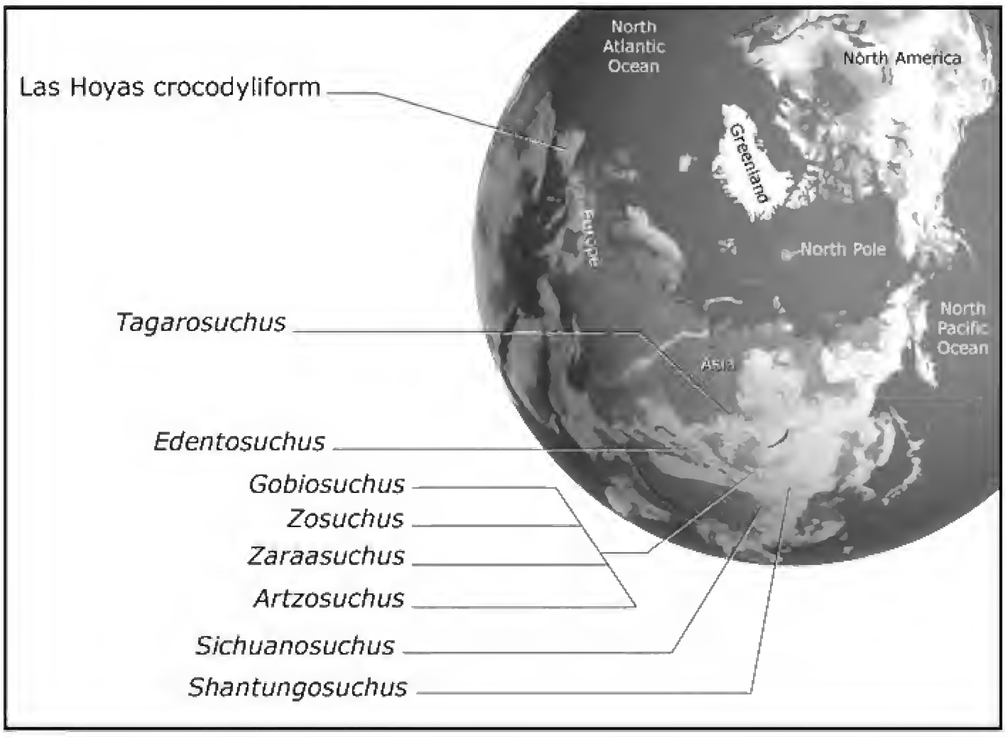

Fig.1- Map of Eurasia showing the places of origin of the species of Cretaceous protosuchians.

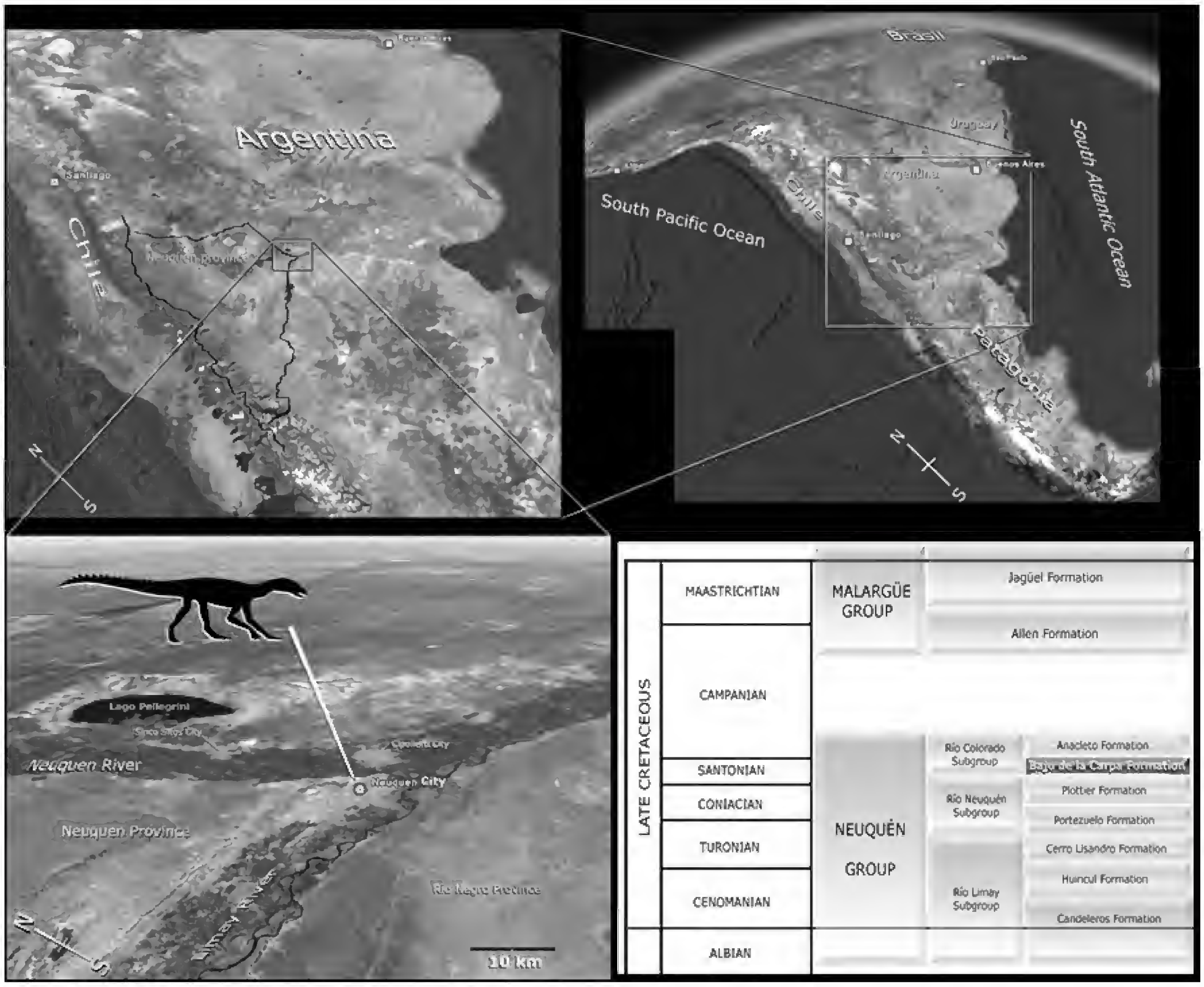

Fig.2- Up right: satellital map showing the location of Argentina and Patagonia in South America; up left: satelital map of Northpatagonic region, showing the location of the Neuquén Province; below left: area of Comahue where were found and collected the materials of *Neuquensuchus universitas*, gen.nov., sp.nov. (scale bar = 10km - right inferior bar). Below right: stratigraphy of the Cretaceous of Neuquén Basin and stratigraphic column of the Neuquén Group (based on LEANZA *et al.*, 2004. (Satellital images taken from GoogleEarth).

RESULTS

GEOLOGY

The Río Colorado subgroup constitutes the top of the Neuquén Group; it is widely distributed in the South of the Neuquén Basin. The subgroup is divided in two formations: Bajo de la Carpa (lower) and Anacleto (upper) (LEANZA *et al.*, 2004) (Fig.2). Bajo de la Carpa Formation is composed of coarse-grained, light violet and pink sandstones of fluvial origin. The age has been dated as Santonian (LEANZA *et al.*, 2004) (Fig.2).

Outcrops in the area have given a wide variety of fauna such as carnotaurine abelisaurid theropod (PORFIRI & CALVO, 2006) and the avian dinosaur *Alvarezsaurus calvoi* BONAPARTE, 1991 and *Velocisaurus unicus* BONAPARTE, 1991; sauropod dinosaurs as cf. *Laplatasaurus* (LEANZA *et al.*, 2004), Titanosauridae indet. (CHIAPPE & CALVO, 1994; pers.obs.), *Neuquensaurus* sp. (pers.obs.), *Antarctosaurus* and the peculiar beaked sauropod *Bonitasaura salgadoi* APESTEGUÍA, 2004. Birds as *Neuquenornis volans* CHIAPPE & CALVO, 1994 and *Patagopteryx deferrariisi* ALVARENGA & BONAPARTE, 1992, snakes as *Dinilysia patagonica* WOODWARD, 1901, bird eggs in nests (SCHWEITZER *et al.*, 2002), dinosaur eggs named *Megaloolithus patagonicus* CALVO *et al.*, 1997. Crocodyles are represented by *Notosuchus terrestris* WOODWARD, 1896, *Comahuesuchus brachybuccalis* BONAPARTE, 1991, *Cynodontosuchus rothi* Woodward, 1896, and postcranials articulated remains of a new peirosaurian crocodyliform (Fiorelli *et al.*, 2007).

The remains of this new "protosuchian" have been gathered on the South margin of Neuquén River (North Neuquén City) increasing the number of crocodyliforms found in the formation.

SYSTEMATIC PALEONTOLOGY

Crocodylomorpha Walker, 1970
Crocodyliformes Hay, 1930
(*sensu* Benton & Clark, 1988)
Mesoeucrocodylia Whetstone & Whybrow, 1983

Neuquensuchus universitas, nov. gen. *et* nov. sp.

Etymology – Generic name *"Neuquén"* in reference to the Neuquén City; "*suchus*", Greek for crocodyle. Specific name "*universitas*" in reference to the universitary campus, where the materials were collected.

Holotype – MUCPv-47 (Fig.3). Six cervical vertebrae, first four dorsal vertebrae, two sacral vertebrae and first five caudal vertebrae. Posterior cervical ribs and anterior dorsal ribs. Fragmentary right scapula, humerus, ulna and rights radius; left scapula and humerus. Right pubis, fragment of right ischium, femur, tibia and right fibula; fragment of the left ilium.

Referred specimens – MUCPv-161 (Fig.3). Proximal end of left tibia, distal end of left fibula and left astragalus.

Type locality – The remains were found in the North of the Neuquén City on the campus of the Universidad Nacional del Comahue (National University of Comahue), Neuquén Province, Argentina (Fig.2).

Type horizon – Bajo de la Carpa Formation, Río Colorado Subgroup, Neuquén Group (Santonian; Leanza *et al.*, 2004) (Fig.2).

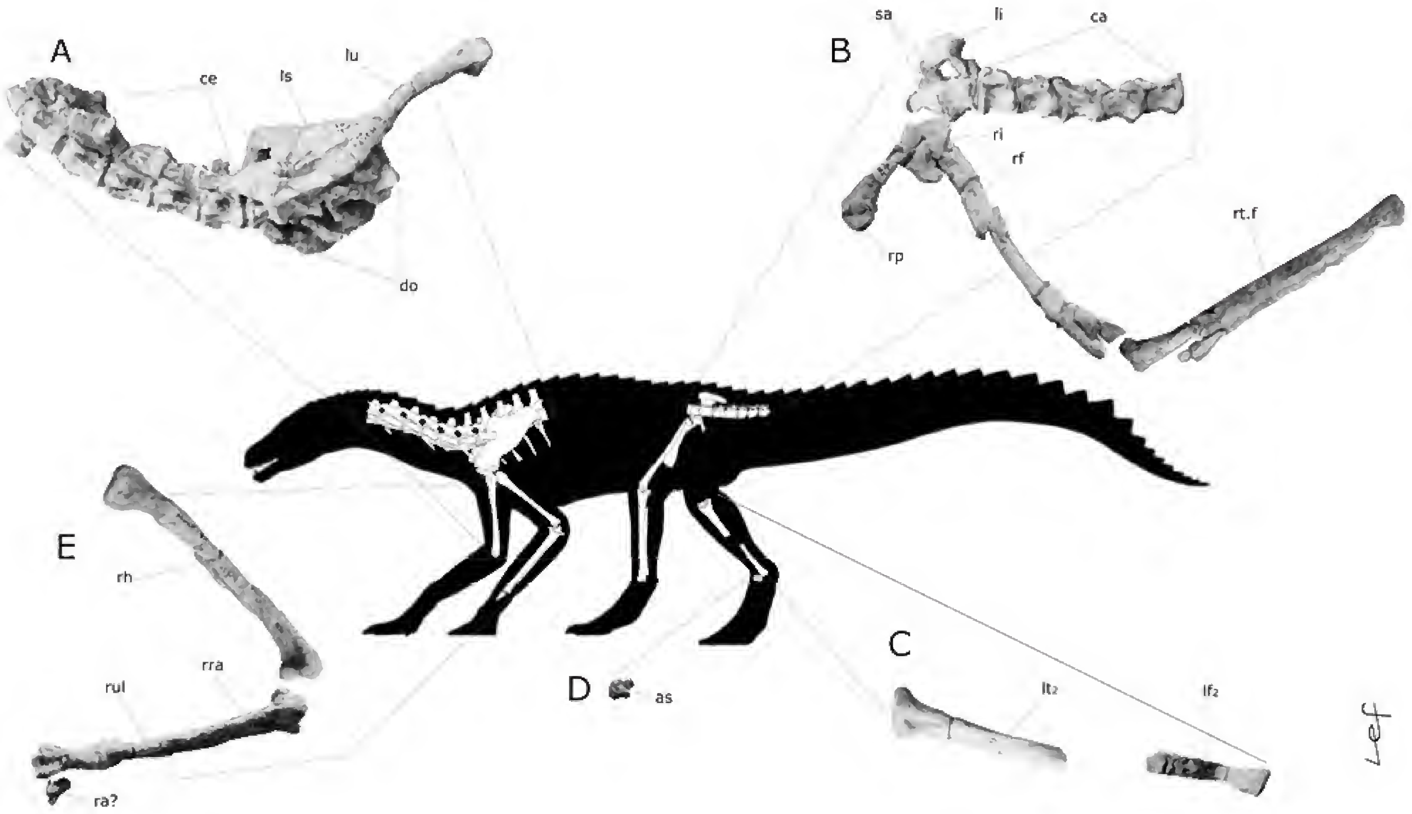

Fig.3- *Neuquensuchus universitas* gen.nov., sp.nov. Referred material. MUCPv-47 (holotype): A, B and E; MUCPv-161 (referred specimens): C and D. A, cervical vertebrae, first dorsal vertebrae, left scapula and left humerus. B, sacral and first caudal vertebrae and right pubis, ischium, femur, tibia and fibula. C, left tibia and fibula. D, left astragalus. E, right humerus, ulna, radius and radial. (Abbreviations in the Appendix IV).

Diagnosis – Relatively small, thin and slender crocodyliform, diagnosed by the following combination of poscranial characters: lengthened cervical vertebrae with low ventral keel, parapophysis and diapophysis anteroposteriorly lengthened. Neural spines elongated in dorsal vertebrae, with their centra lengthened without ventral keel but with a very low anterior hypapophysis. Two laterally enlarged sacral vertebrae. First caudal vertebra with a tenuous opisthocoelous and elongated anterior caudal vertebra, relatively low. Scapula with an important dorsal expansion and a good development of the posterodorsal hook. Humerus with a good development of the lateroproximal expansion, long and thin diaphysis of the humerus with the medial condyle biggest than the lateral one. Very lengthened and thin ulna, with olecranon process. Very thin and proximally expanded radius. Thin and long pubis with a very light distal expansion. Non-sigmoid and lengthened femur, smaller than the tibia.

DESCRIPTION AND COMPARISIONS

AXIAL SKELETON

The specimen MUCPv-47 of *Neuquensuchus universitas* possesses incomplete axial remains but in good preservation state. It includes the last six articulate cervical vertebrae with the first four dorsal, two sacral vertebrae and relatively well preserved five anterior caudal vertebrae that are articulated to the sacral vertebra.

Regarding the cervical section (Fig.4), this specimen possesses a relatively long and thin neck, similar to those other basal crocodylomorphs, as for example *Terrestrisuchus* (CRUSH, 1984) and *Gobiosuchus* (OSMÓLSKA *et al.*, 1997). On the cervical sequence, the first one, here considered the fourth, is incomplete, preserving just the posterior portion of the centrum (Fig.4). All cervical vertebrae and preserved dorsal are slightly amphicoelous. The long and thin cervical centra are parallelogram-shaped in lateral view, with an elevation of the anterior face of the centrum, similarly to *Terrestrisuchus* (CRUSH, 1984), *Dibothrosuchus elaphros* (WU & CHATTERJEE, 1993), *Zaraasuchus* (POL & NORELL, 2004b, IGM 100/1321), *Shantungosuchus* (YOUNG, 1961, IVPP V2484; WU *et al.*, 1994, IVPP V10097) and other cervicals of Crocodylia (ROMER, 1956; HOFFSTETTER & GASC, 1969). *Neuquensuchus* possess medially constricted, well marked cervical centra, similar to some basal crocodyliforms, such as *Zaraasuchus* (POL & NORELL, 2004b) and *Shantungosuchus* (YOUNG, 1961; WU *et al.*, 1994) and different to other protosuchids and mesoeucrocodylians, as *Edentosuchus* (LI, 1985) and Notosuchia (WU & SUES, 1996; FIORELLI, 2005; POL, 2005), that possess short and compressed cervical centra, without medial constriction.

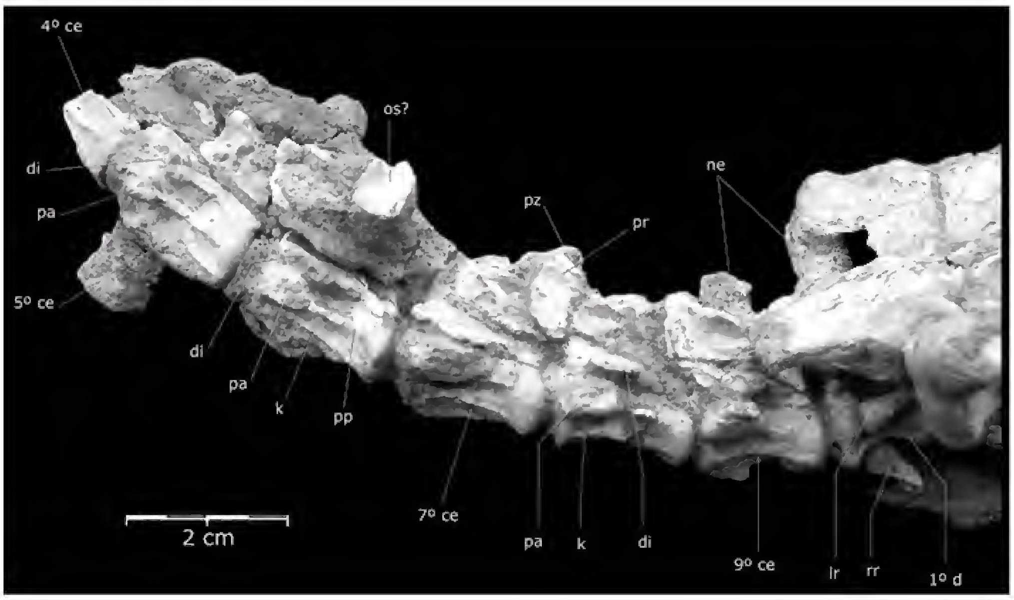

Fig.4- *Neuquensuchus universitas* gen.nov., sp.nov., MUCPv-47. Cervical vertebrae in left lateral view. (Abbreviations in the Appendix IV).

This structure indicates wide lateral movements of the long neck in this basal patagonian crocodyliform. In another sense, each one of the cervical centra possesses a long keel that runs anteroposteriorly in the whole ventral surface, forming deep furrows toward both sides of this and ventrally to the parapophysis (Figs.5B, 5C, 5D). Even so, the ninth centrum also possesses a less marked and lower keel, with shallow lateral furrows than those present in anterior cervicals. These keels are similar to those observed in "protosuchians" and notosuchians, like in the axis of *Shantungosuchus hangjinensis* (Wu *et al.*, 1994, IVPP V10097), in the cervical vertebrae of *Protosuchus* (Colbert & Mook, 1951), *Sichuanosuchus huidongensis* (Peng, 1996), *Notosuchus* (Pol, 2005; Fiorelli, 2005, MACN-RN 1037 and MUCPv-137) and *Chimaerasuchus* (Wu & Sues, 1996, p.692-693, IVPP V8274) but the long extension is a plesiomorphic character. The parapophysis are very wide, well developed and robust with a lengthened articulate facet for the capitulum of the cervical ribs (Figs.5C, 5D). The articulated facets of these parapophysis possess an antero-lateroventral direction, similar to other basal crocodylomorphs as in the first cervical ones of *Terrestrisuchus* (Crush, 1984), in the posterior cervical vertebra of *Zaraasuchus* (Pol & Norell, 2004b) or in the axis of *Shantungosuchus* (Young, 1961; Wu *et al.*, 1994). Lateroventrally projected parapophysis of *Neuquensuchus universitas* possesses a long parapophyseal ridge posteriorly. Posterior cervical vertebrae have the surfaces for the capitulum enlarged and lengthen, covering practically the anterior half of the extensive centrum (Fig.5D). Between the parapophysis and diapophysis there is a prolonged depression, this character has been recorded in *Zaraasuchus* (Pol & Norell, 2004b) and *Protosuchus* (Colbert & Mook, 1951). The diapophyses are lengthened in the first cervical vertebra and they are anteriorly located below the neurocentral sutures. Nevertheles, in the seventh cervical, the diapophyses are anteroventrally located on the suture. In the eighth cervical, the diapophysis spreads rounding the tubercular process. Lastly, in the ninth cervical, the diapophysis is located more dorsally, as in *Terrestrisuchus*. All cervicals possess an important postdiapophyseal ridge, like in *Zaraasuchus*. The neural spines are not complete but they seem to be high and dorsoventrally lengthened, centrally located in the neural arches, contrary to the posterior cervical vertebrae of *Zaraasuchus* (Pol & Norell, 2004b). Laterally, in the base of the neural spines, there is a cavity between the pre and postzygapophysis, nearly delimited by a small developed suprapostzygapophyseal lamina (Fig.5A). Prezygapophysis and postzygapophysis, in dorsal view are robust, laterally high and slightly curved laterally. Prezygapophysis articulate facets are dorsomedially directed and postzygapophysis articulate facets are lateroventrally directed, like in *Zaraasuchus*. Ventrally, the prezygapophysis possesses a well developed lamina posteroventrally directed, that continues with the anterior border of diapophysis; it directs anterodorsally the prezygapophysis base (Fig.5D). There is a very marked border, that extends toward posterior among the articular facets of the pre and postzigapophysis, on the whole lateral surface of the neural pedicelous. Similar condition has been observed in *Zaraasuchus* (Fig.5D).

Regarding the dorsal vertebrae, only the first four have been preserved, with their corresponding articulate ribs (Fig.6). It is observed that these dorsals, corresponding to the tenth to twelfth vertebrae, possess the same anteroposterior lenght, but they fall in relation with the posterior cervical ones. In *Notosuchus* and other Metasuchia there is a light increase in the longitude of the tenth (last cervical in *Notosuchus*) and eleventh dorsal centrum, compared with the short cervical ones (Pol, 2005; Fiorelli, 2005). All the centra are amphicoelous and strongly constrained in the half section. Therefore, proximal and distal facets are very wide and inflated (Figs.6C, 6D) like in *Sichuanosuchus huidongensis* (Peng, 1996). The first dorsal vertebra does not possess a ventral kill and a true reduced hypapophysis appears (Fig.6D). In the first two dorsal vertebrae, the parapophyses are anteriorly located, ventrally directed and rounded. The third dorsal vertebra has the parapophysis small and dorsoventrally longer. Diapophyses are well developed. The cavities in the base of the neural spines are wider and shallower, not very deep but limited posteriorly by high and well-developed suprapostzygapophyseal laminae (Figs.6A, 6B). In lateral view, neural spines in anterior dorsals are very elongated and laminar (Figs.6A, 6B).

In MUCPv-47, the poorly preserved sacral vertebrae are articulated with the anterior five caudals (Fig.7). They are jointed by a suture. Centra are short and very wide, flat and massive. (Figs.7C, 7E). The preserved transverse processes seem to have been wide, similar to those of basal crocodylomorphs as *Dromicosuchus* (Sues *et al.*, 2003).

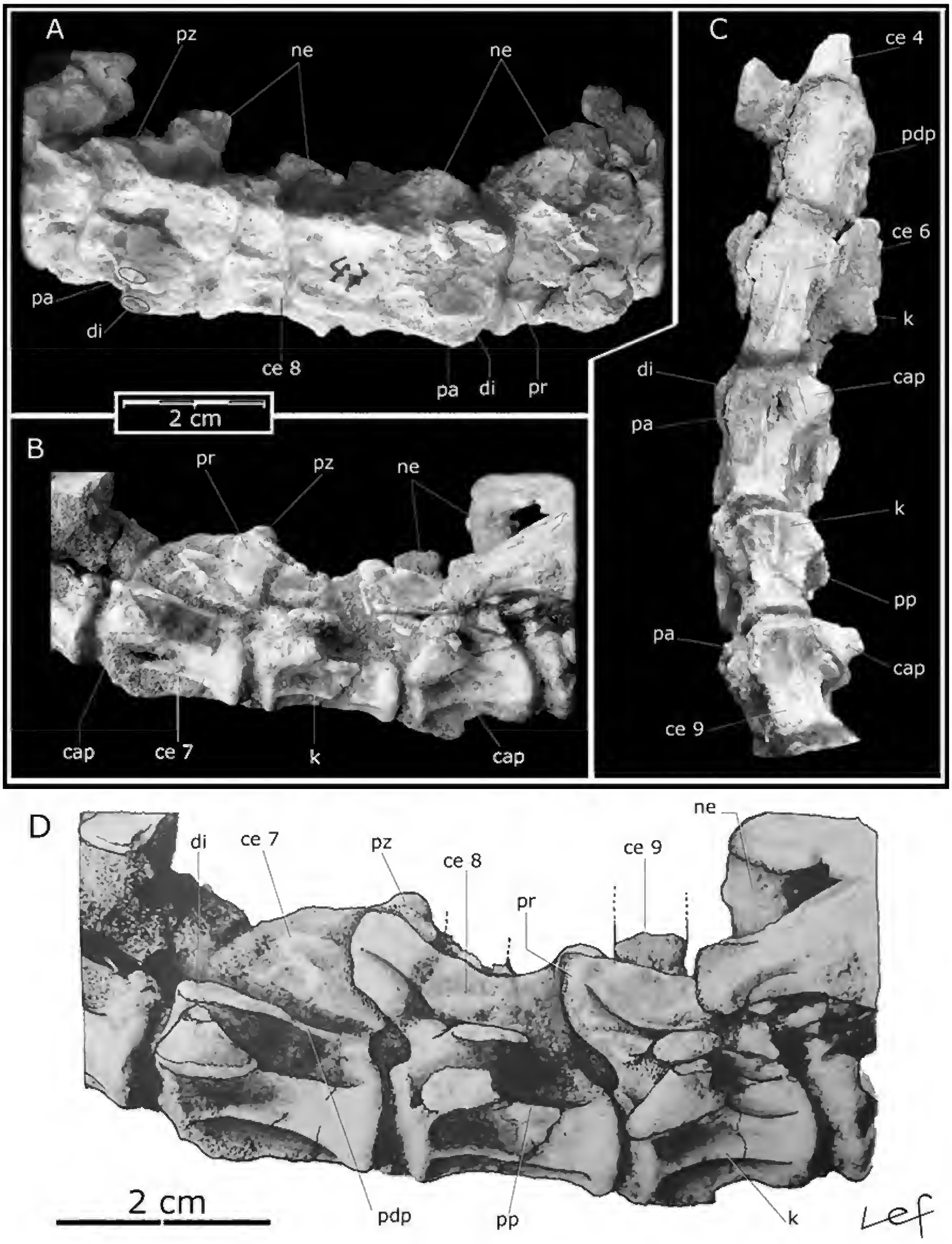

Fig.5- *Neuquensuchus universitas* gen.nov., sp.nov., MUCPv-47. Posterior cervical vertebrae. A, right lateral view; B and D, left lateral view; C, ventral view. (Abbreviations in the Appendix IV).

Anterior caudals correspond to the five firsts (Figs.7A, 7B). Just centra and some pre and postzygapophyses are preserved; they are more rounded and lengthened than in *Notosuchus*. In *Neuquensuchus universitas* centra are similar to the first caudal vertebrae of *Shantungosuchus* (Wu *et al.*, 1994) and other basal crocodyliforms. The first caudal possesses a centrum very slightly opisthocoelic. Transverse processes in the second and third caudals are slightly square in transverse section and they placed at the same level than the zygapophysis. Pre and postzygapophyses, in caudals, do not possess an extensive dorsal development as those in *Notosuchus* and other notosuchian and neosuchian, such as in *Mahajangasuchus* (Buckley & Brochu, 1999) and Dyrosauridae (Schwarz *et al.*, 2006). Articulation surfaces of the prezygapophysis, in the third and fourth caudals, are inclined ventromedially. Hemals arches have not been preserved but the articulated surfaces for the same one appear from the second caudal vertebra.

Appendicular skeleton

MUCPv-47 includes both scapulae, the left humerus (Fig.6), ulna and right radius, left ilium, right pubis, proximal right ischium, femur, tibia and fragment of the right fibula. MUCPv-161 includes a very well preserved proximal left tibia, distal left fibula, and fragmentary remains of tarsus – left astragalus (Fig.3). It is referred to *Neuquensuchus* due to their characters and similar proportions with MUCPv-47.

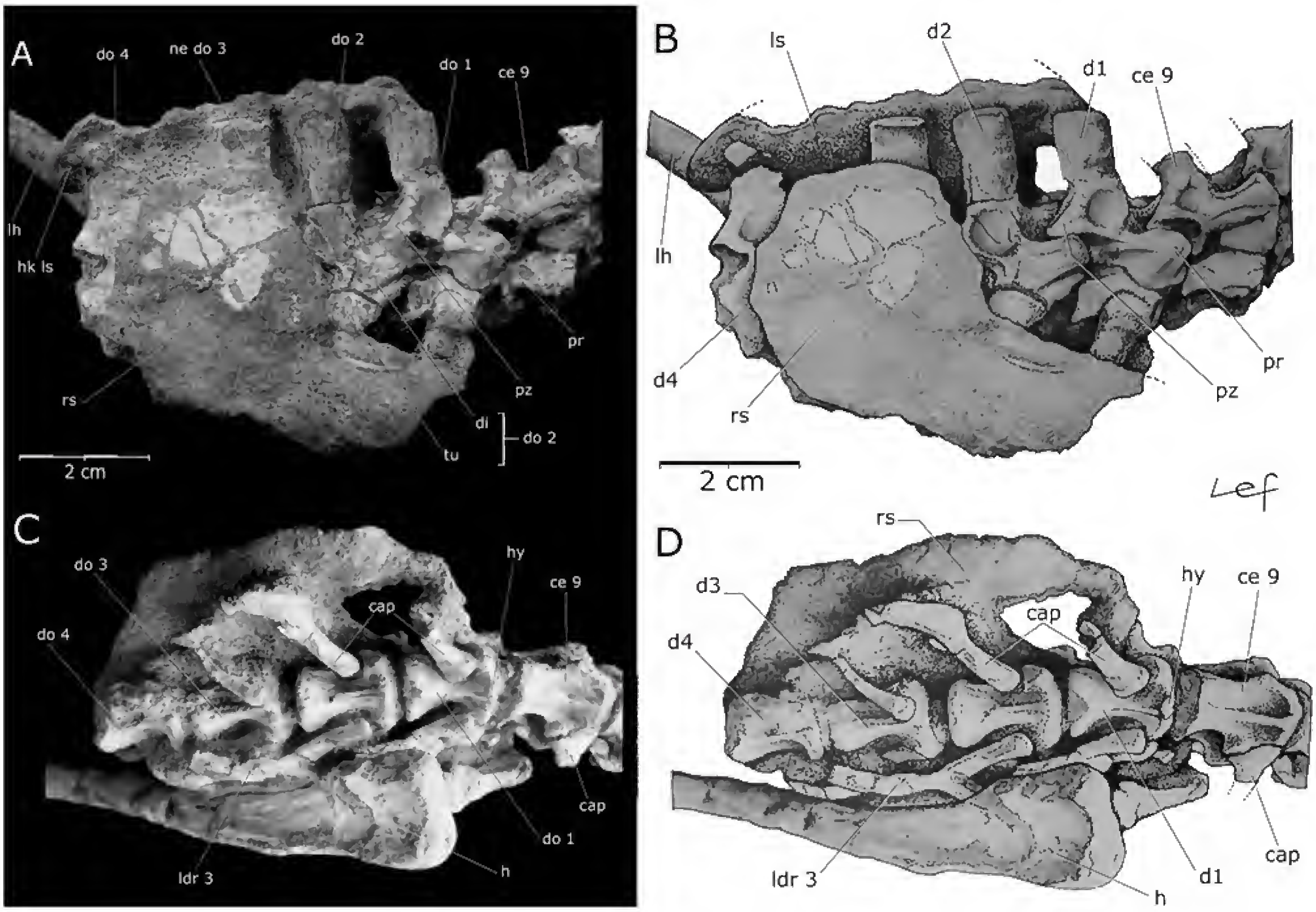

Fig.6- *Neuquensuchus universitas* gen.nov., sp.nov., MUCPv-47. First dorsal vertebrae. A and B, right lateral view; C and D, ventral view. (Abbreviations in the Appendix IV).

SCAPULA

The scapula of *Neuquensuchus universitas* (Figs.6, 8) is quite similar to that of *Notosuchus* (POL, 2005; FIORELLI, 2005) and *Sichuanosuchus shuhanensis* (WU *et al.*, 1997, IVPP V12088). However it differs from *Notosuchus* in having a less marked constriction above the ventral expansion and a slender dorsal expansion. In notosuchians the dorsal expansion is very developed and more anteroposteriorly extensive (POL, 2005; FIORELLI, 2005). As in *S. shuhanensis*, *Neuquensuchus universitas* has the anterior concave border of the scapular blade wider than the posterior one and a well-developed acromial ridge, extended along the anterior margin of ventral portion (Fig.8). The hook, or projection in the posterodorsal vertex, is posteriorly directed and the dorsal border is convex. It is only shared with *Sichuanosuchus shuhanensis* (WU *et al.*, 1997) and also in part with *Sichuanosuchus huidongensis* (PENG, 1996). The hook is also visible in some sphenosuchians as in *Pseudhesperosuchus* but in this Triassic crocodylomorph the posterior border is much wider and it borns abruptly and more centrally (BONAPARTE, 1971). However, in *Junggarsuchus* (CLARK *et al.*, 2004) the hook is dorsoposteriorly directed and the dorsal border is slightly concave.

Another important characteristic is the relationship between the dorsoventral length of scapula and the total length of the humerus; only in *Terrestrisuchus*, *Gobiosuchus*, *Sichuanosuchus* and *Neuquensuchus universitas* this scapular longitude represents less than 70% of the longitude of the humerus, while in the remaining crocodylomorphs – included all the Metasuchia –, it is always bigger.

HUMERUS

MUCPv-47 preserves both humera (Figs.9-10). They are very long and thin (100.8mm), and similar in all its proportions and characteristic to that of *Gobiosuchus kielanae* (OSMÓLSKA *et al.*, 1997, ZPAL MgR-II/67), *Zaraasuchus* (POL & NORELL, 2004b, IGM 100/1321), and *Sichuanosuchus shuhanensis* (WU *et al.*, 1997, IVPP V12088). The relationship between the distal extension of the deltopectoral crest and the total length of humerus in *Neuquensuchus universitas* is 23.5%. In *Sichuanosuchus* it is also 23.5% and in *Shantungosuchus* it is 23% (WU *et al.*, 1997). This is different to the other Metasuchia where this relationship is always bigger than 27%.

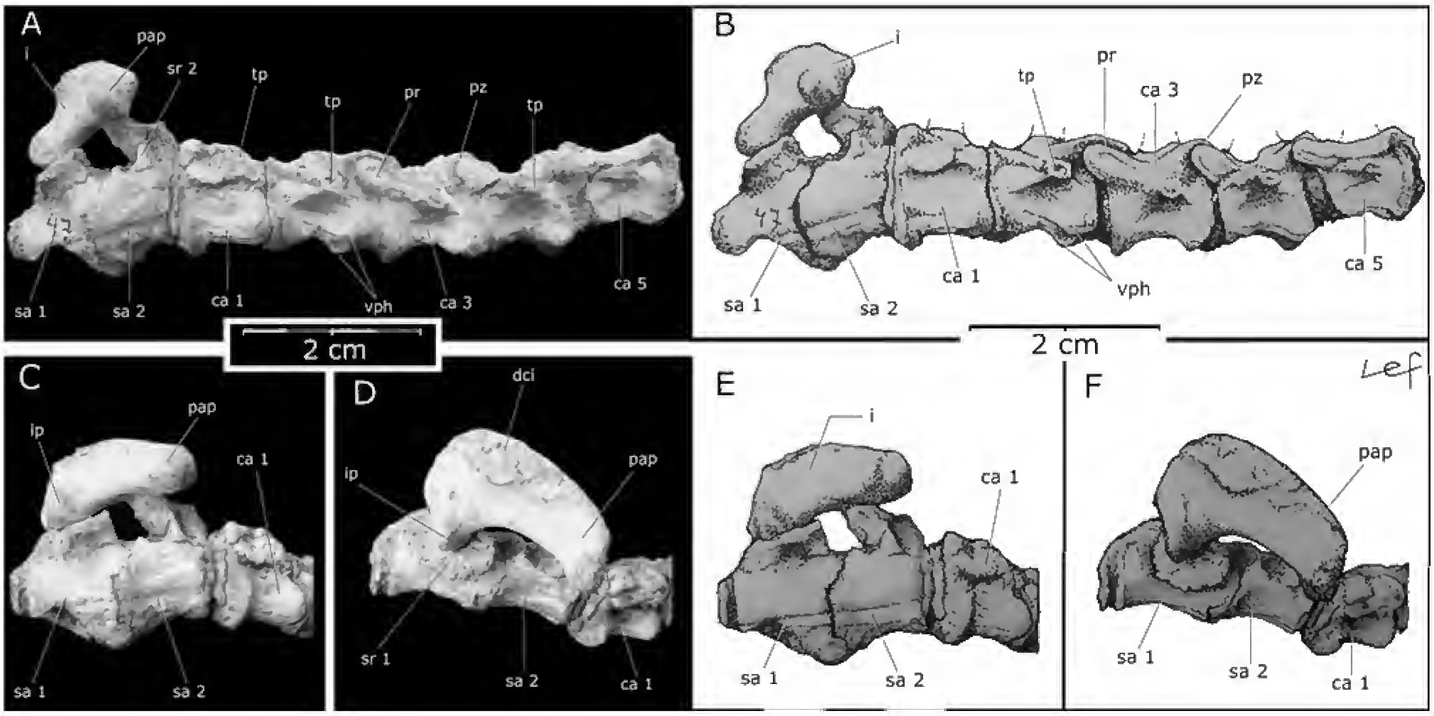

Fig.7- *Neuquensuchus universitas* gen.nov., sp.nov., MUCPv-47. Sacral and first caudal vertebrae and left ilium. A and B, in left lateral view. C and E, sacral and left ilium in ventral view. D and F, sacral and left ilium in left lateral view. (Abbreviations in the Appendix IV).

On the other hand, the diameter of the shaft in relation to the total length of the humerus is, in *Neuquensuchus* (6.5%) similar to the other named "protosuchians" (e.g., *Sichuanosuchus*, *Shantungosuchus*, and *Zaraasuchus*), where it never overcomes 7%, but this contrast with the mesoeucrocodylians Metasuchia where this relationship is always bigger than 9%. Moreover, in *Neuquensuchus universitas* the relationship between the total length and width of the proximal end of the humerus is approximately 5%, similar to those of Crocodylia, sphenosuchians, Protosuchia and more basal crocodyliform, while in Metasuchia non-Crocodylia it is not bigger than 4%.

The proximal end of the humerus shows the articular surface lateromedially elongated, strongly curved medially and relatively thin anteroposteriorly, like that present in *Gobiosuchus* and *Sichuanosuchus* (Fig.10C). The lateroproximal expansion and the rectangular proximal shape of the humerus of *Neuquensuchus universitas* (Fig.10C) are very similar to those of *Notosuchus* (Pol, 2005, MACN-RN 1037 and 1042), *Chimaerasuchus paradoxus* (Wu & Sues, 1996, IVPP V8274), and *Araripesuchus patagonicus* (Ortega *et al.*, 2000, MUCPv-267), suggesting some relationships between *Neuquensuchus* and these notosuchians. However, this characteristic is also similar to *Sichuanosuchus shuhanensis* (Wu *et al.*, 1997, IVPP V12088) and some Protosuchia and sphenosuchians, as for example *Dibothrosuchus* (Wu & Chatterjee, 1993, IVPP V7907). This indicates that the character in question does not throw overwhelming phylogenetic information because it possesses a high distributional disparity inside Crocodylomorpha representing possible convergences in the different groups. However, the internal tuberosity of *Neuquensuchus universitas* is more similar to that of *Sichuanosuchus* (Wu *et al.*, 1997). The lateral facet of the deltopectoral crest has the border anterolaterally directed like in *Notosuchus* and in the rest of the crocodyliforms it is laterally directed; however, in *Sichuanosuchus shuhanensis* (Wu *et al.*, 1997, IVPP V12088) this lateral facet is seemingly also anterolaterally directed.

Distally, the medial condyle is bigger than the lateral one and its general form and proportions are identical to *Sichuanosuchus shuhanensis* (Wu *et al.*, 1997). The posterolateral surface of the humerus is strongly concave and the posterior intercondylar groove is broad, like in *Sichuanosuchus huidongensis* (Peng, 1996, ZDM 3404).

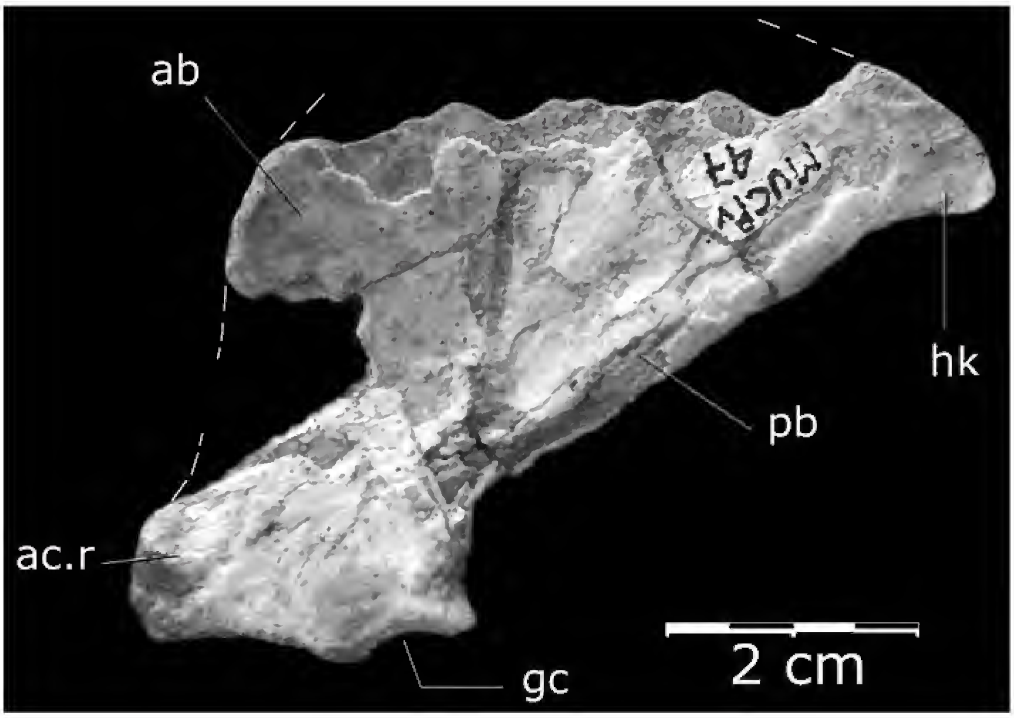

Fig.8- *Neuquensuchus universitas* gen.nov., sp.nov., MUCPv-47. Left scapula in lateral view. (Abbreviations in the Appendix IV).

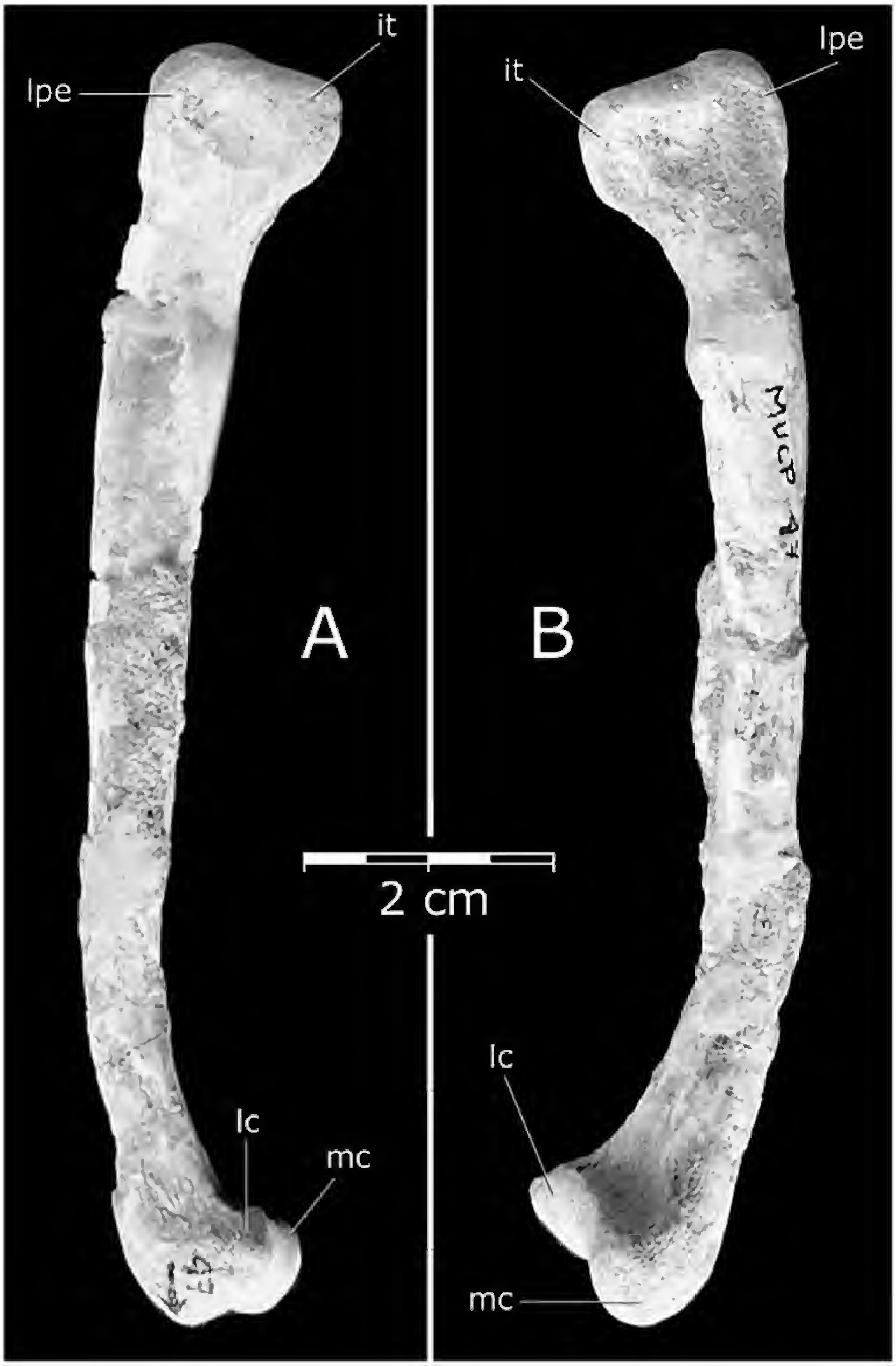

Fig.9- *Neuquensuchus universitas* gen.nov., sp.nov., MUCPv-47. Right humerus in anterior (A) and posterior (B) views. (Abbreviations in the Appendix IV).

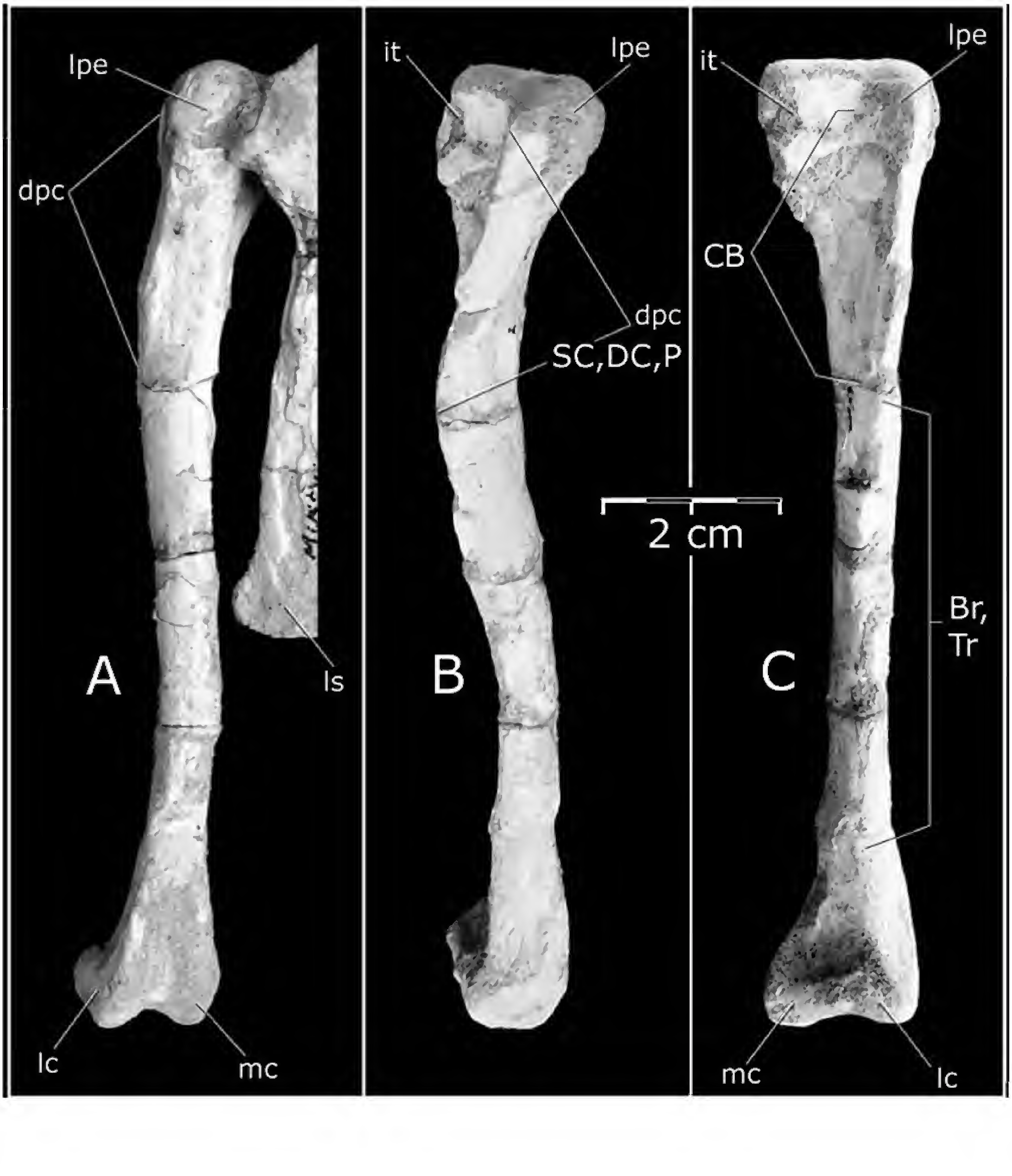

Fig.10- *Neuquensuchus universitas* gen.nov., sp.nov., MUCPv-47. Left humerus in posterolateral (A), lateral (B) and anterior view (C). (Abbreviations in the Appendix IV).

ULNA

The ulna of *Neuquensuchus universitas* is straight (Fig.11), with a long and thin shaft, slightly compressed lateromedially as in *Sichuanosuchus*. It possesses a small proximal expansion, and a convex surface for the lateral condyle of the humerus. As in other basal crocodylomorphs, like some sphenosuchians but contrary to notosuchians, the ulna possesses a prominent olecranon process. The right ulna, although incomplete, has a length of 107.5 mm and it is longer than the humerus. This character is only shared with some sphenosuchians (e.g., *Terrestrisuchus*, *Dibothrosuchus*, and *Dromicosuchus*), representing an autapomorphy of *Neuquensuchus* and a convergent feature shared with these sphenosuchians but related to the cursorial habits of this crocodyliforms. However, in *Neuquensuchus universitas* the relationship between the width of the shaft (5.7mm) and their total length (107.5mm) is 5.3%; it is comparable to other “protosuchian” forms (*Zaraasuchus* <6%; *Gobiosuchus* = 5%; *Shantungosuchus* = 5.6%; *Sichuanosuchus* = 5.3%) and differs from other mesoeucrocodylians metasuchian where it is bigger than 7% (notosuchians and neosuchians).

RADIUS

The right radius (Fig.11) is a very long and thin bone. It is similar in its general form to *Sichuanosuchus shuhanensis* (WU *et al.*, 1997, IVPP V12088). Its proximal end is strongly expanded and the thin shaft is circular in transverse section. The relationship between the diameter of the shaft (3.9mm) and total length of the radius (105mm) in *Neuquensuchus universitas* is 3.7%, which is similar to *Sichuanosuchus shuhanensis* (3.6%). By contrast in *Terrestrisuchus* it is 2.9% and in the other sphenosuchians it is bigger (for example in *Pseudhesperosuchus* it is 5% and in *Hesperosuchus* it is 5.75%). In more derived members of Mesoeucrocodylia this relationship always surpasses 5% (*Araripesuchus patagonicus*: 5.5%; *Notosuchus*: 8.05%; *Chimaerasuchus*: >8%; *Simosuchus*: >8%; Crocodylia: = 8%) contrary to *Araripesuchus tsangatsangana* (TURNER, 2006) where it is 4.52%.

The specimen MUCPv-47 possesses a small proximal fragment of the radial, articulated to the end of the right radius, which is very similar to *Sichuanosuchus shuhanensis* (WU *et al.*, 1997).

ILIUM

Only the posterior fragment of the left ilium has been preserved in MUCPv-47 (Fig.7). It includes the posterior border of the acetabular cavity, the ischiadic peduncle and postacetabular process. The posterior part of dorsal crest in *Neuquensuchus universitas* is low and snub, different to Notosuchia (POL, 2005; FIORELLI, 2005) where there is a very laterally extended marked acetabular roof. The length between the dorsal end of the crest and the distal end of the ischiadic peduncle is very short, indicating an ilium dorsoventrally low. It differs from more derived Mesoeucrocodylia (Metasuchia) where the ilium is very wide dorsoventrally. The ischiadic peduncle is small and the surface for the articulation of the ischium is reduced. The postacetabular process is dorsoventrally thin and markedly posteriorly projected, with its distal extreme lateroventrally directed, like in *Protosuchus* (COLBERT & MOOK, 1951) and other “protosuchian” forms.

PUBIS

The right pubis of *Neuquensuchus universitas* (MUCPv-47) is practically complete. It is associated to the proximal end of the right ischium, sacral and caudal vertebrae, left ilium and femur, tibia and right fibula (Figs.12-13). The pubis is a long and thin bone (rod-like shaped), mainly in the section of the shaft, similar to basal forms of Crocodylomorpha, as *Terrestrisuchus* (CRUSH, 1984), *Protosuchus* (COLBERT & MOOK, 1951), *Sichuanosuchus* (IVPP V12088), and a basal innominated form of China (POL *et al.*, 2004, GMPKU-P 200102). The small proximal expansion supports a convex facet for the ilium and for the pubic process of the ischium (Fig.12B). This character is similar to that of *Sichuanosuchus* and other “protosuchians”, and it implies that the pubis is partially introduced inside the acetabulum. The pubis is slightly expanded distally, as in GMPKU-P 200102 (POL *et al.*, 2004) and *Sichuanosuchus*. In *Neuquensuchus universitas* the relationship between the length of the pubis (39.5mm) and the width of the distal expansion (10.8mm) is 27%, similar to *Sichuanosuchus* (26%) and *Gobiosuchus* (23-24%). In more derived Mesoeucrocodylia – metasuchian forms –, this proportion is always superior to 30%. Lastly, the diameter of the pubic shaft, in relation to the total length, resembles that of other “protosuchians”. In *Neuquensuchus*, this relationship is 7%, similar to *Sichuanosuchus*

(6.5%) and *Gobiosuchus* (<7%) and very different from Metasuchia (>8%).

The existent relationship between the total length of the pubis and the total length of femur is a characteristic only shown by *Gobiosuchus*, *Shantungosuchus* and *Neuquensuchus* being smaller than 45%, while in *Terrestrisuchus*, *Protosuchus*, and Metasuchia the proportion between pubis and femur is always bigger due mainly to the reduction of the pubis, to exception of *Mahajangasuchus*.

ISCHIUM

Only the proximal end of the right ischium has been preserved in MUCPv-47, together with a slight impression (Fig.12B). It is very similar in its construction to *Protosuchus*, *Sichuanosuchus* and GMPKU-P 200102 (POL *et al.*, 2004). The pubis process of ischium is slightly narrower than the proximal end of the pubis, like in *Sichuanosuchus*, and it contacts with the pubis in its posterodorsal extreme. For this reason, the ischium partially excludes the pubis of the acetabulum. The half section of the proximal shaft shows that it is quite narrow but it spreads to distally expanded according to the impression of the same similar to *Protosuchus* and *Gobiosuchus*.

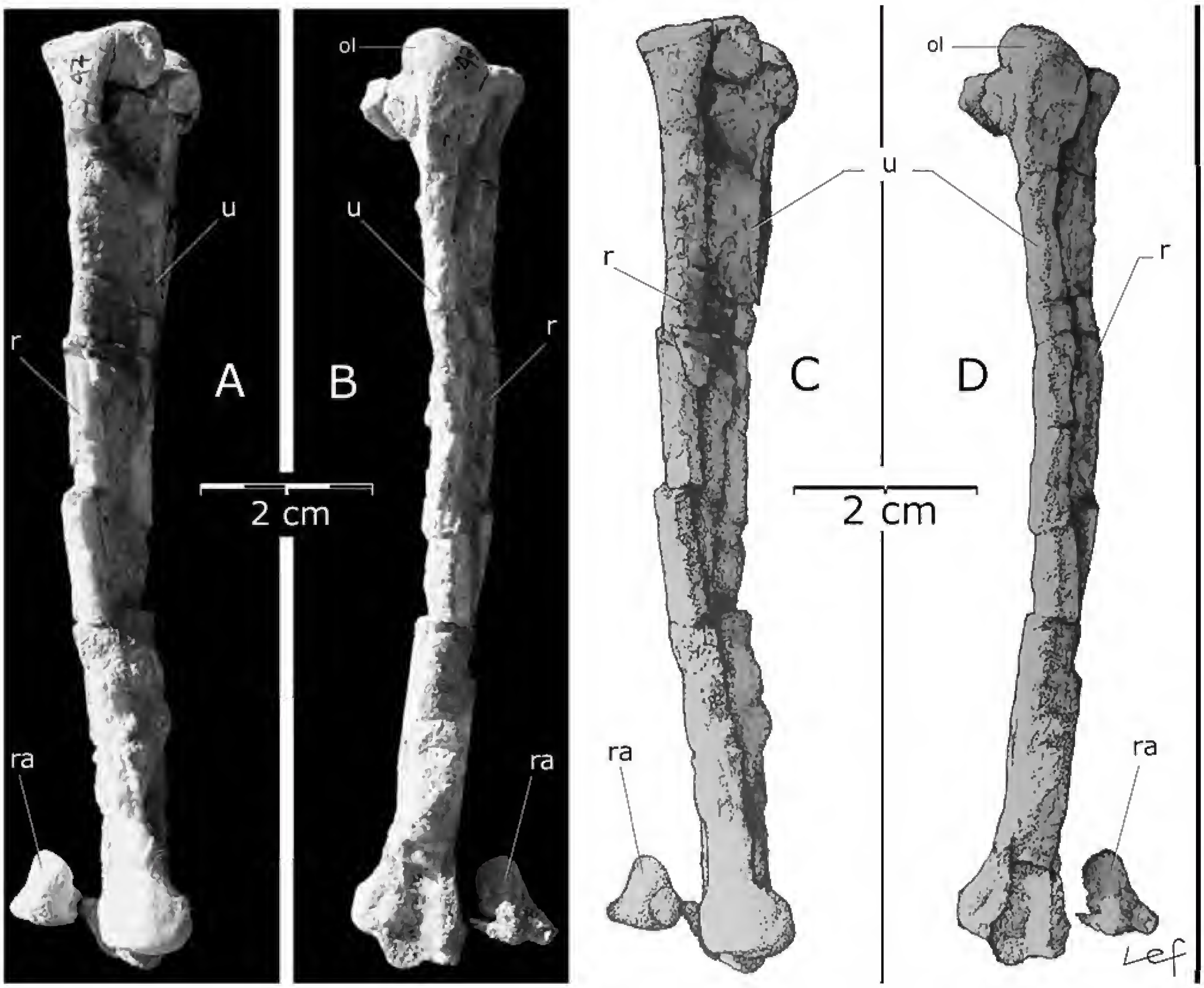

Fig.11- *Neuquensuchus universitas* gen.nov., sp.nov., MUCPv-47. Right ulna, radius and radial in lateral (A and C) and medial (B and D) views. (Abbreviations in the Appendix IV).

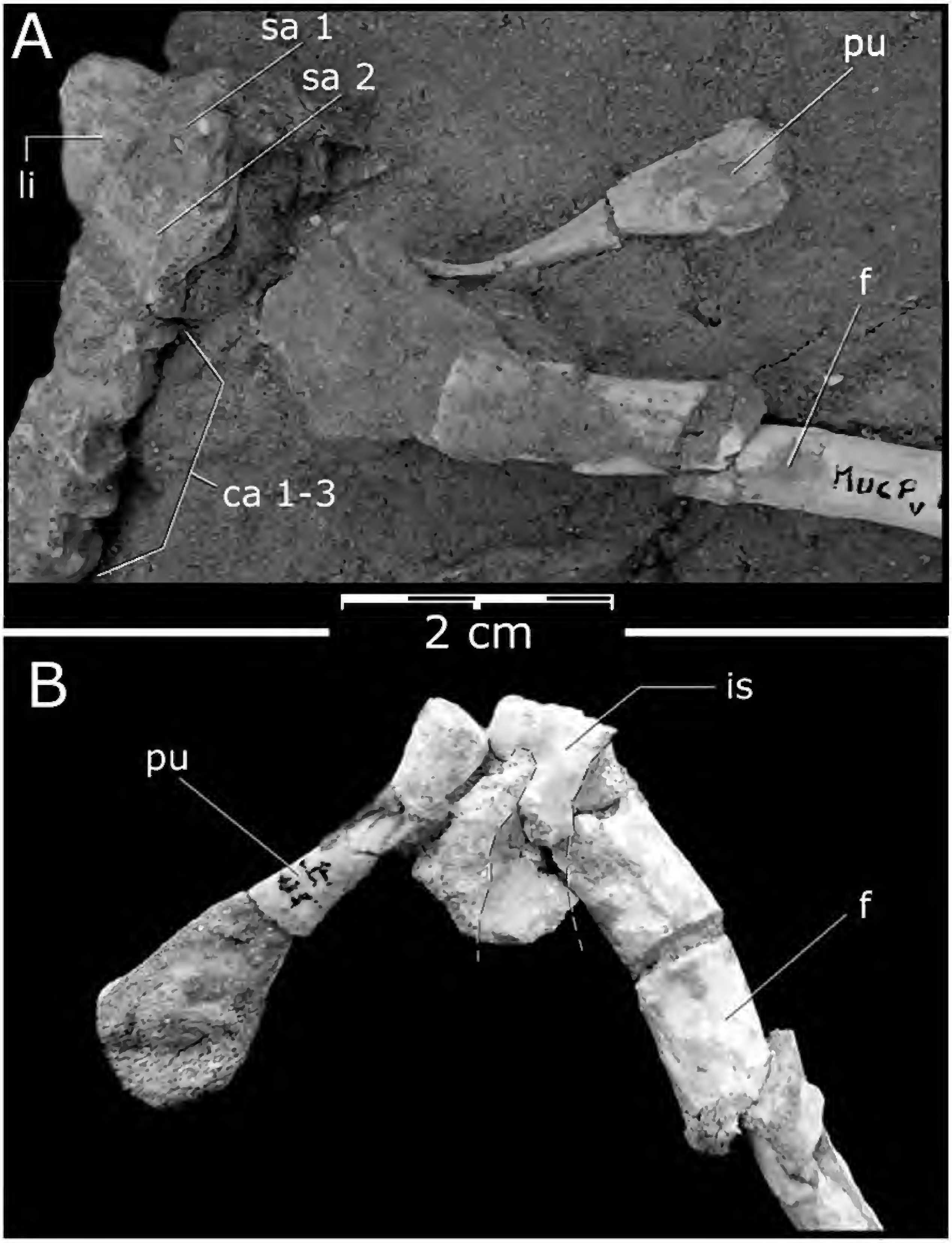

Fig.12- *Neuquensuchus universitas* gen.nov., sp.nov., MUCPv-47. A, right pubis and femur in lateral view; B, right pubis, ischium and femur in medial view. (Abbreviations in the Appendix IV).

FEMUR

Only in the specimen MUCPv-47 of *Neuquensuchus universitas* the right femur have been preserved (Figs.3D, 13, 14). In the holotype, the right femur articulates with the tibia and fibula (Figs.12-13) as likewise with the right ilum, sacral and first caudals vertebrae. The long and thin femur is like in basal crocodylomorphs. It is mostly practically straigth and the sigmoid form is not conspicuous or not very marked. The condyle on the femoral head is slightly expanded (Fig.14). This characteristic differs from other sphenosuchians, such as *Terrestrisuchus* (CRUSH, 1984), *Dromicosuchus* (SUES *et al.*, 2003, UNC 15574), *Macelognathus* (GÖHLICH *et al.*, 2005, LACM 4684/128272), and derived mesoeucrocodylians. The femur of *Neuquensuchus universitas* possesses a lengthened furrow similar in its proportions and muscular dispositions to that observed in the femoral fragment of *Shantungosuchus hangjinensis* (WU *et al.*, 1994, IVPP V10097). *Neuquensuchus universitas* as in other basal crocodyliforms lacks of a prominent anteromedial process of the femur medially placed on the proximal end of shaft. This process is very marked in Notosuchia (POL, 2005; FIORELLI, 2005; fig. 14B) and other metasuchians such as *Mahajangasuchus* (BUCKLEY & BROCHU, 1999). Although in MUCPv-47 the distal end is damaged we can observe that the lateral condyle (fibular c.) is slightly bigger with respect to the medial one. An important character in *Neuquensuchus* is the relationship of the diaphyseal width (7mm) and the total length of the femur (94mm) equal to 7.5%. This is similar to some basal crocodyliforms (*Gobiosuchus* = 6.3%; *Shantungosuchus* = 7.6%), differing from *Protosuchus* and more derived mesoeucrocodylians – Metasuchia – where it is always bigger than 9%.

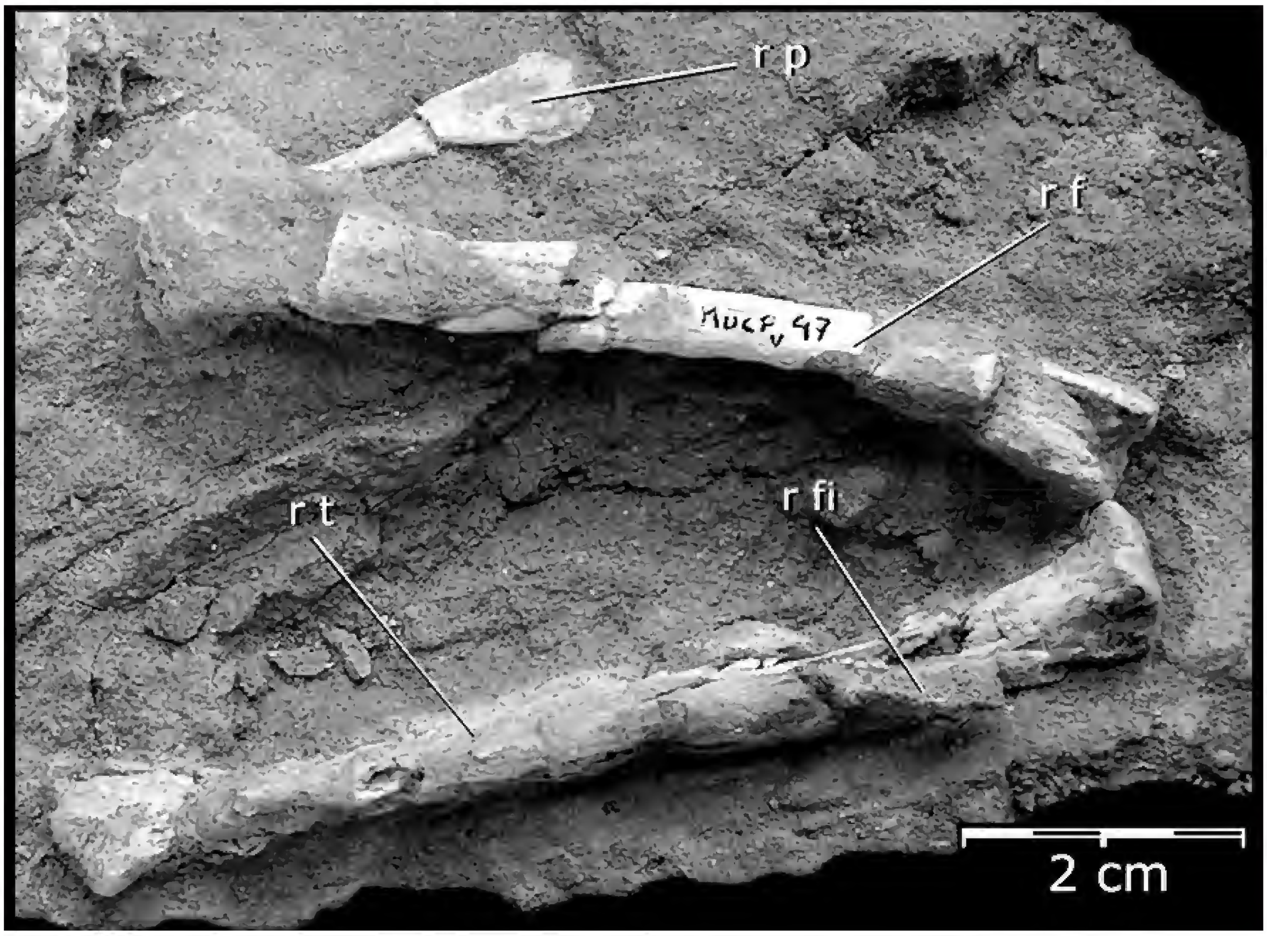

Fig.13- *Neuquensuchus universitas* gen.nov., sp.nov., MUCPv-47. Right pubis, femur, tibia and fibula in lateral view. (Abbreviations in the Appendix IV).

TIBIA

The right tibia in MUCPv-47 is complete (Fig.13), while in MUCPv-161 just the proximal end is preserved (Fig.14). The tibia possesses a very long, straigth and thin shaft, similar to that present in some most basal Crocodylomorpha, as in sphenosuchians like *Macelognathus*, *Dromicosuchus*, *Hesperosuchus*, and *Terrestrisuchus* (CRUSH, 1984; CLARK *et al.*, 2000; SUES *et al.*, 2003; GÖHLICH *et al.*, 2005). However, in some "protosuchian" forms the tibia is too similar, such as in *Shantungosuchus chuhsienensis* (YOUNG, 1961; WU *et al.*, 1994, IVPP V2484) and *Gobiosuchus kielanae* (OSMÓLSKA, 1972; OSMÓLSKA *et al.*, 1997, ZPAL MgR-II/67). The proximal end is broad and the distal end has a small lateromedial expansion. *Neuquensuchus universitas* does not possess a developed cnemial crest and the femoral condyles form a marked notch in the distal end (Figs.14A, 14C).

In MUCPv-47, the tibia (105.3mm) is longer than the femur (94.5mm) comprising 89.7% of the tibial length. This possibly represents one of the most important characters in the species because this feature character is only shared with *Shantugosuchus*, where the length of the femur is 95% of the tibial length (WU *et al.*, 1994) (see Fig.13). By contrast in all other crocodyliforms the femur is always longer than the tibia (WU *et al.*, 1994). Even so, in early ontogenetic states of Crocodylia the femur is always longer than the tibia (DODSON, 1975). Inside Crocodylomorpha, some sphenosuchians as *Terrestrisuchus* or *Macelognathus* have the tibia longer than the femur (SERENO, 1991; CRUSH, 1984; GÖHLICH *et al.*, 2005). On the other hand, the relationship between the diaphyseal width (5.6mm) and the tibia length (105mm; 5.3%) is identical to that of *Shantungosuchus* (5.3%), differing from those of *Protosuchus* and Metasuchia that is always bigger then 8%. The discussions and evolutionary consequences on these characteristics are offered later on (see Discussion).

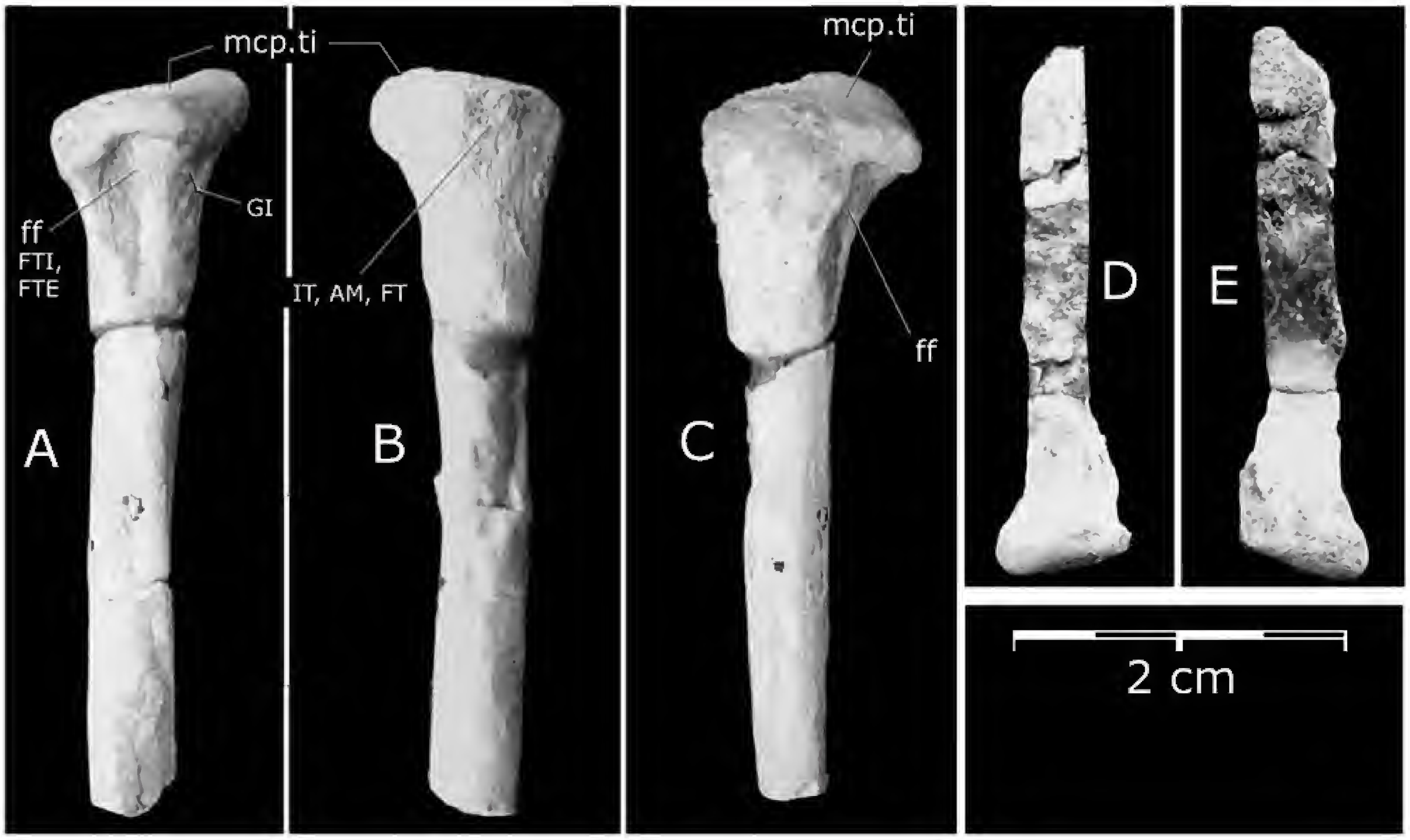

Fig.14- *Neuquensuchus universitas* gen.nov., sp.nov., MUCPv-161. A, B and C, proximal end of left tibia; D and E, distal end of left fibula. Tibia in posterior (A), anterior (B) and lateral (C) view. Fibula in medial (D) and lateral (E) views. (Abbreviations in the Appendix IV).

Fibula

Few fibular materials have been preserved. In MUCPv-47, the partial and very fragmentary right fibula (Fig.13) is thin and long. In MUCPv-161 the distal end of fibula possesses a thin shaft with D-shaped in cross-section (Figs.14D, 14E).

Tarsus

Only conserved in MUCPv-161, the left astragalus is incompletely preserved (Fig. 3D). In spite of it, we can see morphological characters in the articulations that are present in typical Crocodyliformes tarsus. For instance, a good marked process supporting the square fibular facet and a lateromedially wide tibial facet. The articulate surface for the metatarsals is rounded and width with a deep anterior hollow.

PHYLOGENETIC RELATIONSHIPS

Although *Neuquensuchus universitas* gen.nov., sp.nov. is represented just by postcranials remains, it was possible to establish its phylogenetic relationships based on parsimony analysis. For this analysis, we used a modified data set taken of recent publications (Pol & Norell, 2004b; Pol *et al.*, 2004), which was based on the addition of several characters of previously published matrix (Clark, 1994; Wu & Sues, 1996; Gomani, 1997; Wu *et al.*, 1997; Buckley *et al.*, 2000; Ortega *et al.*, 2000). We have included new characters not included in previous publications that were defined by Wu & Sues (1996), Martinelli (2003), and Fiorelli (2005). Moreover, sixteen new characters were added and new taxa were included. The matrix includes 231 characters and 51 taxa (see appendixes I and II). The present work tries to focus mainly in non-neosuchian basal crocodyliforms. In the present analysis, characters were taken with equal weight using NONA (Goloboff, 1993) and published with Winclada (Nixon, 1999). An heuristic tree search was performed consisting of 1000 replicates of RAS + TBR with a final round of TBR (mult*1000; max*;), holding 20 trees per replication (hold/20;). Thirty six (36) most parsimonious trees of 839 steps (CI 0.34; RI 0.65) were found in all of replications. The 36 phylogenetic hypotheses differ in the relationships of some neosuchian crocodyliforms like for instance Peirosaurid forms and derived neosuchian group. However, Notosuchia as well as the basal groups of crocodyliformes stayed constant in the different hypotheses as we can observe in the strict consensus tree (Fig.15).

In all more parsimonious hypotheses, *Neuquensuchus universitas* represents the sister taxa of *Shantungosuchus hangjinensis* from the Lower Cretaceous of Inner Mongolia (Northern China). Both shared the character 91 “hypapophyses present only in cervical vertebrae” and character 226 “Tibia longer than the femur” (Node 11 of the figure 15). This last character is ambiguous in *Sichuanosuchus shuhanensis* and *Zosuchus davidsoni*. In another sence, just two diagnostic character separating *Neuquensuchus* from *Shantungosuchus* (olecranon well developed [character 173-0] and the relationship between the ulna length and the humerus length [Character 220]; Node 12). The absence of additional autapomophies in *Neuquensuchus* can be due to the fragmentarity of the available material, which does not possess cranial remains, the reason why we support the erection of this new taxon. The temporal and geographical separation goes in favor of this proposal. The resulting clade shows that *Neuquensuchus* and *Shantungosuchus* are the sister group of *Sichuanosuchus shuhanensis* from the Early Cretaceous of Sichuan, China (Node 10). This node is diagnosed by two unambiguous synapomorphies (palatines form palatal shelves that do not meet [Character 37]; posteroventral edge of mandibular ramus markedly deflected [Character 170]). However, both characters are ambiguous in *Neuquensuchus*. *Zosuchus davidsoni* from Upper Cretaceous of Gobi Desert (Mongolia), represents the sister taxa of the resulting node of the three previously taxa (Node 9), diagnosed by five unambiguous synapomorphies (characters 55, 143, 163, 169 and 178; see Appendix I).

The clade conformed by Fruita form, *Zosuchus*, *Sichuanosuchus*, *Shantungosuchus*, and *Neuquensuchus* (Node 8 from the figure 15), is closely related to *Hsisosuchus* and more derived mesoeucrocodilians than other Protosuchia (*Gobiosuchus*, *Protosuchus* and all their descendants). This conclusion is similar to that obtained in other works (Pol, 2003; Pol & Norell, 2004a, 2004b; Pol *et al.*, 2004; Fiorelli, 2005; Pol & Apesteguía, 2005; Zaher *et al.*, 2006), but differs of those in that it postulates a monophyly of protosuchids and “protosuchians” (e.g., Wu *et al.*, 1994; Wu & Sues, 1996; Wu *et al.*, 1997; Tykoski *et al.*, 2002).

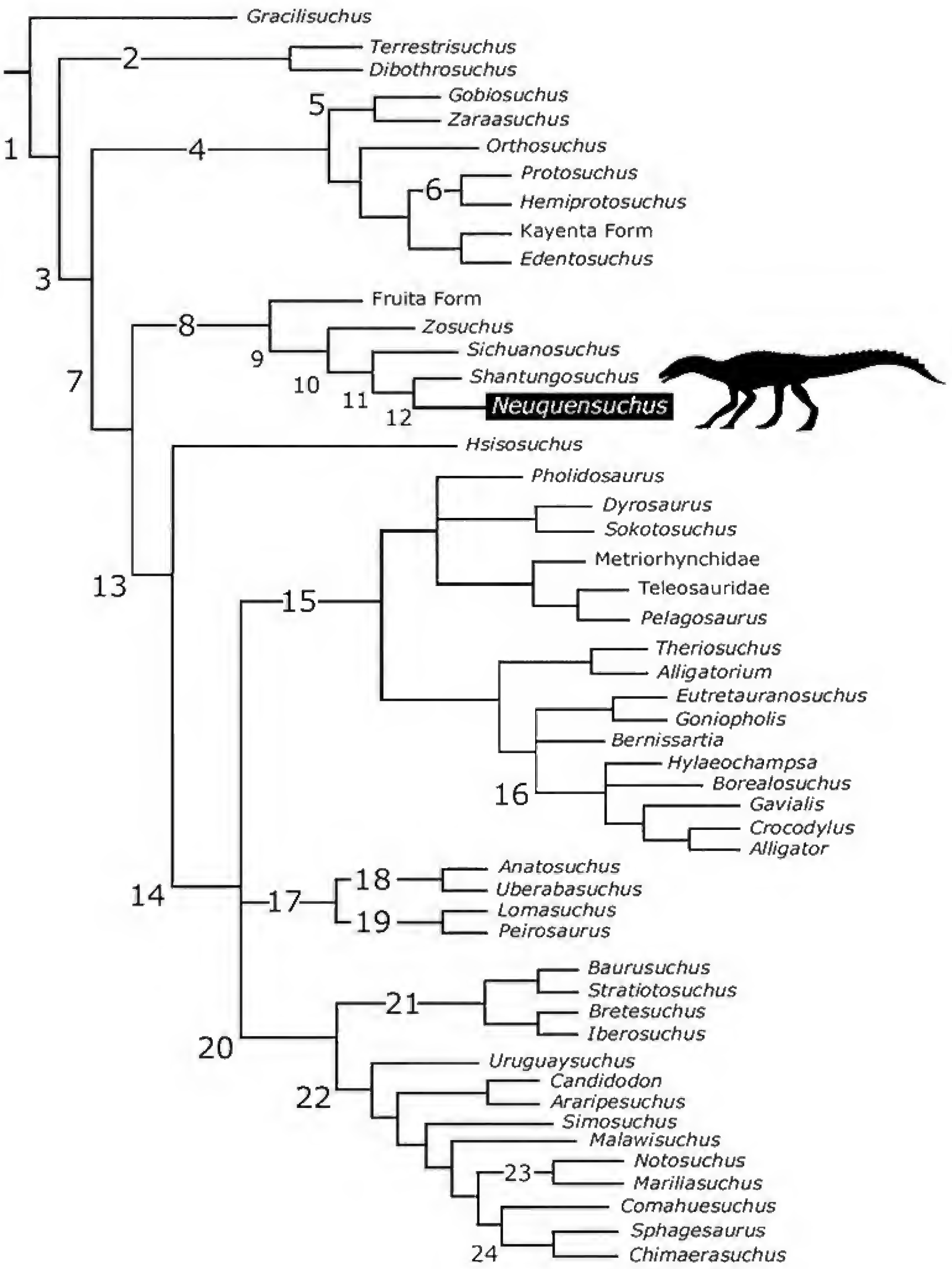

Fig.15- Strict consensus of the 36 most parsimonious topologies that resulted from a strict parsimony analysis obtained with NONA and published with Winclada. Tree length is 839 with a CI of .33 and a RI of .65. The tree shows the phylogenetic relationships of *Neuquensuchus universitas* gen.nov., sp.nov. performed a basal mesoeucrocodylia. 1: Crocodylomorpha; 2: "Sphenosuchia"; 3: Crocodyliformes; 4: Protosuchia; 5: Gobiosuchidae; 6: Protosuchidae; 7: Mesoeucrocodylia; 8, 9, 10 and 11: Innominated; 12: *Neuquensuchus universitas* gen.nov., sp.nov.; 13: "Mesosuchia"; 14: Metasuchia; 15: Neosuchia; 16: Eusuchia; 17: Peirosauridae; 18 and 19: Innominated; 20: Notosuchia; 21: Sebecosuchia; 22: Innominated; 23: Notosuchidae; 24: Sphagesauridae. *Araripesuchus* is used here like a terminal taxon although in the analyses it was used *A. gomesii* and *A. patagonicus*. Explanation and definitions of suprageneric taxa see Appendix V.

On the other hand and in contrast to some recent phylogenetic analysis (e.g., CLARK, 1994; BUCKLEY *et al.*, 2000; ORTEGA *et al.*, 2000; TURNER, 2004; 2006; TURNER & CALVO, 2005) that placed *Araripesuchus* like basal member of Neosuchia, in our analyses this taxon appears as a basal member of notosuchian clade, an important result comparable with other recent phylogenetic studies (POL, 2003; POL & NORELL, 2004a, 2004b; POL *et al.*, 2004; FIORELLI, 2005; POL & APESTEGUÍA, 2005; ZAHER *et al.*, 2006).

DISCUSSION

Neuquensuchus universitas gen.nov., sp.nov. represents the first basal Mesoeucrocodylia non Metasuchia from the Cretaceous, not only from Argentina but also from South America and Gondwana (Fig.16). Mesoeucrocodylia is defined here like the most inclusive clade containing *Crocodylus* but not *Protosuchus* (BENTON & CLARK, 1988; CLARK, 1994; *sensu* SERENO *et al.*, 2001; 2005).

Without doubts, the Triassic argentinean and gondwanic forms of basal crocodyliforms, such as *Hemiprotosuchus* (BONAPARTE, 1967; 1971), *Protosuchus* sp. (ALCOBER *et al.*, 2004), *Orthosuchus (*NASH, 1975*), and Baroqueosuchus haughtoni* (BUSBEY & GOW, 1984) are not related directly to *Neuquensuchus universitas*, because it integrates the most basal group of Mesoeucrocodylia (Figs.15-16) due to the intimate relationships with other so formerly called "protosuchians" and more derived form like *Hsisosuchus*. Then, it demonstrates that *Neuquensuchus* does not represent a derived form from the Upper Triassic/Early Jurassic Gondwana taxa. Therefore, it comes from highly more derived taxa from the Early Cretaceous of Central Asia, such as *Shantungosuchus* and *Sichuanosuchus* (Figs. 15, 16). It would be possible that related form of "Las Hoyas crocodyliform" is closely related, but there is not a detailed data of this specimen to include it in the phylogenetic analyses, although in recent studies "Las Hoyas crocodyliform" is intimately related to *Gobiosuchus* (see ORTEGA *et al.*, 2000). Regarding to the Cretaceous paleobiogeography, *Neuquensuchus universitas* throws more problems than answers inside the classics paleogeographic models used until now (e.g., BONAPARTE, 1986; BUFFETAUT, 1982; SERENO, 1999). This problematic disjunct distributional Cretaceous pattern is similar to that observed in other groups of very diverse tetrapods, as for example Lissamphibia (Discoglossidae, *Callobatrachus*), Mammaliamorpha (e.g., Peramura), Notosuchia (*Chimaerasuchus*) and Atoposauridae (cf. *Theriosuchus*). Even in countless groups of dinosaurs, for example Rebbachisauridae, Nemegtosauridae, Saltasauridae, Abelisauroidea, Spinosauroidea, Carcharodontosauridae, Deinonychosauria, Alvarezsauria, and some Ornithischia (*Valdosaurus*, *Ouranosaurus*). Summing up, it was suggested by different authors (e.g., WU & SUES, 1996; POL, 2003), that this rises many questions to the hypothesis of faunistic endemism in Gondwana during Cretaceous times, a classic hypothesis assumed by several authors (GASPARINI, 1971; BONAPARTE, 1986; 1991; CLARK *et al.*, 1989). The occurrence of *Neuquensuchus* in Gondwana does not indicate the presence of Pangeic lineage of this clade in Southern lands. The presence of this basal mesoeucrocodylian is more probably due to subsequent dispersion, as it has been postulated in recent studies by JUÁREZ VALLIERI & FIORELLI (2002; 2003) and FIORELLI (2005). These authors propose a dispersion event among Gondwana, Europe and Central Asia during the Early Cretaceous (Berriasian–Aptian), producing a faunistic interchange poorly recognized previously (BRETT-SURMAN, 1979). Probably it occurred in both ways: from Central Asia to Gondwana through Europe as well as in the opposite direction. This new hypothesis agrees with the distributional pattern of all fossil groups and is perfectly adjusted with recent genetic studies carried out on current vertebrates (see HAY *et al.*, 1995; HEDGES & POLING, 1999; HEDGES, 2001; COOPER *et al.*, 2001; MURPHY *et al.*, 2001; MEYER & ZARDOYA, 2003).

These basals mesoeucrocodylian non-Metasuchia were abundant during Jurassic and Cretaceous in Asia. Undoubtedly they came from basal forms of Upper Triassic or Early Jurassic times, which have suffered an adaptative radiation in that continent. Posteriorly in the Early Cretaceous, after the contact between Gondwana and Asia (JUÁREZ VALLIERI & FIORELLI, 2002; 2003; FIORELLI, 2005), dispersion toward Southern continents of well derived forms took place and for this reason *Neuquensuchus universitas* occurs in Northern Patagonia. Summing up, *Neuquensuchus* represents a clade of mesoeucrocodylian basal form with a purely Asian origin and dispersal center, at least during the Upper Jurassic, and with dispersion out of Asia toward Europe and Gondwana during the Early Cretaceous.

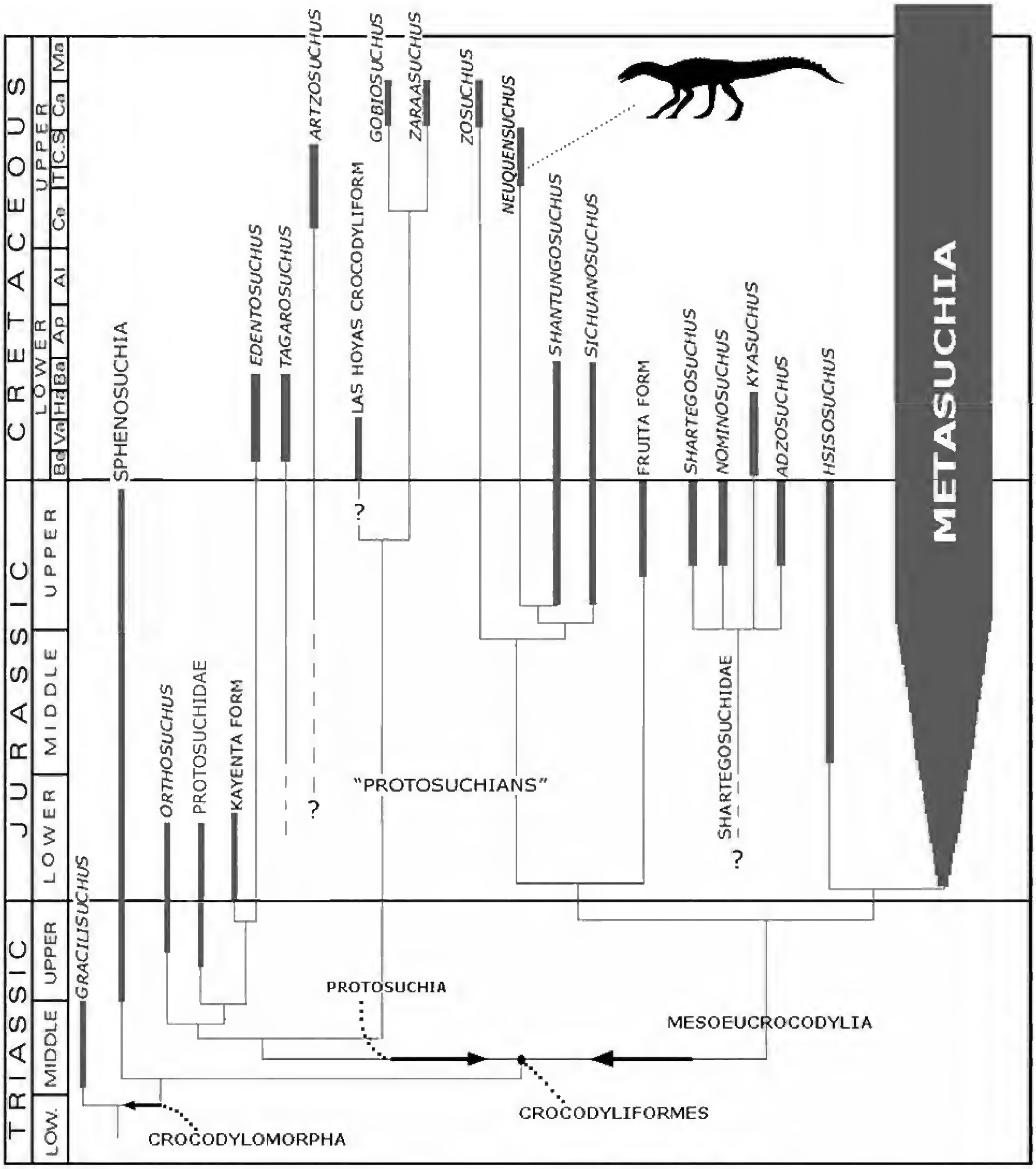

Fig.16- Chronological distribution of Crocodylomorpha. The “Shartegosuchidae” (Efimov, 1988) and other taxa not included in the phylogenetics analysis alone indicating here the highly endemic fauna of Crocodyliformes present in Central Asia during Jurassic and Cretaceous times; they do not indicate phylogenetic relationships with other groups in this chronology.

In the opposite way, we can explain the presence in the Early Cretaceous of China of the derived notosuchian *Chimaerasuchus paradoxus* (Wu & Sues, 1996; Martinelli, 2003; Pol, 2003; Pol & Norell, 2004a; 2004b; Pol, 2005; Fiorelli, 2005) or the atoposarid neosuchian cf. *Theriosuchus* sp. (Wu *et al.*, 1996, IVPP V 10613). It seems that derived basal Crocodyliformes had an important adaptative success in Central Asia during Cretaceous times, for example by the occurrence of *Edentosuchus*, *Tagarosuchus*, *Artzosuchus*, *Gobiosuchus*, *Zaraasuchus*, *Shantungosuchus*, *Sichuanosuchus*, and *Zosuchus*. By contrast, in Neopangea it did not happen this way. The fact that in Gondwana, and mainly in South America, exist an acceptable Cretaceous crocodyliform record, the fragmentary remains of *Neuquensuchus* probably indicate their low abundance. Moreover they did not suffer an apparent adaptative radiation, as it occurred with Notosuchia, a properly gondwanic group. Together with previous protosuchid and "protosuchians" Asian taxa, the Upper Jurassic and Early Cretaceous forms includes in "Shartegosuchidae" – *Shartegosuchus* (Efimov, 1988), *Nominosuchus* (Efimov, 1996; Kurzanov *et al.*, 2003), *Kyasuchus* (Efimov & Leshchinskiy, 2000), and *Adzosuchus* (Efimov *et al.*, 2000) (see Fig.16) –, it is indicating the highly endemic fauna of Crocodyliformes present in Central Asia during Jurassic and Cretaceous times. In a recent work (Fiorelli *et al.*, 2006), it was demonstrated the monophyly and the Shartegosuchidae's endemic group, and they represent the most basal group of the mesosuchian clade (Fiorelli *et al.*, in prep.). The crocodyliforms fauna and other Asian continental tetrapods are correlated with the biogeographical hypothesis proposed by Russell (1993) of a sequential partition of Pangea. He postulated the Asian isolation of Neopangea during the Upper Triassic or Early Jurassic.

In another sense, an interesting aspect that presents *Neuquensuchus universitas* derivated from the present study is the important character related to the longitudinal ratio between the femur and tibia. Previously it was aforementioned that the femur comprises 89.7% of the tibial length, feature character only shared with *Shantugosuchus*, with a femoral length of 95% of the total tibial length (Wu *et al.*, 1994) (see Fig.13). In the other crocodyliforms the femur is always longer than the tibia (Wu *et al.*, 1994), even so in early ontogenetics states of Crocodylia (Dodson, 1975). Within Crocodylomorpha, only in some sphenosuchians like *Terrestrisuchus* or *Macelognathus* the tibia is longer than the femur (Sereno, 1991; Crush, 1984; Göhlich *et al.*, 2005). Undoubtedly, this convergent characteristic was acquired independently by both groups, sphenosuchians – some species – and these two basal mesoeucrocodylian taxa, *Shantungosuchus* and *Neuquensuchus*.

As it has been suggested by diverse authors (Crush, 1984; Sereno, 1991; Sereno & Wild, 1992; Clark *et al.*, 2000; Sues *et al.*, 2003; Clark *et al.*, 2004; Göhlich *et al.*, 2005), sphenosuchians such as *Terrestrisuchus*, *Macelognathus, Junggarsuchus*, *Dromicosuchus*, and *Hesperosuchus*, would have presented a high capacity cursorial for the diverse characteristics of their extremities, mainly by the long and thin bones. Also, Wu *et al.* (1994) suggested that *Shantungosuchus* had a high cursorial capacity instead of very quick terrestrial displacement. The close relationships of forelimb with *Neuquensuchus* allow us to expect the same capacity of movement and cursorial capacity. In the more related taxa (*Sichuanosuchus* and *Zosuchus*), this characteristic – tibia > femur – is ambiguous. These important cursorial characteristic present in these crocodylomorphs possibly had a great influence in their spatial ranges and the amplification of ecological and territorial niches, allowing a bigger dispersal capacity.

Although postcranials remains of *Neuquensuchus universitas* gen.nov., sp.nov. reported here represent the first evident crocodyliform non-Metasuchia in gondwanic Cretaceous lands, we do not know too much about their anatomy and relationships. We believe that the strong phylogenetic relationships of *Neuquensuchus* produce important implications and give novel light about the paleobiogeographic issues. New exploratory works with the purpose of finding new remains of these original taxa, mainly cranial materials, will help to elucidate and know with more details their anatomy and phylogenetic relationships.

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APPENDIX I

LISTS OF CHARACTERS CORRESPONDING TO THE DATA MATRIX (SEE APPENDIX III) USED IN THE PHYLOGENETIC ANALYSES

Definitions of the characters 1-101 were taken from CLARK (1994) and they have the same numeration like in the original publication. The character 5 was excluded of this analysis (due to the dependence with the modified definition of the character 6). Nevertheless, this exclusion does not affect the result of these analyses. The following ones, 102 to 192 characters, were taken from POL & NORELL (2004b). They are listed in order in relation to the same publication and the source mentioned together with the number of original character. The characters 193 and 194 were taken and designated by POL *et al.* (2004), corresponding originally to the characters 164 and 179, respectively. The characters 195, 196, and 197 were taken from WU & SUES (1996) that originally corresponded to the characters 6, 17 and 31, respectively. Although the characters 198 and 199 were taken from MARTINELLI (2003) they originally corresponded to the respective characters 35 and 36. The characters 200 and 210 were designated by FIORELLI (2005) and the numerations are the same ones. The characters 215 and 218 were taken and modified from POL (1999a) corresponding to the characters 192 and 191, respectively. Character 226 is taken and modified from SERENO (1991) corresponding to the character 27. The characters 1, 3, 6, 23, 37, 45, 49, 65, 67, 69, 73, 77, 79, 90, 91, 96, 97, 103, 104, 105, 107, 126, 143, 149, and 165 were taken as aditives characters (also marked with "+" in this list). For finish, the characters 211–214, 216, 217, 219–225, and 227–231 are new, designated by the authors.

CHARACTER 1 (modified from CLARK, 1994: character 1): + External surface of dorsal cranial bones: smooth (0), slightly grooved (1) and heavily ornamented with deep pits and grooves (2).
CHARACTER 2 (modified from CLARK, 1994: character 2): Skull expansion at orbits: gradual (0), or abrupt (1).
CHARACTER 3 (modified from CLARK, 1994: character 3): + Rostrum proportions: narrow oreinirostral (0), broad oreinirostral (1), nearly tubular (2), or platyrostral (3).
CHARACTER 4 (CLARK, 1994: character 4): Premaxilla participation in internarial bar: forming at least the ventral half (0), or with little participation (1).
CHARACTER 5 (CLARK, 1994: character 5): Premaxilla anterior to nares: narrow (0), or broad (1).
CHARACTER 6 (modified from CLARK, 1994: character 6): + External nares facing anterolaterally or anteriorly (0), dorsally not separated by premaxillary bar from anterior edge of rostrum (1), or dorsally separated by premaxillary bar (2).
CHARACTER 7 (CLARK, 1994: character 7): Palatal parts of premaxillae: do not meet posterior to incisive foramen (0), or meet posteriorly along contact with maxillae (1).
CHARACTER 8 (CLARK, 1994: character 8): Premaxilla-maxilla contact: premaxilla loosely overlies maxilla (0), or sutured together along a butt joint (1).
CHARACTER 9 (modified from CLARK, 1994: character 9): Ventrally opened notch on ventral edge of rostrum at premaxilla-maxilla contact: absent (0), present as a notch (1), or present as a large fenestra (2).
CHARACTER 10 (CLARK, 1994: character 10): Posterior ends of palatal branches of maxillae anterior to palatines: do not meet (0), or meet (1).
CHARACTER 11 (CLARK, 1994: character 11): Nasal contacts lacrimal (0), or does not contact (1).
CHARACTER 12 (CLARK, 1994: character 12): Lacrimal contacts nasal along medial edge only (0), or medial and anterior edges (1).
CHARACTER 13 (CLARK, 1994: character 13): Nasal contribution to narial border: yes (0), or no (1).
CHARACTER 14 (CLARK, 1994: character 14): Nasal-premaxilla contact: present (0), or absent (1).
CHARACTER 15 (modified from CLARK, 1994: character 15): Descending process of prefrontal: does not contact palate (0), or contacts palate (1).
CHARACTER 16 (CLARK, 1994: character 16): Postorbital-jugal contact: postorbital anterior to jugal (0), or postorbital medial to jugal (1), or postorbital lateral to jugal (2).
CHARACTER 17 (CLARK, 1994: character 17): Anterior part of the jugal with respect to posterior part: as broad (0), or twice as broad (1).
CHARACTER 18 (CLARK, 1994: character 18): Jugal bar beneath infratemporal fenestra: flattened (0), or rod-shaped (1).
CHARACTER 19 (CLARK, 1994: character 19): Quadratojugal dorsal process: narrow, contacting only a small part of postorbital (0), or broad, extensively contacting the postorbital (1).
CHARACTER 20 (CLARK, 1994: character 20): Frontal width between orbits: narrow, as broad as nasals (0), or broad, twice as broad as nasals (1).
CHARACTER 21 (CLARK, 1994: character 21): Frontals: paired (0), unpaired (1).
CHARACTER 22 (CLARK, 1994: character 22): Dorsal surface of frontal and parietal: flat (0), or with midline ridge (1).
CHARACTER 23 (modified from CLARK, 1994: character 23 by BUCKLEY & BROCHU, 1999: character 81): + Parieto-postorbital suture: absent from dorsal surface of skull roof and supratemporal fossa (0), absent from dorsal surface of skull roof but broadly present within supratemporal fossa (1), or present within supratemporal fossa and on dorsal surface of skull roof (2).

Character 24 (Clark, 1994: character 24): Supratemporal roof dorsal surface: complex (0), or dorsally flat "skull table" developed, with postorbital and squamosal with flat shelves extending laterally beyond quadrate contact (1).
Character 25 (modified from Clark, 1994: character 25) Postorbital bar: sculpted (if skull sculpted) (0), or unsculpted (1).
Character 26 (modified from Clark, 1994: character 26): Postorbital bar: transversely flattened (0), or cylindrical (1).
Character 27 (Clark, 1994: character 27): Vascular opening in dorsal surface of postorbital bar: absent (0), or present (1).
Character 28 (modified from Clark, 1994: character 28): Postorbital anterolateral process: absent or poorly developed (0), or well developed, long, and acute (1).
Character 29 (Clark, 1994: character 29): Dorsal part of the postorbital: with anterior and lateral edges only (0), or with anterolaterally facing edge (1).
Character 30 (Clark, 1994: character 30): Dorsal end of the postorbital bar broadens dorsally, continuous with dorsal part of postorbital (0), or dorsal part of the postorbital bar constricted, distinct from the dorsal part of the postorbital (1).
Character 31 (Clark, 1994: character 31): Bar between orbit and supratemporal fossa broad and solid, with broadly sculpted dorsal surface (0), or bar narrow, sculpting restriced to anterior surface (1).
Character 32 (modified from Clark, 1994: character 32): Parietal: with broad occipital portion (0), or without broad occipital portion (1).
Character 33 (Clark, 1994: character 33): Parietal: with broad sculpted region separating fossae (0), or with sagittal crest between supratemporal fossae (1).
Character 34 (Clark, 1994: character 34): Postparietal (dermosupraoccipital): a distinct element (0), or not distinct (fused with parietal?) (1).
Character 35 (Clark, 1994: character 35): Posterodorsal corner of the squamosal: squared off, lacking extra "lobe" (0), or with unsculptured "lobe" (1).
Character 36 (modified from Clark, 1994: character 36): Posterolateral process of squamosal: poorly developed and projected horizontally at the same level of the skull (0), elongated, thin, and posteriorly directed, not ventrally deflected (1), or elongated, posterolaterally directed, and ventrally deflected (2).
Character 37 (Clark, 1994: character 37): + Palatines: do not meet on palate below the narial passage (0), form palatal shelves that do not meet (1), or meet ventrally to the narial passage, forming part of secondary palate (2).
Character 38 (Clark, 1994: character 38): Pterygoid: restricted to palate and suspensorium, joints with quadrate and basisphenoid overlapping (0), or pterygoid extends dorsally to contact laterosphenoid and form ventrolateral edge of the trigeminal foramen, strongly sutured to quadrate and laterosphenoid (1).
Character 39 (modified from Clark, 1994: character 39): Choanal opening: continuous with pterygoid ventral surface except for anterior and anterolateral borders (0), or opens into palate through a deep midline depression (choanal groove) (1).
Character 40 (Clark, 1994: character 40): Palatal surface of pterygoids: smooth (0), or sculpted (1).
Character 41 (Clark, 1994: character 41): Pterygoids posterior to choanae: separated (0), or fused (1).
Character 42 (modified from Clark, 1994: character 42 by Ortega *et al.*, 2000: character 139): Depression on primary pterygoidean palate posterior to choana: absent or moderate in size being narrower than palatine bar (0), or wider than palatine bar (1).
Character 43 (Clark, 1994: character 43): Pterygoids: do not enclose choana (0), or enclose choana (1).
Character 44 (modified from Clark, 1994: character 44): Anterior edge of choanae situated near posterior edge of suborbital fenestra (or anteriorly) (0), or near posterior edge of pterygoid flanges (1).
Character 45 (Clark, 1994: character 45): + Quadrate: without fenestrae (0), with single fenestrae (1), or with three or more fenestrae on dorsal and posteromedial surfaces (2).
Character 46 (Clark, 1994: character 46): Posterior edge of quadrate: broad medial to tympanum, gently concave (0), or posterior edge of quadrate narrow dorsal to otoccipital contact, strongly concave (1).
Character 47 (Clark, 1994: character 47): Dorsal, primary head of quadrate articulates with squamosal, otoccipital, and prootic (0), or with prootic and laterosphenoid (1).
Character 48 (Clark, 1994: character 48): Ventrolateral contact of otoccipital with quadrate: very narrow (0), or broad (1).
Character 49 (Clark, 1994: character 49): + Quadrate, squamosal, and otoccipital: do not meet to enclose cranioquadrate passage (0), enclose passage near lateral edge of skull (1), or meet broadly lateral to the cranioquadrate passage (2).
Character 50 (Clark, 1994: character 50): Pterygoid ramus of quadrate: with flat ventral edge (0), or with deep groove along ventral edge (1).
Character 51 (Clark, 1994: character 51): Ventromedial part of quadrate: does not contact otoccipital (0), or contacts otoccipital to enclose carotid artery and form passage for cranial nerves IX–XI (1).
Character 52 (Clark, 1994: character 52): Eustachian tubes: not enclosed between basioccipital and basisphenoid (0), or entirely enclosed (1).
Character 53 (Clark, 1994: character 53): Basisphenoid rostrum (cultriform process): slender (0), or dorsoventrally expanded (1).

Character 54 (Clark, 1994: character 54): Basipterygoid process: prominent, forming movable joint with pterygoid (0), or basipterygoid process small or absent, with basisphenoid joint suturally closed (1).
Character 55 (modified from Clark, 1994: character 55 by Ortega *et al.*, 2000: character 68): Basisphenoid ventral surface: shorter than the basioccipital (0), or wide and similar to, or longer in length than basioccipital (1).
Character 56 (Clark, 1994: character 56): Basisphenoid: exposed on ventral surface of braincase (0), or virtually excluded from ventral surface by pterygoid and basioccipital (1).
Character 57 (Clark, 1994: character 57): Basioccipital: without well-developed bilateral tuberosities (0), or with large pendulous tubera (1).
Character 58 (Clark, 1994: character 58): Otoccipital: without laterally concave descending flange ventral to subcapsular process (0), or with flange (1).
Character 59 (Clark, 1994: character 59): Cranial nerves IX–XI: pass through common large foramen vagi in otoccipital (0), or cranial nerve IX passes medial to nerves X and XI in separate passage (1).
Character 60 (Clark, 1994: character 60): Otoccipital: without large ventrolateral part ventral to paroccipital process (0), or with large ventrolateral part (1).
Character 61 (Clark, 1994: character 61): Crista interfenestralis between fenestrae pseudorotunda and ovalis nearly vertical (0), or horizontal (1).
Character 62 (Clark, 1994: character 62): Supraoccipital: forms dorsal edge of the foramen magnum (0), or otoccipitals broadly meet dorsal to the foramen magnum, separating supraoccipital from foramen (1).
Character 63 (Clark, 1994: character 63): Mastoid antrum: does not extend into supraoccipital (0), or extends through transverse canal in supraoccipital to connect middle ear regions (1).
Character 64 (Clark, 1994: character 64): Posterior surface of supraoccipital: nearly flat (0), or with bilateral posterior prominences (1).
Character 65 (modified from Clark, 1994: character 65): + One small palpebral present in orbit (0), one large palpebral (1), or two large palpebrals (2).
Character 66 (Clark, 1994: character 66): External nares: divided by a septum (0), or confluent (1).
Character 67 (Clark, 1994: character 67): + Antorbital fenestra: as large as orbit (0), about half the diameter of the orbit (1), much smaller than the orbit (2), or absent (3).
Character 68 (modified from Clark, 1994: character 68 by Ortega *et al.*, 2000: character 41): Supratemporal fenestrae extension: relatively large, covering most of surface of skull roof (0), or relatively short, fenestrae surrounded by a flat and extended skull roof (1).
Character 69 (modified from Clark, 1994: character 69): + Choanal groove: undivided (0), partially septated (1), or completely septated (2).
Character 70 (Clark, 1994: character 70): Dentary: extends posteriorly beneath mandibular fenestra (0), or does not extend beneath mandibular fenestra (1).
Character 71 (modified from Clark, 1994: character 71): Retroarticular process: absent or extremely reduced (0), very short, broad, and robust (1), with an extensive rounded, wide, and flat (or slightly concave) surface projected posteroventrally and facing dorsomedially (2), posteriorly elongated, triangular-shaped and facing dorsally (3), or posteroventrally projecting and paddleshaped (4).
Character 72 (Clark, 1994: character 72): Prearticular: present (0), or absent (1).
Character 73 (modified from Clark, 1994: character 73): + Articular without medial process (0), with short process not contacting braincase (1), or with process articulating with otoccipital and basisphenoid (2).
Character 74 (Clark, 1994: character 74): Dorsal edge of surangular: flat (0), or arched dorsally (1).
Character 75 (Clark, 1994: character 75): Mandibular fenestra: present (0), or absent (1).
Character 76 (Clark, 1994: character 76): Insertion area for M. pterygoideous posterior: does not extend onto lateral surface of angular (0), or extends onto lateral surface of angular (1).
Character 77 (modified from Clark, 1994: character 77): + Splenial involvement in symphysis in ventral view: not involved (0), involved slightly in symphysis (1), or extensively involved (2).
Character 78 (Clark, 1994: character 78): Posterior premaxillary teeth: similar in size to anterior teeth (0), or much longer (1).
Character 79 (modified from Clark, 1994: character 79): + Maxillary teeth waves: absent, no tooth size variation (0), one wave of teeth enlarged (1), or enlarged maxillary teeth curved in two waves ("festooned") (2).
Character 80 (Clark, 1994: character 80): Anterior dentary teeth opposite premaxilla-maxilla contact: no more than twice the length of other dentary teeth (0), or more than twice the length of other dentary teeth (1).
Character 81 (modified from Clark, 1994: character 81): Dentary teeth posterior to tooth opposite premaxilla-maxilla contact: equal in size (0), or enlarged dentary teeth opposite to smaller teeth in maxillary toothrow (1).
Character 82 (modified from Clark, 1994: character 82 by Ortega *et al.*, 2000: character 120): Anterior and posterior scapular edges: symmetrical in lateral view (0), anterior edge more strongly concave than posterior edge (1), or dorsally narrow with straight edges (2).

Character 83 (modified from Clark, 1994: character 83 by Ortega *et al.*, 2000: character 121): Coracoid length: up to two-thirds of the scapular length (0), or subequal in length to scapula (1).
Character 84 (Clark, 1994: character 84): Anterior process of ilium: similar in length to posterior process (0), or one-quarter or less of the length of the posterior process (1).
Character 85 (Clark, 1994: character 85): Pubis: rodlike without expanded distal end (0), or with expanded distal end (1).
Character 86 (Clark, 1994: character 86): Pubis: forms anterior half of ventral edge of acetabulum (0), or pubis at least partially excluded from the acetabulum by the anterior process of the ischium (1).
Character 87 (Clark, 1994: character 87): Distal end of femur: with large lateral facet for the fibula (0), or with very small facet (1).
Character 88 (Clark, 1994: character 88): Fifth pedal digit: with phalanges (0), or without phalanges (1).
Character 89 (Clark, 1994: character 89): Atlas intercentrum: broader than long (0), or as long as broad (1).
Character 90 (modified from Clark, 1994: character 90): + Cervical neural spines: all anteroposteriorly large (0), only posterior ones rodlike (1), or all spines rodlike (2).
Character 91 (modified from Clark, 1994: character 91 by Buscalioni & Sanz, 1988: character 37 and by Brochu, 1997a: character 7): + Hypapophyses in cervicodorsal vertebrae: absent (0), present only in cervical vertebrae (1), present in cervical and the first two dorsal vertebrae (2), present up to the third dorsal vertebra (3), or present up to the fourth dorsal vertebrae (4).
Character 92 (Clark, 1994: character 92): Cervical vertebrae: amphicoelous or amphyplatian (0), or procoelous (1).
Character 93 (Clark, 1994: character 93): Trunk vertebrae: amphicoelous or amphyplatian (0), or procoelous (1).
Character 94 (Clark, 1994: character 94): All caudal vertebrae: amphicoelous or amphyplatian (0), first caudal biconvex with other procoelous (1), or procoelous (2).
Character 95 (Clark, 1994: character 95): Dorsal osteoderms: rounded or ovate (0), or rectangular, broader than long (1), or square (2).
Character 96 (modified from Clark, 1994: character 96, and Brochu, 1997a: character 40): + Dorsal osteoderms: without articular anterior process (0), with a discrete convexity on anterior margin (1), or with a well-developed process located anterolaterally in dorsal parasagittal osteoderms (2).
Character 97 (modified from Clark, 1994: character 97 by Ortega *et al.*, 2000: characters. 107 and 108): + Rows of dorsal osteoderms: two parallel rows (0), more than two rows (1), or more than four rows with “accessory ranges of osteoderms” (sensu Frey, 1988) (2).
Character 98 (Clark, 1994: character 98): Osteoderms: some or all imbricated (0), or sutured to one another (1).
Character 99 (Clark, 1994: character 99): Tail osteoderms: dorsal only (0), or completely surrounded by osteoderms (1).
Character 100 (Clark, 1994: character 100): Trunk osteoderms: absent from ventral part of the trunk (0), or present (1).
Character 101 (Clark, 1994: character 101): Osteoderms: with longitudinal keels on dorsal surfaces (0), or without longitudinal keels (1).
Character 102 (Wu & Sues, 1996: character 14): Jugal: participating in margin of antorbital fossa (0), or separated from it (1).
Character 103 (modified from Wu & Sues, 1996: character 23): + Articular facet for quadrate condyle: equal in length to the quadrate condyles (0), slightly longer (1), or close to three times the length of the quadrate condyles (2).
Character 104 (modified from Wu & Sues, 1996: character 24 and Wu *et al.*, 1997: character 124): + Jaw joint: placed at level with basioccipital condyle (0), below basioccipital condyle about above level of lower toothrow (1), or below level of toothrow (2).
Character 105 (modified from Wu & Sues, 1996: character 27 and Ortega *et al.*, 2000: character 133): + Premaxillary teeth: five (0), four (1), three (2), or two (3).
Character 106 (modified from Wu & Sues, 1996: character 29): Unsculptured region along alveolar margin on lateral surface of maxilla: absent (0), or present (1).
Character 107 (Wu & Sues, 1996: character 30): + Maxilla: with eight or more teeth (0), seven teeth (1), six teeth (2), five teeth (3), or four teeth (4).
Character 108 (Wu & Sues, 1996: character 33): Coracoid: without posteromedial or ventromedial process (0), with elongate posteromedial process (1), or distally expanded ventromedial process (2).
Character 109 (Wu & Sues, 1996: character 40): Radiale and ulnare: short and massive (0), or elongate (1).
Character 110 (Wu & Sues, 1996: character 41): Postacetabular process: directed posteroventrally or posteriorly (0), or directed posterodorsally and much higher in position than preacetabular process (1).
Character 111 (modified from Gomani, 1997: character 4): Prefrontals anterior to orbits: elongated, oriented parallel to anteroposterior axis of the skull (0), or short and broad, oriented posteromedially-anterolaterally (1).
Character 112 (modified from Gomani, 1997: character 32): Basioccipital and ventral part of otoccipital: facing posteriorly (0), or facing posteroventrally (1).
Character 113 (Buscalioni & Sanz, 1988: character 35): Vertebral centra: cylindrical (0), or spool shaped (1).
Character 114 (modified from Buscalioni & Sanz, 1988: character 39): Transverse process of posterior dorsal vertebrae

dorsoventrally low and laminar (0), or dorsoventrally high (1).

Character 115 (Buscalioni & Sanz, 1988: character 44): Number of sacral vertebrae: two (0), or more than two (1).

Character 116 (Buscalioni & Sanz, 1988: character 49): Supra-acetabular crest: present (0), or absent (1).

Character 117 (Buscalioni & Sanz, 1988: character 54): Proximal end of radiale expanded symmetrically, similarly to the distal end (0), or more expanded proximomedially than proximolaterally (1).

Character 118 (Ortega *et al.*, 1996: character 5): Lateral surface of the dentary: without a longitudinal depression (0), or with a longitudinal depression (1).

Character 119 (Ortega *et al.*, 1996: character 9): Ventral exposure of splenials: absent (0), or present (1).

Character 120 (Ortega *et al.*, 1996: character 11, Ortega *et al.*, 2000: character 100): Tooth margins: with denticulate carinae (0), or without carinae or with smooth or crenulated carinae (1).

Character 121 (modified from Pol, 1999a: character 133 and Ortega *et al.*, 2000: character 145): Lateral surface of anterior process of jugal: flat or convex (0), or with broad shelf below the orbit with triangular depression underneath it (1).

Character 122 (Pol, 1999a: character 134): Jugal: does not exceed the anterior margin of orbit (0), or exceeds the anterior margin of orbit (1).

Character 123 (Pol, 1999a: character 135): Notch in premaxilla on lateral edge of external nares: absent (0), or present on the dorsal half of the external nares lateral margin (1).

Character 124 (Pol, 1999a: character 136): Dorsal border of external nares: formed mostly by the nasals (0), or by both the nasals and premaxilla (1).

Character 125 (Pol, 1999a: character 138): Posterodorsal process of premaxilla: absent (0), or present extending posteriorly wedging between maxilla and nasals (1).

Character 126 (Pol, 1999a: character 139 and Ortega *et al.*, 2000: character 9): + Premaxilla-maxilla suture in palatal view, medial to alveolar region: anteromedially directed (0), sinusoidal, posteromedially directed on its lateral half and anteromedially directed along its medial region (1), or posteromedially directed (2).

Character 127 (Pol, 1999a: character 140): Nasal lateral border posterior to external nares: laterally concave (0), or straight (1).

Character 128 (Pol, 1999a: character 141): Nasal lateral edges: nearly parallel (0), oblique to each other converging anteriorly (1), or oblique to each other diverging anteriorly (2).

Character 129 (Pol, 1999a: character 143): Palatine anteromedial margin: exceeding the anterior margin of the palatal fenestrae wedging between the maxillae (0), or not exceeding the anterior margin of palatal fenestrae (1).

Character 130 (Pol, 1999a: character 144): Dorsoventral height of jugal antorbital region respect to infraorbital region: equal or lower (0), or antorbital region more expanded than infraorbital region of jugal (1).

Character 131 (Pol, 1999a: character 145): Maxilla-lacrimal contact: partially included in antorbital fossa (0), or completely included in antorbital fossa (1).

Character 132 (Pol, 1999a: character 146): Lateral eustachian tube openings: located posteriorly to the medial opening (0), or aligned anteroposteriorly and dorsoventrally (1).

Character 133 (Pol, 1999a: character 147): Anterior process of ectopterygoid: developed (0), or reduced–absent (1).

Character 134 (Pol, 1999a: character 148): Posterior process of ectopterygoid: developed (0), or reduced-absent (1).

Character 135 (Pol, 1999a: character 149 and Ortega *et al.*, 2000: character 13): Small foramen located in the premaxillo-maxillary suture in lateral surface (not for big mandibular teeth): absent (0), or present (1).

Character 136 (Pol, 1999a: character 150): Jugal posterior process: exceeding posteriorly the infratemporal fenestrae (0), or not (1).

Character 137 (Pol, 1999a: character 151): Compressed crown of maxillary teeth: oriented parallel to the longitudinal axis of skull (0), or obliquely disposed (1).

Character 138 (Pol, 1999a: character 152): Large and aligned neurovascular foramina on lateral maxilary surface: absent (0), or present (1).

Character 139 (modified from Pol, 1999a: character 153): External surface of maxilla and premaxilla: with a single plane facing laterally (0), or with ventral region facing laterally and dorsal region facing dorsolaterally (1).

Character 140 (Pol, 1999a: character 154 and Ortega *et al.*, 2000: character 104): Maxillary teeth: not compressed laterally (0), or compressed laterally (1).

Character 141 (Pol, 1999a: character 155): Posteroventral corner of quadratojugal: reaching the quadrate condyles (0), or not reaching the quadrate condyles (1).

Character 142 (Pol, 1999a: character 156): Base of postorbital process of jugal: directed posterodorsally (0), or directed dorsally (1).

Character 143 (Pol, 1999a: character 157): + Postorbital process of jugal: anteriorly placed (0), in the middle (1), or posteriorly positioned (2).

Character 144 (Pol, 1999a: character 158 and Ortega *et al.*, 2000: character 36): Postorbital-ectopterygoid contact: present (0), or absent (1).

Character 145 (Pol, 1999a: character 161): Quadratojugal: not ornamented (0), or ornamented in the base (1).

Character 146 (Pol, 1999a: character 162): Prefrontal-maxillary contact in the inner anteromedial region of orbit: absent (0), or present (1).

Character 147 (Pol, 1999a: character 163): Basisphenoid: without lateral exposure (0), or with lateral exposure on the braincase (1).

Character 148 (Pol, 1999a: character 165): Quadrate process of pterygoids: well developed (0), or poorly developed (1).

Character 149 (modified from Pol, 1999a: character 166 and Ortega *et al.*, 2000: character 44): + Quadrate major axis directed: posteroventrally (0), ventrally (1), or anteroventrally (2).

Character 150 (Pol, 1999a: character 167): Quadrate distal end: with only one plane facing posteriorly (0), or with two distinct faces in posterior view, a posterior one and a medial one bearing the foramen aereum (1).

Character 151 (Pol, 1999a: character 168): Anteroposterior development of neural spine in axis: well developed covering all the neural arch length (0), or poorly developed, located over the posterior half of the neural arch (1).

Character 152 (Pol, 1999a: character 169): Prezygapophyses of axis: not exceeding anterior edge of neural arch (0), or exceeding the anterior margin of neural arch (1).

Character 153 (Pol, 1999a: character 170): Postzygapophyses of axis: well developed, curved laterally (0), or poorly developed (1).

Character 154 (modified from Pol, 1999b: character 212): Shape of dentary symphysis in ventral view: tapering anteriorly forming an angle (0), Ushaped, smoothly curving anteriorly (1), or lateral edges longitudinally oriented, convex anterolateral corner, and extensive transversally oriented anterior edge (2).

Character 155 (Pol, 1999b: character 213): Unsculpted region in the dentary below the tooth row: absent (0), or present (1).

Character 156 (Ortega *et al.*, 1996: character 13 and Buckley *et al.*, 2000: character 117): Cheek teeth: not constricted at base of crown (0), or constricted at base of crown (1).

Character 157 (Ortega *et al.*, 2000: character 42): Outer surface of squamosal laterodorsally oriented: extensive (0), or reduced and sculpted (1), or reduced and unsculpted (2).

Character 158 (Ortega *et al.*, 2000: character 74): Length/height proportion of infratemporal fenestra: higher than long or subequal (0), or very anteroposteriorly elongated (1).

Character 159 (Ortega *et al.*, 2000: character 90): Foramen intramandibularis oralis: small or absent (0), or big and slotlike (1).

Character 160 (Ortega *et al.*, 2000: character 146): Ectopterygoid medial process: single (0), or forked (1).

Character 161 (modified from Gomani, 1997: character 46 and Buckley *et al.*, 2000: character 113): Cusps of teeth: unique cusp (0), one main cusp with smaller cusps arranged in one row (1), one main cusp with smaller cusps arranged in more than one row (2), several cusps of equal size arranged in more than one row (3), or multiple small cusps along edges of occlusal surface (4).

Character 162 (Pol & Norell, 2004a: character 164): Cross section of distal end of quadrate: mediolaterally wide and anteroposteriorly thin (0), or subquadrangular (1).

Character 163 (Pol & Norell, 2004a: character 165): Palatine-pterygoid contact on palate: palatines overlie pterygoids (0), or palatines firmly sutured to pterygoids (1).

Character 164 (Wu *et al.*, 1997: character 103): Squamosal descending process: absent (0), or present (1).

Character 165 (modified from Wu *et al.*, 1997: character 105): + Development of distal quadrate body ventral to otoccipital-quadrate contact: distinct (0), incipiently distinct (1), or indistinct (2).

Character 166 (Wu *et al.*, 1997: character 106): Pterygoid flanges: thin and laminar (0), or dorsoventrally thick, with pneumatic spaces (1).

Character 167 (Wu *et al.*, 1997: character 108): Postorbital participation in infratemporal fenestra: almost or entirely excluded (0), or bordering infratemporal fenestra (1).

Character 168 (Wu *et al.*, 1997: character 109): Palatines: form margin of suborbital fenestra (0), or excluded from margin of suborbital fenestra (1).

Character 169 (Wu *et al.*, 1997: character 110): Angular posterior to mandibular fenestra: widely exposed on lateral surface of mandible (0), or shifted to the ventral surface of mandible (1).

Character 170 (Wu *et al.*, 1997: character 112): Posteroventral edge of mandibular ramus: straight or convex (0), or markedly deflected (1).

Character 171 (modified from Wu *et al.*, 1997: character 119): Quadrate ramus of pterygoid in ventral view: narrow (0), or broad (1).

Character 172 (Wu *et al.*, 1997: character 121): Pterygoids: not in contact anterior to basisphenoid on palate (0), or pterygoids in contact (1).

Character 173 (Wu *et al.*, 1997: character 122): Olecranon: well developed (0), or absent (1).

Character 174 (Wu *et al.*, 1997: character 123): Cranial table width respect to ventral portion of skull: as wide as ventral portion of skull (0), or narrower than ventral portion of skull (1).

Character 175 (Wu *et al.*, 1997: character 127): Depression on posterolateral surface of maxilla: absent (0), or present (1).

Character 176 (Wu *et al.*, 1997: character 128): Anterior palatal fenestra: absent (0), or present (1).
Character 177 (Pol & Norell, 2004a: character 179): Paired ridges located medially on ventral surface of basisphenoid: absent (0), or present (1).
Character 178 (Pol & Norell, 2004a: character 180): Posterolateral end of quadratojugal: acute or rounded, tightly overlapping the quadrate (0), or with sinusoidal ventral edge and wide and rounded posterior edge slightly overhanging the lateral surface of the quadrate (1).
Character 179 (Pol & Norell, 2004a: character 181): Orientation of quadrate body distal to otoccipital-quadrate contact in posterior view: ventrally (0), or ventrolaterally (1).
Character 180 (Gasparini *et al.*, 1993: character 3): Wedgelike process of the maxilla in lateral surface of premaxilla-maxilla suture: absent (0), or present (1).
Character 181 (Pol & Norell, 2004b: character 181): Palpebrals: separated from the lateral edge of the frontals (0), or extensively sutured to each other and to the lateral margin of the frontals (1).
Character 182 (Pol & Norell, 2004b: character 182): External surface of ascending process of jugal: exposed laterally (0), or exposed posterolaterally (1).
Character 183 (Pol & Norell, 2004b: character183): Longitudinal ridge on lateral surface of jugal below infratemporal fenestra: absent (0), or present (1).
Character 184 (Pol & Norell, 2004b: character 184): Dorsal surface of posterolateral region of squamosal: without ridges (0), or with three curved ridges oriented longitudinally (1).
Character 185 (Pol & Norell, 2004b: character 185): Ridge along dorsal section of quadrate-quadratojugal contact: absent (0), or present (1).
Character 186 (Pol & Norell, 2004b: character 186): Sharp ridge along the ventral surface of angular: absent (0), or present (1).
Character 187 (Pol & Norell, 2004b: character 187): Longitudinal ridge along the dorsolateral surface of surangular: absent (0), or present (1).
Character 188 (Pol & Norell, 2004b: character 188): Dorsal surface of osteoderms ornamented with anterolaterally and anteromedially directed ridges (fleur de lys pattern of Osmólska *et al.*, 1997): absent (0), or present (1).
Character 189 (Pol & Norell, 2004b: character 189): Cervical region surrounded by lateral and ventral osteoderms sutured to the dorsal elements: absent (0), or present (1).
Character 190 (Pol & Norell, 2004b: character 190): Appendicular osteoderms: absent (0), or present (1).
Character 191 (Ortega *et al.*, 2000: character 72): Supratemporal fenestra: present (0), or absent (1).
Character 192 (Pol & Norell, 2004a: character 183): Choanal opening: opened posteriorly and continuous with pterygoid surface (0), or closed posteriorly by an elevated wall formed by the pterygoids (1).
Character 193 (Pol *et al.*, 2004: caract. 164) Major axis of ectopterygoid body oriented: anterolaterally (0), or anteriorly (1).
Character 194 (Pol *et al.*, 2004: character 179): Ventral margin of infratemporal bar of jugal: straight (0), or dorsally arched (1).
Character 195 (Wu & Sues, 1996: character 6): Premaxilla-maxilla segment longer than (0) or shorter than (1) remainder of skull in lateral view.
Character 196 (Wu & Sues, 1996: character 17): Mandibular symphysis deep (0) or shallow and spatulate anteriorly (1).
Character 197 (Wu & Sues, 1996: character 31): Maxillary tooth row extending posterior to anterior border of orbit (0) or terminating in front of orbit (1) in lateral view.
Character 198 (Martinelli, 2003: character 35): Ectopterygoid does not contact posterior part of palatine (0), or contact palatine, excluding the pterygoid of the posterior edge of the fenestra palatina (1).
Character 199 (Martinelli, 2003: character 36): Nasal-frontal suture transversely oriented (0) or obliquely oriented (1).
Character 200 (Fiorelli, 2005): Hipapophysis in cervical vertebrae: absent (0), like a vertical thorn slightly or well marked (1) or like keel-shaped running anteroposteriorly in ventral surface of centrum (2).
Character 201 (Fiorelli, 2005): First and second pair of mandibular teeth directed, in relation to the vertical one, toward up practically vertical (0) or directed anterodorsally in an angle approximate of 45º-50º (1).
Character 202 (Fiorelli, 2005): Postcanines teeth (molariforms) triangular in transverse section (0), rounded, cuspidate or tablets laterally (Ziphodont or basal type) (1).
Character 203 (Fiorelli, 2005): Small and big neurovascular foramina aligned on lateral surface of dentary: absent (0) or present (1).
Character 204 (Fiorelli, 2005): Anteroposterior crest directed in the glenoid fossa on articular shelf separating the articulation cavities for the respective condyles of quadrate: absent (0) or present (1).
Character 205 (Fiorelli, 2005): Posterior Buttress on shelf of articular like top for the quadrate: absent (0) or present (1).
Character 206 (Fiorelli, 2005): Rounded cervical centra (0) in transverse section or irregulary polygonal (heptagonal) formed one of their vertexes the ventral keel (hipapophysis) (1).
Character 207 (Fiorelli, 2005): Development of thin pre and postspinals sheets in anterior dorsal vertebrae: absent or little developed (0) or developed (1).

Character 208 (Fiorelli, 2005): Suprapostzygapophyseal laminae in cervical and cervicodorsal vertebrae: absent (0) or present (1).
Character 209 (Fiorelli, 2005): Development of the acetabular roof of ilium with a deep acetabular cavity: not developed (0) or well developed (1).
Character 210 (Fiorelli, 2005): Prominent process on femur (for *m. coccygeofemoralis*) located medially in the proximal end of shaft: absent or slightly developed (0) or very developed (1).
Character 211 Cervical vertebrae centra very anteroposteriorly lengthened (0), or shorter and tablets in anteroposterior sense (1).
Character 212 Articulation surface of the parapophysis for the chapter of the ribs in cervical vertebrae: anteroposteriorly lengthened –double long than wide or more– (0) or practically square or rounded – as long as wide – (1).
Character 213 Long postparapophyseal border in cervical vertebrae, anteroposteriorly directed until the posterior border of the centrum, forming deep furrows toward both sides (up and below) of the parapophyseal border: absent (0), present (1).
Character 214 Hook or expansion in the posterior vertex of the scapula formed by the posterior and dorsal border: absent (0), present (1).
Character 215 (Pol, 1999a: character192) Lateral expansion in proximal extreme of the humerus: absent (0), present (1).
Character 216 Proportion among the long of the deltopectoral crest (Dc) in relation to the total length (TL) of the humerus (= Dc hu / TL hu): smaller than 25 % (0) or bigger than 25 % (1).
Character 217 Proportion among the diameter of the shaft (Dsh) of the humerus measured in half of their longitude in relation to the total length (TL) of the humerus (= Dsh hu/ TL hu): smaller or similar to 7 % (0) or bigger than 7 % (1).
Character 218 (modified from Pol, 1999a: character 191) + Proportion among the total length of humerus and wide of proximal expansion: in the range between 2.15 and 2.3 (0), between 2.8 and 3.2 (1), bigger at 3.7 and 4.74 (2), same or bigger at 5.0 (3).
Character 219 Proportion among the diameter of the shaft (Dsh ra) of the radius measured in half of their longitude in relation to the total length (TL ra) of the radius (= Dsh ra / TL ra): smaller or similar to 4 % (0), between 4 % and 6 % (1) or bigger than 6 % (2).
Character 220 Relationship between the total length of the ulna and the total length of the humerus (= TL ul / TL hu): ulna < humerus (0) or ulna > humerus (1).
Character 221 Relationship between the broad of the shaft of ulna and their total length (= BS ul / TL ul): smaller than 5 % (0), between 5 % and 7 % (1) or bigger than 7 % (2).
Character 222 Broad of the femoral shaft in relation to their total length (= BS fe / TL fe): smaller than 9 % (0) or bigger than 9 % (1).
Character 223 Broad of the tibial shaft in relation to their total length (= BS ti / TL ti): smaller or similar to 7 % (0) or bigger than 7 % (1).
Character 224 Relationship among the broad of the distal expansion of pubis (B.d.e pu) and the total length (TL pu) of the same one (= B.d.e pu / TL pu): smaller or similar to 30 % (0) or bigger than 30 % (1).
Character 225 Relationship among the diameter of the pubic shaft (D.sh.pu) and the total length (TL pu) of the same one (= D.sh.pu / TL pu): smaller than 8 % (0) or bigger than 8 % (1).
Character 226 (modified from Sereno, 1991: character 27): Relationship between the total length of the femur and the total length of the tibia (= TL fe / TL ti): femur > tibia (0) or femur < tibia (1).
Character 227 Anteroposterior longitudinal relationship between the ventral scapular section (v.S) and dorsal scapular blade (d.S) [= v.S/d.S]: smaller than 55 % (0); between 55 % and 70 % (1); between 70 % and 100 % (2) or bigger than 100 % (3).
Character 228 Relationship between the anteroposterior length of dorsal scapular blade (d.S) and the major dorsoventral longitudinal axis (m.l.a.S) of the same one [= d.S/m.l.a.S]: smaller than 40 % (0); between 40 % and 55 % (1) or bigger than 55 % (2).
Character 229 Relationship between the diameter of the scapular half constriction (S.h.c) and the major dorsoventral longitudinal axis (m.l.a.S) of the same one [= S.h.c/ m.l.a.S]: less than 15 % (0); between 15 % and 20 % (1) or more than 20 % (2).
Character 230 Relationship between the major dorsoventral longitudinal axis of scapula (m.l.a.S) and the total length of the humerus (t.l.hu) [= m.l.a.S/t.l.hu]: less than 70 % (0) or more than 70 % (1).
Character 231 Relationship between the total length of the pubis (t.l.pu) and the total length of femur (t.l.fe) [= t.l.pu/t.l.fe]: less than 45 % (0) or more than 45 % (1).

APPENDIX II

List of the 51 taxa used in the phylogenetic analysis (taken from Pol & Norell, 2004b; Pol *et al.*, 2004). *Anatosuchus*, *Mariliasuchus*, *Candidodon*, *Stratiotosuchus*, and *Uberabasuchus* are new taxa included in this paper.

Gracilisuchus stipanicicorum (Romer, 1972)
Terrestrisuchus gracilis (Crush, 1984)
Dibothrosuchus elaphros (Wu & Chatterjee, 1993)
Protosuchus richardsoni (Colbert & Mook, 1951)
Hemiprotosuchus leali (Bonaparte, 1971)
Kayenta Form (Clark, 1986)
Edentosuchus tienshanensis (Young, 1973; Pol *et al.*, 2004)
Orthosuchus stormbergi (Nash, 1975)
Gobiosuchus kielanae (Osmólska, 1972)
Zaraasuchus shepardi (Pol & Norell, 2004b)
Shantungosuchus hangjinensis (Wu *et al.*, 1994)
Neuquensuchus universitas (MUCPv-47, MUCPv-161)
Sichuanosuchus shuhanensis (Wu *et al.*, 1997)
Zosuchus davidsoni (Pol & Norell, 2004a)
Fruita Form (Clark, 1985, 1994)
Hsisosuchus chungkingensis (Young & Chow, 1953; Li *et al.*, 1994; Wu *et al.*, 1994)
Notosuchus terrestris (Woodward, 1896; Gasparini, 1971)
Anatosuchus minor (Sereno *et al.*, 2003)
Comahuesuchus brachybuccalis (Bonaparte, 1991)
Mariliasuchus amarali (Carvalho & Bertini, 1999)
Uruguaysuchus aznarezi (Rusconi, 1933)
Chimaeresuchus paradoxus (Wu & Sues, 1996)
Malawisuchus mwakasyungutiensis (Clark *et al.*, 1989; Gomani, 1997)
Candidodon itapecuruense (Carvalho, 1994; Nobre & Carvalho, 2002)
Simosuchus clarki (Buckley *et al.*, 2000)
Sphagesaurus huenei (Price, 1950; Pol, 2003)
Araripesuchus gomesii (Price, 1959)
Araripesuchus patagonicus (Ortega *et al.*, 2000)
Baurusuchus pachecoi (Price, 1945)
Stratiotosuchus maxhechti (Campos *et al.*, 2001)
Bretesuchus bonapartei (Gasparini *et al.*, 1993)
Iberosuchus macrodon (Antunes, 1975; Ortega *et al.*, 2000)
Lomasuchus palpebrosus (Gasparini *et al.*, 1991)
Peirosaurus torminni (Price, 1955; Gasparini *et al.*, 1991)
Uberabasuchus terrificus (Carvalho *et al.*, 2004)
Theriosuchus pusillus (Owen, 1879; Clark, 1986, 1994; Ortega *et al.*, 2000)
Alligatorium (Wellnhofer, 1971; Clark, 1986, 1994)
Eutretauranosuchus delfsi (Mook, 1967; Clark, 1986, 1994)
Goniopholis (Mook, 1942; Clark, 1986, 1994; Salisbury *et al.*, 1999)
Pholidosaurus decipiens (Owen, 1878; Clark, 1986, 1994)
Dyrosaurus phosphaticus (Buffetaut, 1978; Clark, 1986, 1994)
Sokotosuchus ianwilsoni (Halstead, 1975; Buffetaut, 1979; Clark, 1986, 1994)
Pelagosaurus typus (Eudes-Deslongchamps, 1863)
Teleosauridae (Buffetaut, 1982; Clark, 1986, 1994)
Metriorhynchidae (Kälin, 1955; Gasparini & Diaz, 1977)
Hylaeochampsa vectiana (Clark & Norell, 1992; Ortega *et al.*, 2000)
Bernissartia fagessi (Buscalioni & Sanz, 1990; Norell & Clark, 1990)
Borealosuchus formidabilis (Erickson, 1976; Brochu, 1997b)
Gavialis gangeticus (Clark, 1994; Brochu, 1997a)
Crocodylus niloticus (Clark, 1994; Brochu, 1997a)
Alligator mississippiensis (Clark, 1994; Brochu, 1997a)

APPENDIX III

Data matrix used in phylogenetic analysis

Gracilisuchus stipanicicorum
000000??0?000000000000?0?000000000?0??0?0?00000?000???0000?0???00000?100000?00000000?011?0000?0?000001012?00?00???00?01?01000??1?01???000001002?0???0000???0?0??0??0000?0000000?00000000?0?00000?00000000100?000?00100111320201??03011?

Terrestrisuchus gracilis
000??00??01?000000?000001000000?110?00000?00000?000??0?000?000???002??0100?00000000010?0000?0200000101 0?01100?100000001001?10?00?11010001?[01]110???00000??0000000?0?0??00??0100??00??000?????00000010100100?0001001100003010000?121001

Dibothrosuchus elaphros
000?00?020??001???000000?????00110000000?00000?0000?00000?0?0101000?010100?0010?000?????2000?0????01010?01100?0?00000001001?10?00?1?000101011100??000001??00000010001000100?0?00000000?000000000001?100100??00100???1??2?110?????????

Protosuchus richardsoni
2100000120?000011010002100000100010001010?00201001111110010101102011?110210001010100011100[1234]00?1200110101110210010100000[01]000000?01??01??10010[01]0101000000???01000000000120000011110??01000?010?0000000000001201100???10111011122011100030011

Hemiprotosuchus leali
?00?00?10??????10010?0??00?0010?11?0??01??0020?00?11?1100101??1?2?11??1?21???01?????????0????1200?1?101??0??????????000?000??10?00???00000??10?????00???????0?000?12???001??10?0?00?01??00???000000000?01?00?????????0????????????????

Kayenta Form
[12]01110?1200000?10010?0??00????0?0???11110?002010011111100001011?2011?0102100?1010??0????00??0?1200101101112?????0????01100?00?01000111?101001?01?10000000011?0??40012??00011??0?00???00????????011100???01?????????????????????????????

Edentosuchus tienshanensis
201?????[12]????0??[01]0??1?0100??0?????02?110?00?????????????????????[12]?311????10?01010?????????[234]??????????????1[23]??????????00110??1?01?1???1000110?11?1????????011????4?0??1????11??0????0100???????00111000??01100???10110??????????????????

Orthosuchus stormbergi
21100001201?0001001000[01]10000010001000?000?002011001111100??1?1?02011?0?0?0?001000100011100000?120010010211421001?10010?100000001?01010000000000?0???00001???000000?12?000011110000100000?000?0000010001?01?00???10?1?00??3?0?1???0?????

Gobiosuchus kielanae
101000?110000011001?[01][01]?1?00001?10?0201000?0020112011111000?1????201???1?20100[01]010?0?0???????0?1010110[01]012002??0000???0010[01]00001000000?00001001211?0000???110000000?121000011?00?0?001111111111000100?1?01?0????100??0000??0100000???00

Zaraasuchus shepardi
10?????????????1?01?01?1000001?10?02??????????????????????????????2?????1??010??????????????[1234]0??1010??0????????????0??????????????????????????0?????1??1?????????1?00????????1?00???0??????1111111111?00????00???000????001???0???1??????????

Shantungosuchus hangjinensis
2?1????1?0???0?1??1????11??????????21?1[01]100020?1?011?1100?10????????101?1?000??10???????0?1????????????1???????1?????0010???????00??10?00??111211??001?????0?0?00????10111111?0?110??0???1?????00[01]1000?201??0???10001??00??0100001????0

Neuquensuchus universitas
??1??0111?11000???????????????0??1?0??0???????????????00?????????2?????0???0001110030110000102100

Sichuanosuchus shuhanensis
[12]01??0?1200[01]00?10010[01]1?110???1?00?021?10?00020?1?011?1100???????2?11????1?000011?1??01????000????????1?11?0?1????0??100100??1??10?0????00111[01]1210??00?????1?????010111011111100?110000100?1???00?01000120 1000?00?0?0111002001??00?0210?

Zosuchus davidsoni
201??0?1200000??001010[01]110?001110?02211010012?1??011?11000?0?1?0211110????0?01111???????????
????????1?12?3????1?????0010001101 1?0001?0?00101 12?[01]?0001???0?00???010111??1011?101110000001 0
0???000010001?011?0???????????????????????????

Fruita Form
201??00120010001000010010000011001022 1?11?0020112?1???0?0??0??1?2?31?????1?0111101011?1?000111
12?0??1???[01]00???1?1001?001?0?0100100??101?0011?01110??0??00?10?0000?1???000????101?0?00000?00
0??0?0??0?????1???????????????????????????????

Hsisosuchus chungkingensis
211??????1??0000001000011000110 00?0221101000[12]??12?11?10000?0?1?0??111?4?00[01]02?1??10???????0
00?1000???101?0021??1?????01001???????0000??00??1?11?1??00????????0??0????10?0?0111[01]?00??00?0?1
000?01?0001012?1?0????????????????02??????2121?

Notosuchus terrestris
101?00110101001110001111100110011022110110021112011?1000010?1102111112101011 10001[01]11101?
210001000??0122011??01100101[01]1101[01]0100100000011111110110000011100100001011101100001 11011
00000000000000100111112101101111111001111 20211??01221?

Mariliasuchus amarali
101?00?1?10?00?11000101111?0111?01022?10???021?120?1?100??1??1??2130?121010111000??1??0??2?000?
???????2201???011?010?01101101001?0?000111111101?0??001???010000?0111?11?0001?101?0?00000000?0
00100111?1?10110?11?1?????????0211??01221?

Anatosuchus minor
203?00?1?11?001?1?00101111?0010101022?1010?01??????????0?????????1212131?10?10101????????????????
????1?1000???0??????01101?01?10?00????00?00111?00??0????10020??0111?1?000???100???0?000000???010
001000??1?00???????????????????????????

Comahuesuchus brachybuccalis
103??0?1011?00?????0112????????0010?2????1??11?1??????????????????131??????0?10101???????????????????
????[01]13???1??????0?10?101201?01?????011??0?1????11???11?00100?1?0??000???100??0?000??0????0?0?1
1?11?111?????????????????????????????

Sphagesaurus huenei
101?000101??00??100?????110?????????21101?00?????011?1000????????13?2????????100????????1??????????
?????312????0???????1111110111111111111111001110101 1?0?11?0??011?0?10??01??000000?00???????0100
1?1????0????????????????????????????????

Chimaerasuchus paradoxus
101?0001111?00??12??0110?01010??1?1?????2100?00????
11[12]?314210??00?0100111111011??????0?0110??????????10?11?????3????????????1?00???0???????????0???11
1?1211?101111?110011?1202????01221?

Malawisuchus mwakasyungutiensis
101?00?1110000?[01]10001[01][01]1100?110001?22110100011??20???1000?10?1?02?111[01]2?0101110001????
1??210000010??01[12]2111???01?0???01100101?11000???110110101?0?0001???0?100??21110?100001110000
000000000???0100110002?1110101??11001112?0211??01221?

Uruguaysuchus aznarezi
201?001101??00??10??1??1????1???01022?101?0011????1?????0??0???01111[12]???000110100??1?1??????000
0?0??01?21002100?00?000?[01]???01?1?00????1?0111?11?????11?????1?0001????????0???10?????00????????0
1?001101?01100?11?11?001111?????????????

Candidodon itapecuruense
201?00???1??00??110010?????0010101022?111?00?????????????????????11212?????????11????????????????????
????1?01?????????????1011010??00????1001111111????11??????1?0??21?1?1???????1?0???00?000?????01101?0
00??1??????????????????????????????

Simosuchus clarki
1030101100000001000101111 10?0110001021?10100011?11011?1000010?1?0201121210101 10000???????02100
?2010?10002010???01??????11011012120000101001110021100120???211[12]0001111011001[01]1?100000000
000100000101101000011 00?????110?????202??????????

Araripesuchus gomesii
201000110100001110001011111011[01]0010221101000111 12011?10000?0?1102011212 10001101[01][01]1[01]
11111?1[234]000100010011110021001001010100100100000010011000210000110?0011[01]00001 1110100
0011100?000000000000000100 10000?01?0??????110011121021111012211

Araripesuchus patagonicus
201000?1010000?1[01]000101111?0111001022?10100011?12?11?1000??0?1?02?11212?0?011[01]1??1?1??????
????1000??0111100???01???0?01?01101?010000??100110102?0??01????0??[01]1000111?0100001110?0000000
000000001001000O?01100?1?11110011121O211??01221?

Baurusuchus pachecoi
100??0?121??00?1101????111?0110?????2?10110011112011?1000?10??10??3111210101111111??????????????
??????12103????1?????110111010101110011001111011O?0111???[01]0[01]1111011101?00001?0001000000000
0???010000101?01000??????????????????????????

Stratiotosuchus maxhechti
100?0??1??0000?11?111101?0???10?11??????????1?1??????????????????130?????????11????????????????????
?0?2103???1??????????1111?10?1????010001101?10??1??????010??01????1??????10??010?0000????00??0??1?
1??1?????????????????????????????

Bretesuchus bonapartei
1[01]0??01121??00???????????0??????????2???10011????????1011?1??????13?1??1?00?10110????????????????
???????100????1???????01??0????01??0???0??1?0???????????[01]0[01]?1?10?1???1??001??00??????????0????1?
?00101?0100??????????????????????

Iberosuchus macrodon
1?0?00012?0?00111000111111?01?000?02??10100111?12??1?101??10?1????111??10?0?1011011??????[12][12
34]00??00???00?[12][01]0?2??0000???11001101010?1?0??100?11001?0??101???[01]?0111?001101?0??01?1000
01000000??0??010?00????0100???????????????????????????

Lomasuchus palpebrosus
201????1211?00?110001011111??110001022?1010001??12??1?100??1??1??2?21?????00??0[12]11?????????????
???????1???00???00?????0?00???1?110?00???00011?0??1??0??????010???0?11??10??01?1000??11000??0???01
?000100??1?????????????????????????????

Peirosaurus torminni
201?011??1??00??????10?1????????0???2?10???????????????????????????1??????????[12]1???????????????????
?????000?????????????0????1???0???????0?1??????????????[01]??????0??????????????00??1??????????0???00?00
??1?????????????????????????????

Uberabasuchus terrificus
201100?1211?00?1100010?1?1?0110101122??0?0001????????????????????111?131110?11[12]11??????????????
??????011000???0??????01101?01?10?00?1?010000101?11??0????10010??00?1??1000???100?0?1?000000???0
?1000100?01001??????????????????????????

Theriosuchus pusillus
2011011111010011000011011110011001 1?211010001?11?01111000?????1?20211?41001010101101111110001
1112001001010002?00?10?110110[01]001?1100?00?0?00100??01??0?00??10100000?11?010??01?10000??0000
??????010?000??1?1?0??0000110??1???0211????????

Alligatorium
?0??????1?0000?1000010?111??0?100?1????0??00??11??1??1000???????20?1????00101?101?011111000???1?0
0100????????????10??1????????????????????0?????????????????????????0???????????????????0???????????????000??[
01]?1000?00001????????0211??0?????

Eutretauranosuchus delfsi
203????1?10010111000100111?00?0001001110?000?1112011?1010??0?1?0?121204?00001020111???1??0??0?
1?????????000???00?????0?100????110????????0??00???1???0????10?2???001?0??000?1?110?01?0000000???01
0?00???????????????????????????0??????? ?????

Goniopholis
203?121111001011100010011 1?0010001002?101000?1112011?1010?10?1?021312?4100[01]0[12]02011?1??1??
0?00?1200?11?0000021000 10?1101100??101100?00001001000 1?1???000011002000001100100001111 0?01000
00000000010000????01?????0001100?11??0211??0?????

Pholidosaurus decipiens
212?111101??11?11101100111?00100010?211?10000111 2111?101??10?100?1311?300???2?0???11?1???0??0??
2?0??????????????????????1????1?110?????0?0010????????????????0?1?0001???10?001?100?010???0??????010?
00????01?????0001100?11??0211??0?????
00?11??021111030111

Dyrosaurus phosphaticus
002??1?101?010?11?00100011?1010011012?10101001112011?1011?10?10101302?3?00??2?000????????0?00?
?????1????????????????????1?????????????????0??0????????????????021?0001????0??????00??1?0000000???010?0
0?11?01?????0001100?11??0211??0?????

Sokotosuchus ianwilsoni
2?2???1101??10????001001???101001?012?1??????1112?11?1?11??0???1?1?0?????????01????????????????????
?????????????????????1?????????????????0??0?????????????????????0?????????????????????????????????00???????
???????????????????????????

Pelagosaurus typus
202?1111110011020101000000000000[01]100211010000001101111001001?10001200?300000200001101111?0
000001200011101?00???10???????1?1??????0000??010010?0010???00????00010000112010000110000001?0000
000???010000???0?1?0???000????????????????????

Teleosauridae
[02]02?11111100110201001000000000000110021?01000?0011011110010111?1?00120003?000?20000210111?0
000?1200010101 1?0???10??01001101??1011000011000010100?0??0000??10001000011?010?011100010100000
000000000100001?12010000000011000110?0211??0?????

Metriorhynchidae
[02]02?12110100111201011000?0000000110021?0?000?0011011110010111?1?001200?30001020000 2101?11?0
000??????0??012?0???100?01001101??1011?000??000010102?0???000????001000011?01000?110000010000000
00???0100001?1?0100000000011000110?0211??0?????

Bernissartia fagessi
203??21111??00111000?00111?001000?002?????0001112?11?10100?0?1???1?1??41001010201 1?1?11??02002
1110110100000??00????????1????1????????0??0?10???01???0????1?12000001????0??????00??10000????0??01
???????1?1?0???0001100?11????????0?????

Hylaeochampsa vectiana
00???????11???11????1?01???0????0?002?1?1011?????????101??1??1?????10?????????????????????????????????
??????????0???????10?????????????0??0??????0?????????????2??00?????????????????????????????01?????????1?0
???000????????????????????

Gavialis gangeticus
212?1211110011111101101111100100010021101011011120111101101011110[01]1310031000120000011111110
131112111100?000002110?100100?101??121100?0000000100010 1?1?00001?0?20?000110010000111000001?0
000000000010000001001001000001100?11??021111030111

Borealosuchus formidabilis
203?1211110010111000100111?00100010021101011111211111010010?110?13100310001 10?011111111131
11?110?00?000002110?100100?101??11110??000000010001?1???0000110?20?000110010000111000010000000
0000001000000100100100000 1100?11??021111030111

Crocodylus niloticus
203012111100[01]0111000102111100100010021 10?01111112011110100101110[01]131003100010010121111 1
1013111202110 0?0000021100100100?101??121100?00000001001101011000 01?0?200000110010000111000001
0000000000001000000100100100000 1100?11??021111030111

Alligator mississippiensis
203112?101?000111000102111100100 0?00211010111111201111010010 1110[01]0312031000100201211111111
1311120211?0?0000021100100100 1101??111000?000000001001[12]01011000011[01]120000011001000011 1000
01000000000000010000001001001000 0011

APPENDIX IV

ANATOMICAL ABREVIATIONS

ab: anterior blade; ac.r: acromial ridge; AM: insertion of the *M. ambiens*; as: astragalus; Br: origin for the *M. brachialis*; ca: caudal vertebrae (1 to 5); cap: capitulum; CB: insertion of the *M. coracobrachialis brevis*; ce: cervical vertebrae (4 to 9); DC: insertion of the *M. deltoideus clavicularis*; dci: dorsal crest of ilium; di: diapophysis; dpc: deltopectoral crest; do: dorsal vertebrae (1 to 4); f: femur; ff: fossa flexoria; FT: insertion of the *M. femorotibialis*; FTE: insertion of the *M. flexortibialis externus*; FTI: insertion of the *M. flexortibialis internus*; gc: glenoid cavity; GI: origin for the *M. gastrocnemius internus*; h: humerus; hk: scapular hook; hy: hypapophysis; i: ilium (= il); ip: ischiadic peduncule; is: ischium; it: inner tuber; IT: insertion of the *M. iliotibialis*; k: keel; lc: lateral condyle; ldr3: third left dorsal rib; lh: left humerus (= lu); lpe: lateroproximal expansion of humerus; lr: left ribs; ls: left scapula; lt2: left tibia (second individual); lf2: left fibula (second individual); mc: medial condyle; mcp.ti: medial condyle process of the femur in the tibia; ne: neural spine; ol: olecranon process; os?: osteoderm?; P: insertion of the *M. pectoralis*; pa: parapophysis; pap: postacetabular process; pb: posterior blade; pdp: postdiapophyseal process; pp: postparapophyseal process; pr: prezygapophysis; pz: postzygapophysis; pu: pubis; r: radius; ra: radial; rh: right humerus; rf: right femur; ri: right ischium; rp: right pubis; rra: right radius; rs: right scapula; rt.f: right tibia and fibula; rul: right ulna; sa: sacral vertebrae (1 to 2); SC: insertion of the *M. scapulocoracoideus*; sr: sacral ribs; tp: transverse processes; Tr: origin for the *M. triceps brevis*; tu: tuberculum; u: ulna; vph: ventroposterior process in caudal vertebrae for hemal arches.

APPENDIX V

Definitions of the nodes used in the text and the phylogenetic results (figure 15) with the diagnoses character of each node. The definitions are based in Sereno *et al.*, 2001 and *sensu* Sereno *et al.*, 2005:

1 – CROCODYLOMORPHA: The most inclusive clade containng *Crocodylus niloticus* but not *Poposarus gracilis*, *Gracilisuchus stipanicicorum*, *Prestosuchus chiniquensis*, *Aetosaurus ferratus*.
2 – "SPHENOSUCHIA": The most inclusive clade containing *Terrestrisuchus gracilis* but not *Crocodylus niloticus*. Characters 33(1), 105(0), 128(0), 197(1), 220(1).
3 – CROCODYLIFORMES: The least inclusive clade containing *Protosuchus richardsoni* and *Crocodylus niloticus*. Characters 1(2), 3(1), 16(1), 24(1), 30(1), 45(1-2), 47(1), 51(1), 65(2), 67(1), 68(1), 80(1), 82(1), 86(1), 95(1), 99(1), 164(1), 166(1), 172(1), 173(1).
4 – PROTOSUCHIA: The most inclusive clade containing *Protosuchus richardsoni* but not *Crocodylus niloticus*. Characters 25(0), 55(1), 60(1), 73(2), 140(0), 165(2), 185(1), 215(0).
5 – GOBIOSUCHIDAE: The least inclusive clade containing *Gobiosuchus kielanae* and *Zaraasuchus shepardi*. Characters 1(1), 32(1), 75(1), 96(0), 97(1), 174(0), 181(1), 182(1), 183(1), 184(1), 186(1), 187(1), 188(1), 189(1), 190(1), 191(1).
6 – PROTOSUCHIDAE: The least inclusive clade containing *Protosuchus richardsoni* and *Hemiprotosuchus leali*. Characters 48(0), 50(1), 74(1), 132(1).
7 – MESOEUCROCODYLIA: The most inclusive clade containing *Crocodylus niloticus* but not *Protosuchus richardsoni*. Characters 37(2), 39(1), 41(1), 66(1), 79(1), 84(1), 141(1).
8 – Innominated. Characters 31(1), 113(1), 176(1).
9 – Innominated. Characters 55(1), 143(2), 163(0), 169(1), 178(1).
10 – Innominated. Characters 37(1), 170(1).
11 – Innominated. Characters 91(1); 226 (1).
12 – *Neuquensuchus universitas*. Characters 173(0), 220(1)
13 – "MESOSUCHIA": not defined. Characters 10(1), 29(1), 73(2), 119(1), 171(0), 192(1), 197(1), 221(2).
14 – METASUCHIA: The least inclusive clade containing *Notosuchus terrestris* and *Crocodylus niloticus*. Characters 15(1), 17(1), 26(1), 67(2), 83(1), 142(0), 167(1).
15 – NEOSUCHIA: The most inclusive clade containing *Crocodylus niloticus* but not *Notosuchus terrestris*. Characters 6(1), 29(0), 36(0), 80(0), 140(0), 166(0), 209(0).
16 – EUSUCHIA: The least inclusive clade containing *Hylaeochampsa vectiana* and *Crocodylus niloticus*. Characters 43(1), 44(1), 69(0), 71(3), 76(1), 90(1), 91(3), 92(1), 93(1), 110(1), 126(1), 200(0).
17 – PEIROSAURIDAE: The most inclusive clade containing *Peirosaurus torminni* but not *Araripesuchus* gomesii, *Simosuchus clarki*, *Notosuchus terrestris*, *Baurusuchus pachecoi*, *Crocodylus niloticus*. Characters 11(1), 81(1), 105(0), 199(0).
18 – Innominated. Characters 32(1), 74(1), 128(0), 139(0), 140(0).
19 – Innominated (Originally Peirosauridae sensu Gasparini *et al.*, 1991). Characters 120(0).
20 – NOTOSUCHIA: The most inclusive clade containing *Notosuchus terrestris* but not *Crocodylus niloticus*. Characters 71(2), 76(1), 90(1), 91(1), 104(2), 123(1), 135(1), 145(0).
21 – SEBECOSUCHIA: No definition has been proposed. Characters 1(1), 3(0), 102(0), 118(1), 120(0), 128(0), 130(1), 156(1), 159(1), 160(1).
22 – Innominated. Characters 9(0), 67(1), 80(0), 156(1), 202(1).
23 – NOTOSUCHIDAE: The most inclusive clade containing *Nototsuchus terrestris* but not *Araripesuchus gomesii*, *Comahuesuchus brachybuccalis*, *Simosuchus clarki*, *Baurusuchus pachecoi*, *Crocodylus niloticus*. Characters 45(2), 105(0), 137(1), 156(0), 176(1), 202(0).
24 – SPHAGESAURIDAE: The most inclusive clade containing *Sphagesaurus huenei* but not *Baurusuchus pachecoi*, *Sebecus icaeorhinus*, *Araripesuchus gomesii*, *Comahuesuchus brachybuccalis*, *Simosuchus clarki*, *Notosuchus terrestris*, *Crocodylus niloticus*. Characters 105(3), 121(1), 124(1).

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AN INCOMPLETE PTEROSAUR SKULL FROM THE CRETACEOUS OF NORTH-CENTRAL QUEENSLAND, AUSTRALIA [1]

(With 6 figures)

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ABSTRACT: An incomplete pterosaur skull was found in the Albian marine Toolebuc Formation near Hughenden, Queensland, Australia. Although only the snout and part of the jaws are preserved, the specimen has two unique characters: posterior dentary teeth relatively large (approximately half the depth of the dentary) and posterior dentary and maxillary teeth relatively widely spaced (only 3 maxillary teeth between the last enlarged tooth and the nasopreorbital opening), and a unique combination of other characters. Thus, it is assigned to the new genus and species, *Mythunga camara* gen.nov., sp.nov., provisionally related to plesiomorphic pterodactyloids. The snout was apparently hollow with a boxlike internal structure, supporting the characterization of pterosaurs as 'optical illusions'. This specimen represents at least the second pterosaur taxon from Queensland.

Key words: Cretaceous. Australia. *Mythunga* gen.nov. Queensland. Albian. Archaeopterodactyloidea. Toolebuc Formation.

RESUMO: Um crânio incompleto de pterossauro do Cretáceo do centro-norte de Queensland, Austrália.

Um crânio incompleto de pterossauro foi encontrado em rochas do Albiano marinho da Formacão Toolebuc próximo a Hughenden, Queensland, Austrália. Apesar de apenas o focinho e mandíbulas incompletas estarem preservadas, o espécime possui duas características únicas: dentes mandibulares posteriores relativamente grandes (aproximadamente metade da altura da a mandíbula) e dentes maxilares e mandibulares posteriores posicionados relativamente distantes uns dos outros (apenas 3 dentes maxilares entre o mais posterior dos grandes dentes e a abertura nasoantorbital) e uma combinação única de outros caracteres. Então, é aqui determinado um novo gênero e espécie, *Mythunga camara*, provisoriamente relacionado aos pterodactilóides plesiomórficos. O focinho era aparentemente oco com uma estrutura interna compartimentada, suportando a caracterização de pterossauros como "ilusões de ótica". Esse espécime representa ao menos o segundo táxon de pterossauro de Queensland.

Palavras-chave: Cretáceo. Australia. *Mythunga* gen.nov. Queensland. Albiano. Archaeopterodactyloidea. Formação Toolebuc.

INTRODUCTION

The anterior portion of a pterosaur skull was discovered in April 1991 by Phillip Gilmore on Dunluce Station, near Hughenden, north-central Queensland. It was embedded in a calcareous nodule from the Toolebuc Formation. This is the first evidence of a pterosaur from north-central Queensland, although this unit has yielded pterosaur material near Boulia, some 500km to the southwest (Fig.1). Broken and dissociated pieces of ichthyosaurs, as well as ammonites and other mollusks were observed in the area where the snout was recovered. This specimen is the most complete pterosaurian cranial material from Australasia.

Sporadic occurrences of other pterosaur material have been reported in Australasia: in addition to the described material from Boulia (Molnar & Thulborn, 1980; Molnar, 1987), a pubis (QM F27104) and flight metacarpal (NMV P197962) indicate substantially larger pterosaurs than previously known. The Lower Cretaceous of Victoria (reported by Rich & Rich, 1989), and the Upper Cretaceous of Western Australia (Bennett & Long, 1991) and New Zealand (Wiffen & Molnar, 1988; Molnar & Wiffen, 1994) have also produced pterosaurs.

Collection designations - AMNH (American Museum of Natural History, New York City); CAMSM (Sedgwick Museum, Cambridge); NMV (Museum of Victoria, Melbourne); QM (Queensland Museum, Brisbane).

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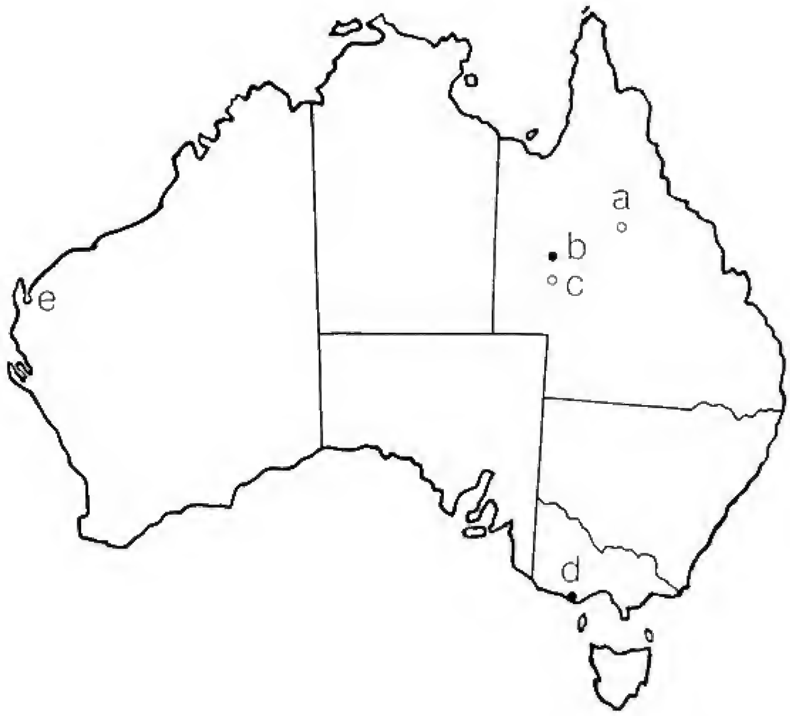

Fig.1- Australian pterosaur localities: (a) Dunluce Station, Albian (*Mythunga camara* sp.nov.); (b) Warra Station, Albian (aff. *Lonchodectes* sp., ?Anhangueridae & NMV P197962); (c) Elizabeth Springs, Albian (QM F27104); (d) Dinosaur Cove, Aptian-Albian (Rich & Rich, 1989); (e) Giralia Range, Maastrichtian (Bennett & Long, 1991).

RESULTS

Systematic Palaeontology

Pterosauria Kaup, 1834
Pterodactyloidea Plieninger, 1901
Archaeopterodactyloidea Kellner, 1996

Genus *Mythunga* gen.nov.

Diagnosis – As for type species, below.

Type species – *Mythunga camara* sp. nov.

Etymology – From 'Mythunga', referring to a star and a hunter of the skies in an unspecified western Queensland aboriginal dialect (Duncan-Kemp, 1968).

Mythunga camara sp.nov.

Diagnosis – Pterodactyloid with straight, slender snout; upper and lower teeth conical, slightly recurved, widely spaced, and lower teeth uniformly decreasing in height posteriorly; upper tooth row extends well back – at least three teeth in both jaws under anterior part of nasopreorbital opening; three maxillary teeth between last enlarged tooth and anterior edge of nasopreorbital fenestra (a); nasopreorbital opening relatively close to posterior margin of symphysis (only two upper teeth between them); nasopreorbital opening anteriorly rounded, not acutely angled; jaw margins strongly corrugated; upper jaw margin straight; anterior teeth enlarged; remainder of teeth relatively large, height of posterior dentary crowns approximately half of jaw depth (a); dentary symphysis narrow. Autapomorphies marked a.

Etymology – From *kamara* (Gr.), chamber, referring to the hollow, boxlike structure of the snout.

Holotype – QM F18896, an incomplete snout and adherent mandible.

Locality – Toolebuc Formation (Late Albian: Exon & Senior, 1976); Dunluce Station, west of Hughenden, north-central Queensland (Fig.1).

Preservation

One-third to one-half of the skull and jaws are preserved (Figs.2-3). The snout and corresponding portions of the mandible, incomplete anteriorly, are preserved back to the anterior part of the nasopreorbital fenestra. The right side has been sheared upwards slightly relative to the left. This resulted in both mandibular rami being visible on the right side of the nodule, whilst only the left is visible on the left. The close interlocking of the upper and lower teeth indicates that the mandible probably remains in the position it held during life.

The snout has been mildly crushed, but there is no indication of plastic deformation. The lower part of the snout on the left has suffered longitudinal fractures, evincing no displacement, that form relatively smooth curves. These bound a depressed region that extends anteriorly at least to the level of the second preserved dentary tooth. The dorsal portion of the snout has been lost, more so on the right than the left. An unknown amount, but likely little (see below), has also been lost from the tip of the snout. The preserved part of the snout is 21.5cm long, and 7.1cm deep at its posterior break.

The dorsal portion and anterior extremity of the nasopreorbital opening are preserved, but ventrally the margin is somewhat broken. Fragments of skull or mandible lay within the nasopreorbital fenestra on the left side, and between the mandibular rami on the right. The mandible is 4cm deep as preserved, and the left ramus shows a longitudinal break, similar to those described for the snout, apparently due to crushing. The ventral margin of the right ramus and anterior portion of the left are eroded (Fig.3).

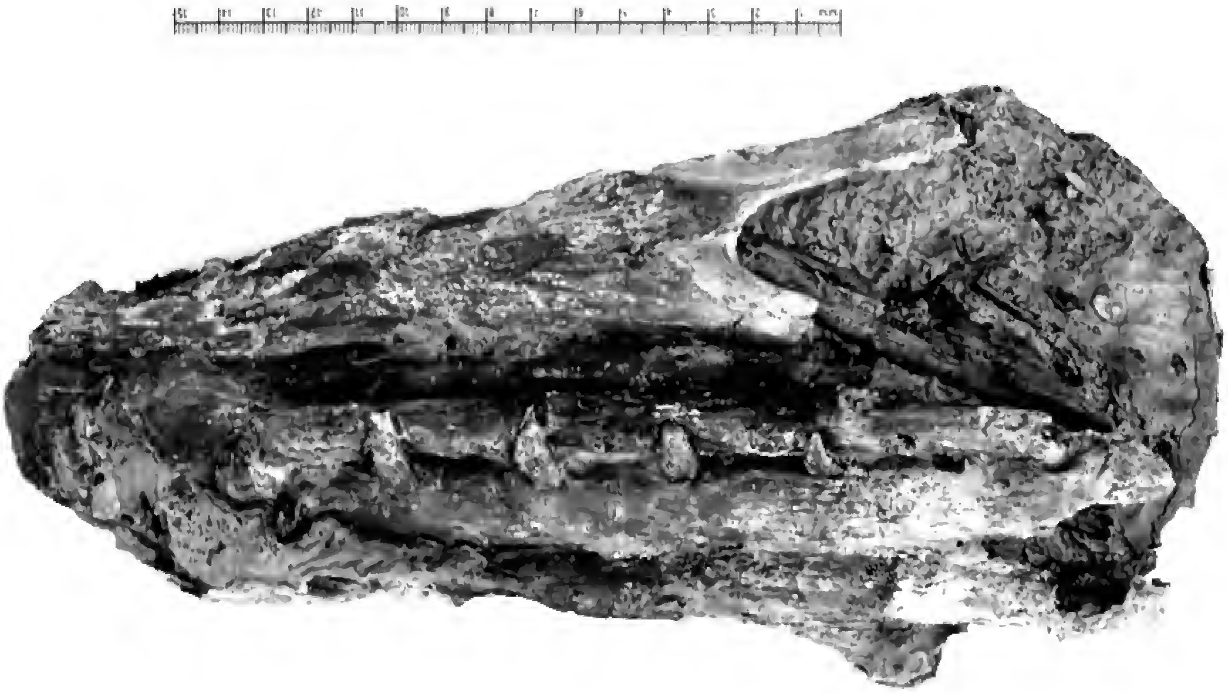

Fig.2- *Mythunga camara* gen.nov, sp.nov. Hughenden region, Queensland, Australia; Toolebuc Formation, Early Cretaceous. Holotype (QM F18896). Snout and mandible, left ventro-lateral view. This is a slightly different perspective from that of figure 4. Scale in mm.

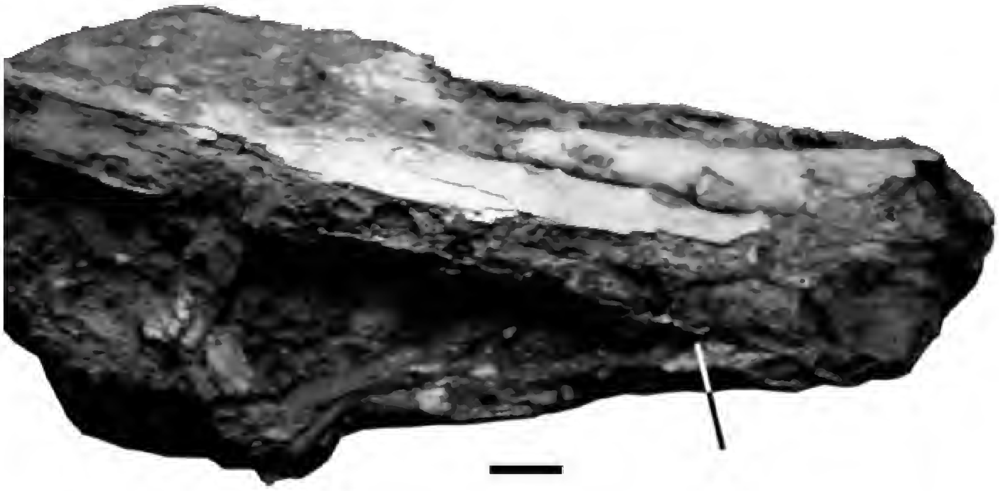

Fig.3- *Mythunga camara* sp.nov. (QM F18896), right lateral view. Bar indicates posterior margin of symphysis. Scale bar = 2cm.

The teeth are fractured, in some cases the enamel is buckled near the base, and the tips (except for the last) are missing, so their form is not entirely clear. All of the left upper teeth but the anteriormost two have been lost, however all save the posteriormost two left mandibular teeth are present. The missing teeth had slipped out of their alveoli, presumably before burial. By contrast all of the crowns, both upper and lower, on the right side have been broken off. Since the teeth that slipped from their sockets were presumably exposed, their absence on the left suggests that the skull came to rest on its right side, and may have been exposed for some time before burial. However, the bones of the left side are well-preserved, whilst substantially less is preserved, or at least exposed, on the right – chiefly the ventral part of the maxilla and much of the dentary. Only small, unidentifiable pieces can be seen in addition to these. This suggests that this side was exposed and that the left lower teeth may have been lost before the skull came to rest in its final position.

DESCRIPTION

The low, slender snout is straight, probably tapering gradually forwards (Figs.2, 4). No clear indication of bony contacts is preserved on the snout, however a fissure extending anteriorly from the nasopreorbital opening may represent part of the maxillary-premaxillary contact. This feature is mildly serrate, rather than smooth as are the breaks, and is at the expected position of this contact. The upper and lower margins of the nasopreorbital opening meet in a smooth curve. The antero-ventral margin of the nasopreorbital opening is not well preserved, and the depression in the lateral face of the snout may represent the contact surface for the jugal. An anterior tongue of the jugal overlies the lateral face of the maxilla at this position in *Araripesaurus santanae* and *Santanadactylus araripensis* (WELLNHOFER, 1985), both now attributed to *Anhanguera*, in *Anhanguera piscator* (KELLNER & TOMIDA, 2000), and in *Tapejara wellnhoferi* (WELLNHOFER & KELLNER, 1991). If this conjecture is correct, the anterior tongue of the jugal was substantially longer than in other known pterosaurs. Because of the loss of the dorsal margin of the snout, there is no indication whether the skull bore a crest.

The first two upper teeth, exposed at the broken front of the snout, are adjacent to one another and very close to the midline, unlike the more posterior teeth, suggesting that they were actually the first two teeth at the tip of the snout. If so, the premaxilla is not clearly separated from the maxilla, which is the case in other large pterosaurs (cf. BENNETT, 2001; EATON, 1910; KELLNER & TOMIDA, 2000; and the figures of WELLNHOFER, 1991a). Also implied is that the snout is relatively short anterior to the nasopreorbital opening, unlike forms such as *Pteranodon, Dsungaripterus, Anhanguera, Gallodactylus*, and *Pterodactylus*.

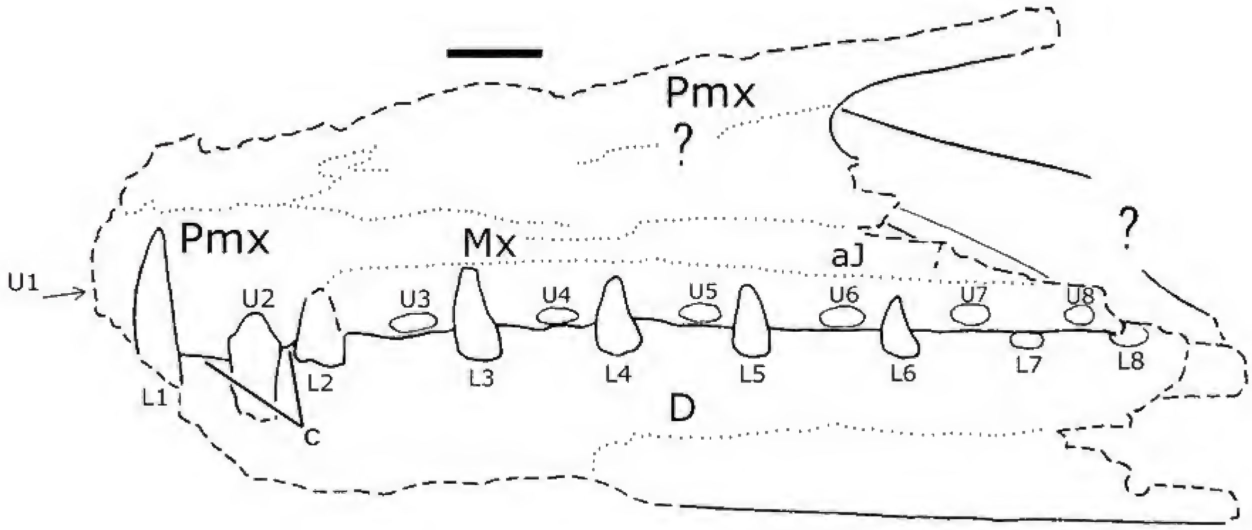

Fig.4- Outline sketch of the snout of *Mythunga camara* sp.nov. (QM F18896) indicating the extent of breakage along the margins of specimen (dashed lines). Abbreviations: (D) dentary; (Mx) maxilla; (Pmx) premaxilla; (aJ) possible articular region for jugal; (c) low collar around the second upper tooth; (U1-8) upper teeth or alveoli; (L1-8) lower teeth or alveoli. U1 indicates the position of the first upper tooth, not visible in lateral view. Scale bar = 2cm.

The mandibular rami appear to have been straight, with dorsal and ventral margins parallel in lateral view. Unfortunately, the ventral surface of the symphyseal region has also been lost, so the presence of a mandibular 'crest' cannot be determined. Owing to the loss of the tip of the jaws, the length of the mandibular symphysis also cannot be determined. The dentigerous margins of both jaws are strongly corrugated, or scalloped, permitting deep interlocking of the upper and lower teeth. That of the upper jaw margin is straight, but descends slightly to form a low conical 'collar', overhanging the lower jaw, around the neck of the first complete tooth. The upper margin of the lower jaw is also straight.

A large, thin walled, apparently hollow element is situated in the nasopreorbital opening. It bears longitudinal grooves and ridges, and may represent the posterior part of the maxilla, or anterior part of the jugal.

Eight teeth are indicated in each jaw on the left side, and four upper and six lower on the right. These are not all visible in the text figure, as the first upper tooth of each side is exposed in the anterior break but is not visible from the side.

The anteriormost left lower tooth preserved is a crown from which the outer bone of the jaw has been broken away: it and the following tooth are about 10% larger (in diameter) than the remainder, as is the anteriormost complete upper tooth (Tab.1). Where reasonably well-preserved, the lowers seem to be smooth near the tip, but bear irregular, longitudinal striae from the neck to about two-thirds the height of the crown. The lower teeth (and the single upper) are conical and slightly recurved, but more strongly flexed in the frontal plane. The depth of the dentary is about twice the height of the preserved dentary teeth. The upper alveoli are widely spaced, but the interval between them decreases, with but a single minor exception, towards the back (Tab.2). The lower teeth seem to gradually decrease in height posteriorly. Both tooth rows have at least three teeth under the anterior region of the nasopreorbital opening and there are two dentary and two upper teeth between the mandibular symphysis and the anterior end of the nasopreorbital opening on the left. The right side shows at least four mandibular alveoli behind the posterior margin of the symphysis, and one left dentary tooth is level with the margin.

ONTOGENETIC AGE

If our interpretation of an exposed maxillary contact surface for the jugal and of a partially open suture between the maxilla and premaxilla is correct, then this skull derives from immature individual (BENNETT, 1993; 2001). The unidentified element preserved in the nasopreorbital opening may have been an element not yet fused to the rest of the skull or mandible, rather than a piece broken free. But since neither end of the piece is preserved, this cannot be determined. The symphyseal region of the mandible is very poorly preserved, but there is no indication that the symphysis was not fused. However, the preservation of the specimen is such that our interpretation of the maxillary depression and the upper break anterior to the nasopreorbital opening might be incorrect, and this represents a mature specimen.

TABLE 1. Antero-posterior diameter of left teeth at base (mm).

NUMBER	2	3	4	5	6	7	8	9
Upper	112	90[1]	86[1]	79[1]	73[1]	63[1]	-	-
Lower	105	94	95	96	84	75	59[1]	53[1]

[1] Measurement of antero-posterior alveolar diameter.

TABLE 2. Spacing of teeth (on left side, mm).

INTERVAL	2-3	3-4	4-5	5-6	6-7	7-8
Upper	35	31	29	30	25	21
Lower	32	31	30	29	25	20

COMPARISON

The most recent and complete phylogenetic analyses are those of KELLNER (2003) and UNWIN (2003). Kellner observed that incompleteness of material (or of preparation) is a major difficulty in understanding pterosaurian relationships: of the 40 characters that he uses pertaining to the cranial skeleton, only 12 can be assessed (or estimated) for *Mythunga camara* sp.nov. These characters are: 3, rostral part of skull anterior to the external naris reduced vs. elongate; 6, position of the external naris above the premaxillary tooth row vs. displaced posterior to the premaxillary tooth row; 8, naris and antorbital fenestra separated vs. confluent; 13, tip of the premaxilla expanded vs. not expanded; 30, mandibular symphysis absent or very short vs. present and at least 30% of mandibular length; 34, position and presence of teeth and distribution along the jaw; 35, largest maxillary tooth positioned posteriorly vs. not so positioned; 36, variation in the size of the anterior teeth with the 5th and 6th smaller than the 4th and 7th vs. lacking this; 37, teeth with a broad and oval base vs. lacking such; 38, multicusped teeth vs. no such teeth; 39, peg-like teeth vs. no such teeth; 40, long, slender teeth vs. no such teeth. Characters 3, 8, and 39 actually have three states, but only those given here are discernible for *M. camara* sp.nov.

In *M. camara* sp.nov. the snout clearly extends well anterior of the nasopreorbital opening and that opening is apparently posterior to the premaxillary toothrow, so indicating that this taxon does not pertain to *Anurognathus* or an asiaticognathid. The confluent nasopreorbital opening implies reference to pterodactyloids. If, as proposed above, the first two upper teeth mark the front of the snout, there is no indication that the tip was expanded. This rules out assignment to the anhanguerids. The mandibular symphysis is clearly neither absent nor very short, indicating assignment to rhamphorhynchids or pterodactyloids. The teeth are evenly distributed along the jaws, thus eliminating reference to dsungaripterids (in which teeth are absent from the front of the jaws) or gallodactylids (in which teeth are restricted to the front of the jaws). Likewise, it could not be referred to *Pteranodon*, azhdarchoids, or nyctosaurids which are edentulous. The largest upper tooth (as determined from the diameter of the base or alveolus) is anterior and not positioned posteriorly thus also eliminating reference to the dsungaripterids. The 5th and 6th teeth are not smaller than the 4th and 7th, thus precluding assignment to *Anhanguera*. The remaining four characters concern unusual tooth forms characteristic of specific pterosaurian taxa. None of these occur in *Mythunga* gen.nov., and thus reference to *Peteinosaurus* or *Eudimorphodon rosenfeldi*, dsungaripterids, ctenochasmatids, *Pterodactylus antiquus, P. kochi* or *Germanodactylus* is ruled out.

Kellner's analysis suggests that *Mythunga* gen.nov. represents a rhamphorhynchid, plesiomorphic archaeopterodactyloid, or advanced pteranodontoid other than an anhanguerid. Confluent naris and preorbital fenestra is a character of pterodactyloids (KELLNER, 2003), so we may eliminate rhamphorhynchids. Kellner mentions only two taxa of pteranodontoids other than *Pteranodon* and anhanguerids, *Istiodactylus* and *Ornithocheirus*. The cranial material of *Istiodactylus latidens* is incomplete, but indicates a low, broad snout, somewhat dorso-ventrally compressed, with closely-spaced teeth (HOWSE *et al.*, 2001). UNWIN (2001) has recently restudied *Ornithocheirus*, synonymising it with *Criorhynchus*, and attributing the much of material previously considered *Ornithocheirus* to *Lonchodectes* and *Anhanguera*. Like that of *I. latidens*, the skull of *Lonchodectes compressirostris* is fragmentary. However, the snout is clearly low, with more closely-spaced teeth than in *Mythunga camara* sp.nov. (OWEN, 1884). Thus *Mythunga* gen.nov. shows no significant similarities to either *Istiodactylus* or *Lonchodectes*. *Ornithocheirus simus*, the type species, is known from fragments of rostral and mandibular symphyses (UNWIN, 2001). In the specimen figured (CAMSM B54.428) by UNWIN (2001), the third and fourth upper alveoli are larger than the second, unlike the condition in *Mythunga* gen.nov.. *Ornithocheirus mesembrinus* had a longer rostrum anterior to the nasopreorbital aperture relative to its depth at the anterior termination of that aperture than appears to have been the case in *M. camara* sp.nov. with ten teeth anterior to the nasopreorbital aperture, and the third upper tooth appears to have been the largest (WELLNHOFER, 1987, Fig.2). Thus, taking into account the fragmentary nature of the material of *M. camara* sp.nov. (and of *O. simus*), we see no significant similarity between *Mythunga* gen.nov. and *Ornithocheirus*. Therefore, we provisionally regard *M. camara* sp.nov. as an archaeopterodactyloid. If the elongate depression of the maxilla does represent the contact surface for the jugal, then the anterior jugal tongue was substantially longer than in any other known pterosaur, and would constitute a third autapomorphy of *M. camara*.

Until recently, archaeopterodactyloids were not known from the Early Cretaceous, but they have now been found from Lower Cretaceous deposits in Liaoning, China (Wang & Lü, 2001).

Unwin's (2003) analysis uses 29 characters of the cranial skeleton, of which only six (17, 19, 24, 43, 55, and 57) are determinable or plausibly inferable. Of these, a bony mandibular symphysis is clearly present (character 17), teeth are present (43), dsungaripterid teeth (as defined by Unwin, 2003) are absent, and the largest teeth are rostral (57). The naris and antorbital opening seem to be confluent (24), and if we have properly interpreted the front of the snout, the first two mandibular teeth are larger than the more posterior teeth (character 19). However, the crown of the second is incomplete, and these teeth do not seem as large relative to the more posterior crowns as in, for example, *Eudimorphodon ranzii*. Thus, we provisionally regard *Mythunga camara* sp.nov. as lacking two large fanglike anterior dentary teeth. If we are wrong, the presence of such teeth is a plesiomorphic state and so does not affect the phylogenetic assessment. These comparisons indicate that the snout derives from a breviquartossan, and plausibly a pterodactyloid, pterosaur, thus agreeing with the results from Kellner's analysis in so far as such agreement is possible given the different bases of the two analyses.

Internal Structure

The internal structure of the snout is exposed anteriorly. The snout is hollow with two longitudinal series of roughly rectangular chambers, 3-5mm long and 4mm wide, separated from one another by struts (Fig.5). Where clearly exposed, the chambers seem floored by a continuous, very thin sheet of bone. The floor of the anteriormost chamber (partially) exposed, however, is penetrated by roughly circular apertures, as are the roofs of the posteriormost chambers visible. Thus the structure of this part of the snout is like a series of adjacent cubic boxes. The lateral surface of the snout at this level is about 0.8mm thick but ventrally, near the alveoli, it is 1.1mm thick, presumably to withstand stresses imposed in biting.

The jaws are also hollow. The medial wall of the left at its posterior break is 2.2mm thick, and the lateral wall is 1.4mm thick near the alveolar margin, and 0.9mm further ventrad. Thus the jaws seem to be essentially hollow tubes, reinforced by very thin internal partitions and struts.

The internal structure of the snout is similar to that illustrated by Dalla Vecchia (1993) for ?*Cearadactylus ligabuei*, but is more regular in form. In ?*C. ligabuei* the chambers were seen only as a single 'layer' between the internal and external sheets of compacta. On the other hand, the structure of *M. camara* sp.nov. seems unlike that of *Tupuxuara leonardii*, figured by Kellner & Campos (1994). There is no indication of a transverse bony sheet as shown in their figure 7, instead the sheet is horizontal. Admittedly in *Mythunga camara* sp.nov. only the dorsal portion of the snout is available for examination, and in *T. leonardii* the dorsal part of the transverse sheet is quite open with large perforations, however the obvious transverse structures in the snout of *Mythunga camara* sp.nov.are rods or struts. Thus there are at least two different kinds of internal structure in pterosaur snouts, one shown by *Mythunga camara* sp.nov. and ?*C. ligabuei*, and the other by *T. leonardii*. The suspicion of Kellner & Campos, that the bones of pterosaur skulls were subdivided into hollow internal chambers, is very likely correct.

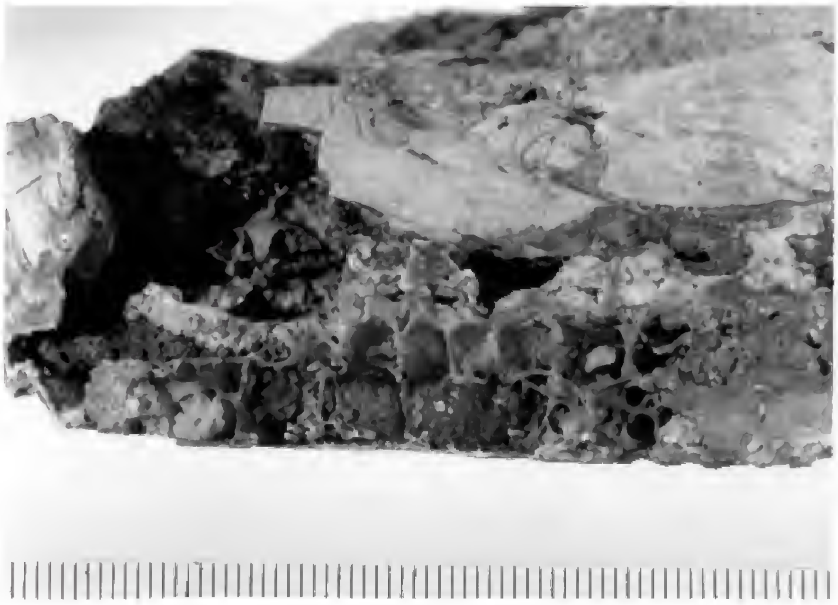

Fig.5- *Mythunga camara* sp.nov. (QM F18896), internal structure of the snout, dorsal view. Anterior is to the right.

PADIAN *et al.* (1992) characterise pterosaurs as 'optical illusions' in that the size of their skeletal elements does not reflect the mass or weight of these elements, an 'illusion' shared with the skulls of toucans. Although the skull is mentioned in this context, their analyses (e.g., VAN DER MEULEN *et al.*, 1992) are restricted to appendicular bones. This specimen, and those of DALLA VECCHIA (1993) and KELLNER & CAMPOS (1994), indicate that the pterosaur skull and mandible were basically composed of hollow boxes and tubes, and suggests that the characterisation of the cranial skeleton as an 'optical illusion' in this sense is quite apt.

WINGSPAN

Besides its intrinsic interest, size has significant palaeoecological implications. In view of the similarities in size and general form, we have chosen to compare the skull of *Mythunga camara* sp.nov. with that of *Anhanguera santanae* (AMNH 22555) in order to estimate the wingspan of *M. camara* sp.nov. WELLNHOFER (1991c) estimated the wingspan of *A. santanae* (AMNH 22555) as 4.15m. The only cranial measurement that can be confidently compared is that of the depth of the skull (not including the crest, if present) at the anterior end of the nasopreorbital fenestra, and even this is not entirely reliable because of the incompleteness of the dorsal margin of the snout of *M. camara* sp.nov. However, the general proportions of the *M. camara* sp.nov. snout suggest that not much of the dorsal region is missing, and any error resulting from this would serve to underestimate the wingspan, and so err on the side of conservatism. From WELLNHOFER (1991c) we find that the depth of the snout of *A. santanae* at this point is about 5cm: that of the *M. camara* sp.nov. snout is 5.7cm. Thus we estimate a wingspan of approximately 4.7m. This is twice as large as the pterosaur reported by MOLNAR & THULBORN (1980), but about the size of the Western Australian specimen (BENNETT & LONG, 1991) and that represented by the pubis (QM F27104) from near Boulia.

If our interpretation of unfused bony contacts in the skull is correct, it implies that the adults of this form were somewhat larger than here estimated.

DISCUSSION

Mythunga camara sp.nov. is plesiomorphic for a Cretaceous pterosaur, e.g., it is not edentulous nor does it have a deep or curved snout. The well-developed, interlocking teeth – together with its occurrence in a marine unit –, suggest that it preyed on fish (cf. WELLNHOFER, 1991a), and the relatively wide spacing of the teeth suggests that relatively large fish were taken.

In view of the recent publications of phylogenetic analyses of the Pterosauria (KELLNER, 2003; UNWIN, 2003), it is appropriate to re-assess the taxonomic affinities of the previously described postcranial material. Initially the pterosaur material from Queensland was attributed, tentatively, to the Ornithocheiridae as aff. *Ornithocheirus* sp. (MOLNAR & THULBORN, 1980). MOLNAR (1987) pointed out the similarities of the pterosaur pelvis from the Toolebuc to that of *Pteranodon*. WELLNHOFER (1991a) followed these comments and attributed the jaw fragment to ?*Ornithocheirus* and the scapulocoracoid and pelvis to an indeterminate pteranodontid. Thus it was suggested in the literature that two families were represented. The recently discovered pubis (QM F27104) (Fig.6), although twice as large as that of the described partial pelvis (QM F12982), closely resembles it and so probably derives from the same taxon. The metacarpal (NMV P197962) has not yet been studied.

Fig.6- Pterosaur. Elizabeth Springs, Queensland, Australia; Toolebuc Fm., Early Cretaceous; QM F27104, pubis in right lateral view. Scale bar = 2mm. Scale in mm.

The Toolebuc scapulocoracoid (QM F10613) derives from a mature individual (BENNETT, 1993), and matches both those of *Anhanguera* (WELLNHOFER, 1991b, 1991c) and *Pteranodon* (EATON, 1910) in possessing a posterior process and a 'bridge' between the scapula and coracoid internal to the glenoid region. It further resembles that of *Anhanguera santanae* in the general form of the glenoid, and the V-shaped fossa on the dorso-lateral surface of the scapula between the posterior process and the anterior moiety of the scapula. *Pteranodon* seems to lack these features (BENNETT, 2001). KELLNER (2003) used three characters of the shoulder girdle that can be assessed for QM F10613. The proximal (glenoid) articular face of the scapula is suboval in form, rather than elongate as in more plesiomorphic taxa. This is a character state of the pteranodontoids. The scapular shaft is relatively stout and slightly constricted. This indicates membership among the advanced pteranodontoids (including anhanguerids). The scapula is substantially shorter than the coracoid, with a ratio of scapular to coracoid length of about 0.8. This is an autapomorphy of *Anhanguera* (KELLNER, 2003). UNWIN's (2003) analysis used only two characters applicable to QM F10613, that the coracoid length is greater than 75% of the scapular length (which only indicates that it pertains to a pterosaur) and that the length of the coracoid is greater than that of the scapula. This indicates that QM F10613 derived from an ornithocheiroid pterosaur. This is consistent with the results from Kellner's analysis, as *Anhanguera* is included in the ornithocheiroids. It thus seems reasonable to suggest that this scapulocoracoid derives from an anhanguerid that may be designated aff. *Anhanguera* sp.

The pubis is separated from the ischium by a deep cleft in *Anhanguera santanae* (WELLNHOFER, 1991b) and an apparently much less prominent one in the Toolebuc pelvis (MOLNAR, 1987), whereas in *Pteranodon* they are fused along their entire contact (EATON, 1910). BENNETT (1993; 1995) argued that this cleft disappears with maturity. That of the Toolebuc pelvis would fall between those of parts 2 and 3 of figure 6 of BENNETT (1995), indicating that the pelvis derived from a nearly mature individual. Because neither KELLNER (2003) nor UNWIN (2003) found pelvic characters useful in analysis, we cannot be certain if apomorphic or plesiomorphic features are involved here (although because the ancestors of pterosaurs almost certainly did not show such fusion of the pubis and ischium, it is probably plesiomorphic). The mandible from near Boulia, however, closely resembles those previously attributed to *Ornithocheirus*, now to *Lonchodectes* (UNWIN, 2001) and so may now be designated aff. *Lonchodectes* sp. UNWIN (2001; 2003) considered *Lonchodectes* not closely related to *Ornithocheirus*, but more closely related to *Pterodactylus*, a member of KELLNER's (2003) Archaeopterodactyloidea, but distinct at the familial level.

Thus, we conclude that as many as three taxa may be represented: an anhanguerid, represented by the scapulocoracoid, *Lonchodectes* or a closely related form, represented by the Boulia mandible, and *Mythunga camara* sp.nov.

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DISCOVERY OF A NEW ORNITHOPOD DINOSAUR FROM THE PORTEZUELO FORMATION (UPPER CRETACEOUS), NEUQUÉN, PATAGONIA, ARGENTINA [1]

(With 14 figures)

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ABSTRACT: We describe the postcranial skeleton of a new Cretaceous ornithopod, *Macrogryphosaurus gondwanicus* gen.nov., sp.nov. from Patagonia, Argentina. The specimen was found in the Portezuelo Formation, Neuquén Group, Upper Cretaceous. *Macrogryphosaurus gondwanicus* gen.nov., sp.nov. is diagnosed by having triradiate sternum with the anterior border tribranched, two laterally placed and outwardly directed, and one centrally placed, smaller, and forwardly directed. Sternal ribs flattened, twisted and distally expanded. Last dorsal vertebra with well-developed hyposphene. A thin plate-like are located in front of the sterna. Together with these autapomorphies, this new species of ornithopod differs from *Talenkauen santacrucensis* by having the pubic peduncle of ilium less developed, a more acute angle between the anterior process of ilium and the pubic peduncle, the acetabular cavity slightly marked. Also present ten cervical vertebrae, fourteen dorsal vertebrae, epipophyses on the third cervical vertebra placed over the distal end of the postzygapophyses and posteriorly projected. The presence of plates on the lateral side of the thorax and well developed epipophyses on the third cervical vertebra, were originally interpreted as autapomorphies for the euiguanodontian *Talenkauen santacrucensis*. These features are also present in *Macrogryphosaurus gondwanicus* gen.nov, sp.nov., and are regarded as synapomorphies defining a new clade of Euiguanodontia dinosaurs comprising the two species: Elasmaria nov.

Key words: *Talenkauen*. Ornithopoda. Elasmaria nov. Portezuelo Formation. *Macrogryphosaurus gondwanicus* gen.nov., sp.nov.

RESUMEN: Hallazgo de un nuevo dinosaurio ornitópodo de la Formación Portezuelo (Cretácico superior) Neuquén, Patagonia, Argentina.

Describimos el esqueleto postcranial de un nuevo ornitópodo Cretácico, *Macrogryphosaurus gondwanicus* gen.nov., sp.nov. de Patagonia, Argentina. El especimen fue hallado en la Formación Portezuelo, Grupo Neuquén, Cretácico tardío. *Macrogryphosaurus gondwanicus* gen.nov., sp.nov. es diagnosticado por tener un esternón trirradiado con el borde anterior triramificado, dos ramas ubicadas lateralmente y dirigidas hacia afuera, y una ubicada centralmente, pequeña y desplazada hacia adelante. Costillas esternales aplanadas, giradas y distalmente expandidas. Última vértebra dorsal con hipósfeno bien desarrollado. Delgadas placas ubicadas frente al esternón. Junto con estas autapomorfias, esta nueva especie de ornitópodo difiere de *Talenkauen santacrucensis* por tener el pedúnculo púbico del ilion menos desarrollado, un ángulo más agudo entre el proceso anterior del ilion y el pedúnculo púbico, cavidad acetabular levemente marcada. Además, presenta diez vértebras cervicales, catorce vértebras dorsales, epipófisis sobre la tercera vértebra cervical ubicadas sobre el extremo distal de las postzigapófisis y proyectadas posteriormente. La presencia de placas sobre los laterales del tórax y epipófisis bien desarrolladas sobre la tercera cervical fueron originalmente interpretadas como autapomorfías del euiguanodonte *Talenkauen santacrucensis*. Estos caracteres también están presentes en *Macrogryphosaurus gondwanicus* gen.nov., sp.nov. y son considerados sinapomorfías de un nuevo clado de dinosaurios Euiguanodontia: Elasmaria nov., que comprende estas dos especies.

Palabras clave: Talenkauen. Ornithopoda. Elasmaria nov. Formación Portezuelo. *Macrogryphosaurus gondwanicus* gen.nov., sp.nov.

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INTRODUCTION

Among Cretaceous dinosaurs discovered in Argentina, the ornithischians are currently represented by several taxa. Among them are basal ornithopods from Río Negro: *Gasparinisaura cincosaltensis* (CORIA & SALGADO, 1996; SALGADO *et al.*, 1997); Neuquén: *Anabisetia saldiviai* (CORIA & CALVO, 2002) and indeterminate ornithopod materials (PORFIRI & CALVO, 2002); Chubut: *Notohypsilophodon comodorensis* (MARTÍNEZ, 1998); and Santa Cruz: *Talenkauen santacrucensis* (NOVAS *et al.*, 2004). Moreover, other ornithischians recorded in this country are the probable ceratopsian *Notoceratops bonarelli* (TAPIA, 1918), the Hadrosauridae *Kritosaurus australis* (BONAPARTE *et al.*, 1984), probable lambeosaurines (POWELL, 1987), and an unnamed nodosaurid ankylosaur (CORIA & SALGADO, 1996).

During a field trip of the Universidad Nacional del Comahue to Mari Menuco lake in May of 1999, an almost complete and articulated skeleton of an ornithopod was unearthed. The specimen has unusual plates on the thorax. Ornithopods with such feature are uncommon. These plates were recorded in *Thescelosaurus* (GILMORE, 1915) and *Talenkauen* (NOVAS *et al.*, 2004). Here we describe this new ornithopod dinosaur, which is the biggest non-hadrosaurian ornithopod from South America known up to now. It shares derived characters with the basal euiguanodontian *Talenkauen santacrucensis* (NOVAS *et al.*, 2004), including the presence of epipophyses on the third cervical, and thin ossified plates on the thorax, suggesting that these two species are closely related, forming a new clade: Elasmaria nov.

Abbreviations: (MUCPv) Museo Universidad Nacional del Comahue, Neuquén, Argentina. (MPM) Museo Padre Molina, Río Gallegos, Santa Cruz, Argentina.

RESULTS

SYSTEMATIC PALEONTOLOGY

Ornithischia SEELEY, 1888
Ornithopoda MARSH, 1881
Euornithopoda SERENO, 1986
Iguanodontia SERENO,1986
Euiguanodontia CORIA & SALGADO, 1996

Elasmaria nov.

Etimology – Elasmaria (Greek), thin plate.

Phylogenetic definition – Elasmaria is phylogenetically defined as *Talenkauen santacrucensis*, *Macrogryphosaurus gondwanicus* gen.nov., sp.nov., their most recent common ancestor plus all the descendants.

Diagnosis – Two unambiguous synapomorphies support the monophyly of Elasmaria: large basal euiguanodontian with well-developed epipophyses on the third cervical and presence of thin ossified plates on thorax.

Macrogryphosaurus gondwanicus gen.nov., sp.nov.

Holotype – MUCPv-321. The specimen was found articulated with the cervical and dorsal series in straight position with the ventral zone upward. Only post-cranial materials are preserved, 8 post-axial cervicals, 14 dorsals, 6 sacrals and 16 caudals, cervical and dorsal ribs, both ilia, pubes, and ischia, one sternum, and 4 thoracic plate.

Etymology – *Macrogryphosaurus,* from Greek m*acro*, big; *grypho*, enigmatic; *saurus*; lizard; and *gondwanicus* in reference to the Gondwana continent.

Locality and horizon – The fossil was found 60 km NW from Neuquén city, on the west coast of the Mari Menuco lake, Neuquén, Argentina. It comes from the Portezuelo Formation (Coniacian), Neuquén Group.

Diagnosis – Triradiate sternum with the anterior border tribranched, two laterally placed and outward directed and one centrally placed smaller and forwardly directed. Sternal ribs flattened, twisted and distally expanded. Last dorsal with well-developed hyposphene. A thin plate-like is located in front of the sterna. Together with these autapomorphies this Elasmarian euiguanodontian differs from *Talenkauen santacrucensis* by having the pubic peduncle of ilium less developed, a more acute angle between the anterior process of ilium and the pubic peduncle, the acetabular cavity slightly marked. Ten cervical vertebrae, fourteen dorsal vertebrae, epipophyses on the 3rd cervical placed over the distal end of the postzygapophyses and posteriorly projected.

DESCRIPTION

We estimate that the holotype specimen of *Macrogryphosaurus gondwanicus* gen.nov., sp.nov. measured no more than 6m long, representing one of the largest known non-hadrosaurian ornithopods yet recorded in South

America. However, the presence of unfused sutures between neural arches and centra in posterior dorsals and proximal caudals suggests that this is probably not a full-grown individual (e.g., GALTON, 1981; SERENO & NOVAS, 1993; BROCHU, 1996). Although the specimen does not preserve cranial and dental elements, which are highly relevant for phylogenetic analysis, the available postcranial bones allow comparisons with other euiguanodontians (e.g., *Gasparinisaura*, *Anabisetia*, *Talenkauen)*.

VERTEBRAL COLUMN

The number of presacral and sacral vertebrae in *Macrogryphosaurus* gen.nov. is 10+14+6. Most basal Ornithopoda (e.g., *Heterodontosaurus, Hypsilophodon, Camptosaurus, Talenkauen*) have 9 cervicals, and the number of sacrals is regular in most of them (except for *Camptosaurus*, with 4-5 sacrals). By contrast, the number of dorsals is more variable among these dinosaurs: 12 in *Heterodontosaurus*, 15 in *Hypsilophodon,* 16 in *Talenkauen* and *Camptosaurus*, and 17 in *Iguanodon*.

Thus, *Macrogryphosaurus* is one of the few Ornithopoda with low number of dorsal vertebrae.

Cervical vertebrae: Eight (8) articulated cervicals were found, the lasts 7 are well preserved. We do not have data on atlas and axis. All cervicals (Figs.1-3) have amphicoelous centra; they are wider than high. In lateral view, they have a rectangular shape and in spite of being a little crushed by compression, they are as elongated as in *Talenkauen*. A ventral keel is present from cervical 4th to 8th. Parapophyses are anteriorly placed, and diapophyses are short, rounded, and ventrally projected. In *Talenkauen*, both pre- and postzygapophyses are elongate, extending beyond centrum level. Cervical 3 bears well-developed epipophyses above the postzygapophyses (Fig.1A). This feature, as well as the elongate condition of most cervical centra, are unusual among ornithischian dinosaurs, and are uniquely shared with *Talenkauen* (NOVAS *et al.*, 2004) (Fig.2). *Lesothosaurus* has epipophyses on the third cervical but they are less developed than in *Macrogryphosaurus* and *Talenkauen*. Moreover, this feature in *Macrogryphosaurus* differs from that of *Talenkauen* because, in the former, the epipophyses are posteriorly projected and placed on the distal end of the postzygapophyses.

In the 4th cervical of *Macrogryphosaurus* gen.nov. (Fig.1B), epipophyses are placed on the proximal end of the postzygapophyses, and they are more reduced and different from those of *Talenkauen*. Neural spines in anterior cervicals are short and placed at mid-length of the centra. The neural canal has a circular shape. From cervicals 5 to 10, the anterior face of the centrum is heart-shaped. The diapophyses are directed caudolaterally and ventrally. Anterior neural spines are higher than posterior ones; they are rounded at the distal end and posteriorly directed. Postzygapophyses are elongated, with the articular surfaces slightly concave. In posteriors cervicals, the neural canal has a quadrangular shape and the diapophyses are caudolaterally projected.

Dorsal vertebrae: The dorsal series was found complete, with 14 vertebrae, and articulated. At both sides of vertebrae 13 and 14, ossified tendons have been preserved. All dorsals are slightly

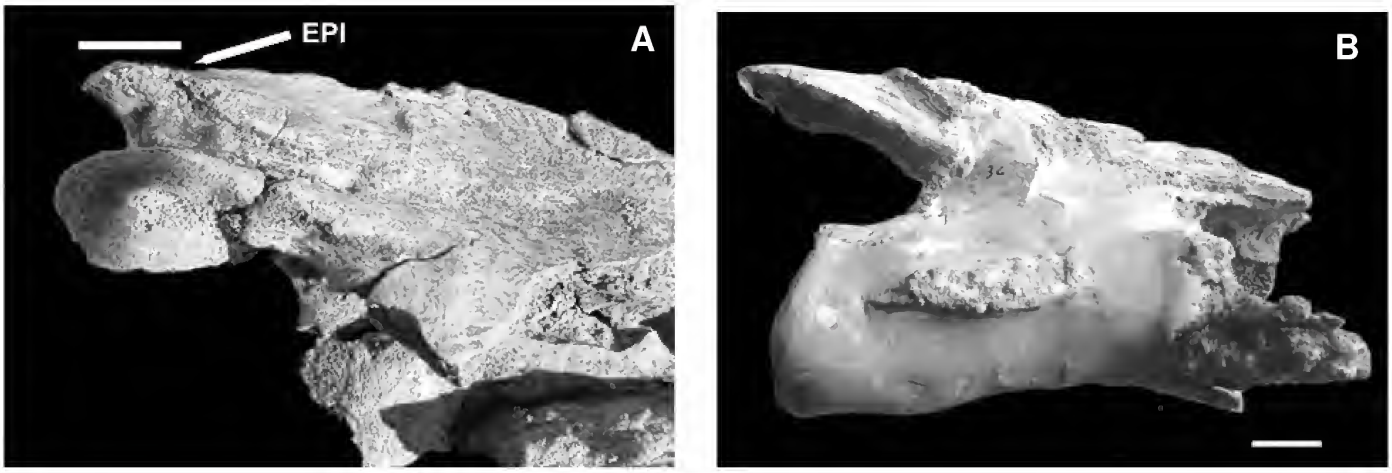


Fig.1- *Macrogryphosaurus gondwanicus* sp.nov. (A-B) third and fourth cervicals in lateral view. Scale bar = 1cm.

amphycoelous. Dorsal 1 is recognized by having the parapophyses on the neurocentral suture. Anterior dorsals have centra transversely compressed, with the ventral surface strongly concave laterally. The parapophyses are small, with oval articular surfaces. Diapophyses are caudally directed. The subcircular and slightly convex articular facets of prezygapophyses are inclined medially 45 degree with respect to the sagittal plane. Neural spines are transversely thin. In dorsal 1, the distal end of the neural spine is rounded, but from dorsal 2 and backwards, it is rectangular-shaped. Centra of posterior dorsals have anterior surfaces slightly smaller than the posterior ones. Ventrally, a keel is present, at least, in dorsals 13 and 14. Its presence on vertebrae 5 to12 is uncertain, because this area is covered by sediments. A pair of foramina is present on both sides of the ventral keel in dorsal 13, but in dorsal 14 both foramina are placed only on the rigth side. Other small foramina are also present on the upper half of the lateral side of the centra. Diapophyses of the posterior dorsals are anterodorsally projected, and parapophyses are small and fused to the proximal part of the diapophyses. The neural canal is small and subcircular. The last dorsal (14th) has a well-developed hyposphene (Fig.4A), a character not documented before in other ornithischian dinosaurs. It is absent in dorsal 13; and in the first sacral, there is no hypantrum.

Caudal vertebrae: 16 caudal vertebrae were found, most of them incomplete, preserving only centra and neural arches, with partial neural spines. All caudal centra are amphyplatian and subcircular in anterior view. Caudal 1 to 3 have a strong hypapophyses. On the lateroventral side of the centra, several foramina are present in these caudals. Two small spinoprezygapophyseal laminae are present. There is a prespinal lamina that reaches the base of the neural arch in caudals 2 and 3. Three anterior neural spines, and two transverse processes without the centra were also recovered. Neural spines are transversely thin and high, and transverse processes are directed backwards. Mid caudals have centra higher than wide. A deep ventral sulcus is present, which becomes less marked in distal caudals. Mid-caudal chevrons are narrowed in lateral view, and slightly curved distally. Contrary to what is observed in mid-caudals, the posterior haemal arches are triangular in lateral view, and have expanded distal ends (Fig.5). Six articulated distal caudals, partially complete, are articulated with their corresponding haemal arches. Neural spines are small, rounded and transversely thin proximally.

PECTORAL GIRDLE

Sternum: The sternum is triradiate; on the anterior border, three branches are present, two laterally placed, and outwardly directed, and one centrally placed, smaller, and forwardly directed (Fig.6). The anterior border is three times wider than the posterior one. Lateral borders are concave.

Sternal ribs: Three sternal ribs were found articulated with the sternum; although four were present originally. They are flattened, twisted and distally expanded.

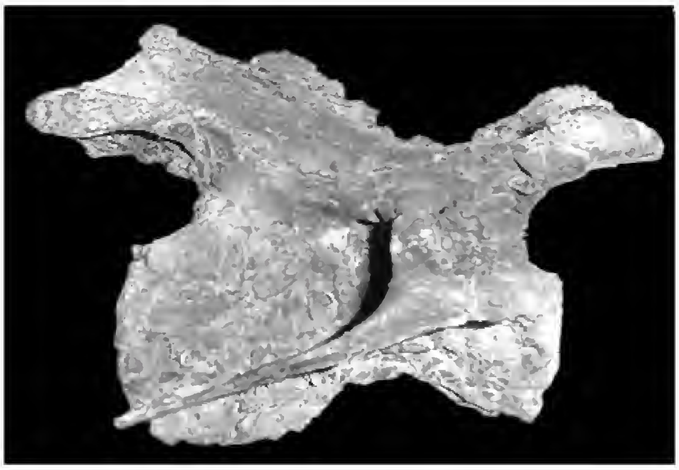


Fig.2- *Talenkauen santacrucensis*. Third cervical in lateral view.

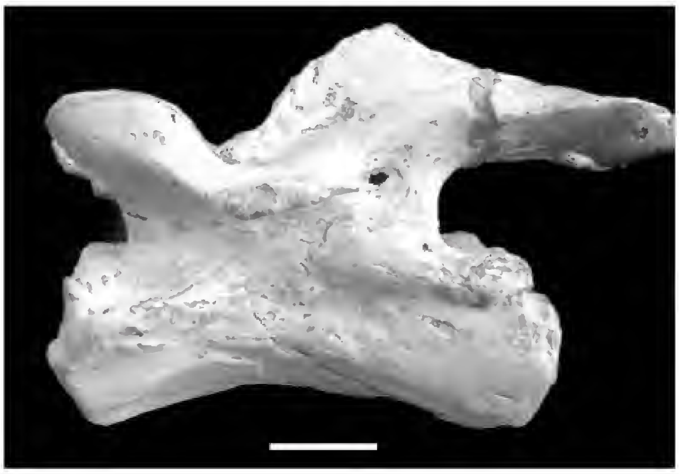


Fig.3- *Macrogryphosaurus gondwanicus* sp.nov. Cervical vertebrae (8th) in lateral view. Scale bar = 1cm.

Fig.4- *Macrogryphosaurus gondwanicus* sp.nov. Dorsal vertebrae (14th) in (A) posterior, and (B) lateral views. Scale bar = 1cm.

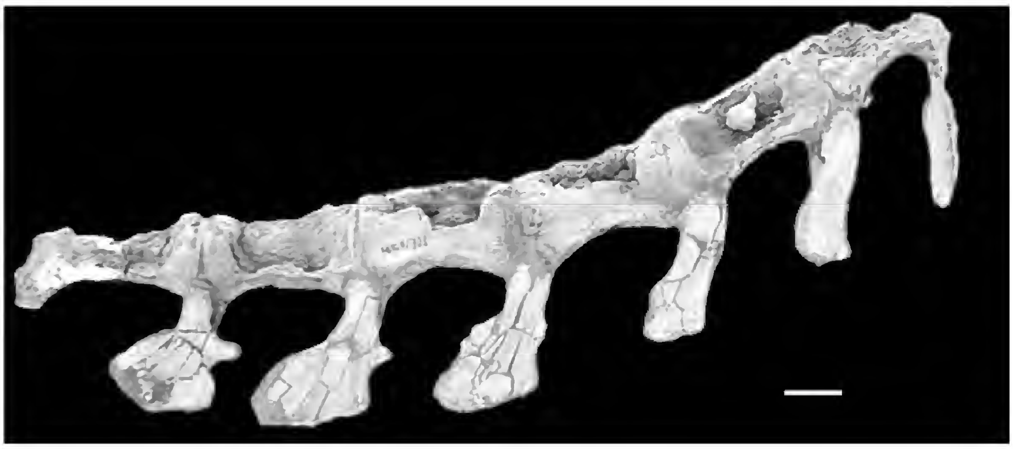
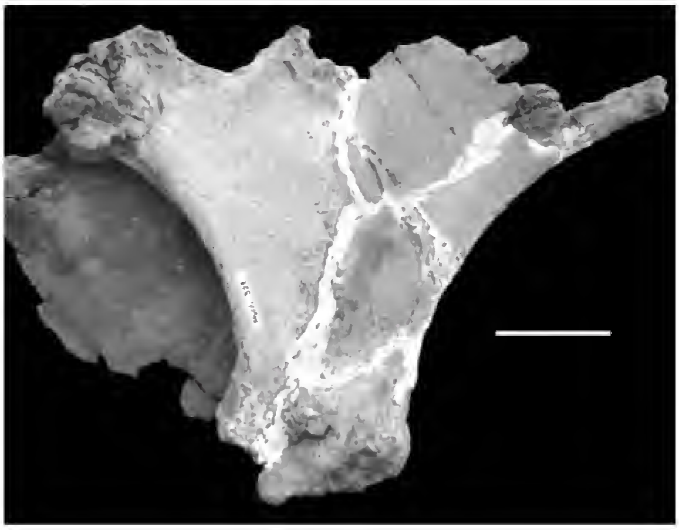


Fig.5- *Macrogryphosaurus gondwanicus* sp.nov. Posterior caudals, in lateral view. Scale bar = 2cm.

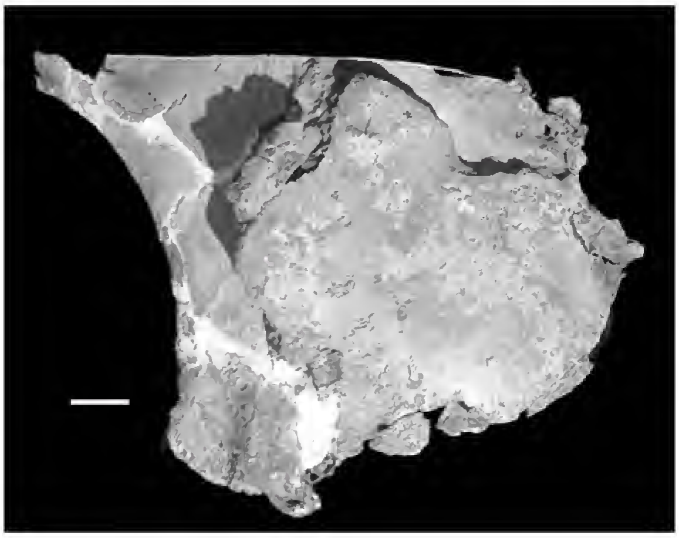
Plates: *Macrogryphosaurus* has ossified plates placed along the dorsal region of the thorax, from ribs 6 to 8 (Figs.7-8). These ossifications are subcircular and thin (1 to 3mm thick) and one of them is placed inside the thorax, with its surface opposed to the internal surfaces of the ribs. Another two ossified plates (with the same morphological characteristics cited above for the internal plates) were recovered above the sternum. Similar ossifications are also documented internally in the articulated skeletons of the Patagonian *Talenkauen* (Fig.10) and the North American *Thescelosaurus*.

Notwithstanding the fact that one plate was placed internally to the thoracic ribs, there is no evidence that it was its real position in life, because it could have been transported after the decaying process.



⮜Fig.6
Macrogryphosaurus gondwanicus sp.nov. Sternum in medial view. Scale bar = 5cm.

Fig.7⮞
Macrogryphosaurus gondwanicus sp.nov. Thoracic plate in lateral view. Scale bar = 1cm.



⮜Fig.8
Macrogryphosaurus gondwanicus sp.nov. Sternum backward of behind the thoracic plate in anterior view. Scale bar = 2cm.

Pelvic Girdle and Hindlimbs

Ilium: Both ilia articulated with the sacrum were recovered (Figs.9A-9B). They are incomplete, lacking the extremities of both pre- and postacetabular processes. The left ilium lacks also the pubic peduncle. The preserved part of the preacetabular process is long and lateroventrally curved. Proximally, it is triangular incross-section, being strongly excavated on its medial side, and slightly concave on its dorsal and ventral sides. The medial surface of this process has a wide but thin horizontal ridge that serves for the attachment of the transverse processes of sacral vertebrae. The three anterior sacrals have keels and foramens as in the dorsals and anterior caudals. The dorsal edge of the ilium is slightly concave above de acetabulum and has a rugose surface. *Macrogryphosaurus* has a "S-shaped" dorsal margin of the iliac blade that is different from those present in Marginocephalia and Hypsilophodontidae, which are convex. Caudally to the acetabulum, the preserved portion of the postacetabular blade is laterally offset. This blade is not expanded dorsoventrally as that present in *Tenontosaurus* (Ostrom, 1970). The postacetabular blade is "L–shaped" in cross section, with a ventral shelf, medially projected forming an angle of more that 100 degree with respect to the axial plane) that connects with the transverse processes of the last sacral vertebra. By contrast, the brevis shelf in dryosaurids is extremely wide (Galton, 1981)

The pubic peduncle of ilium is more slender than in *Talenkauen* (Fig.9B) and the angle that it forms with the preacetabular process is less sharp (Fig.11).

Ischial and pubic peduncles are poorly developed, forming a small acetabulum. It is different from that of *Talenkauen*. The morphology of the acetabulum cavity has more resemblance with that observed in *Hypsilophodon* and *Gasparinisaura*.

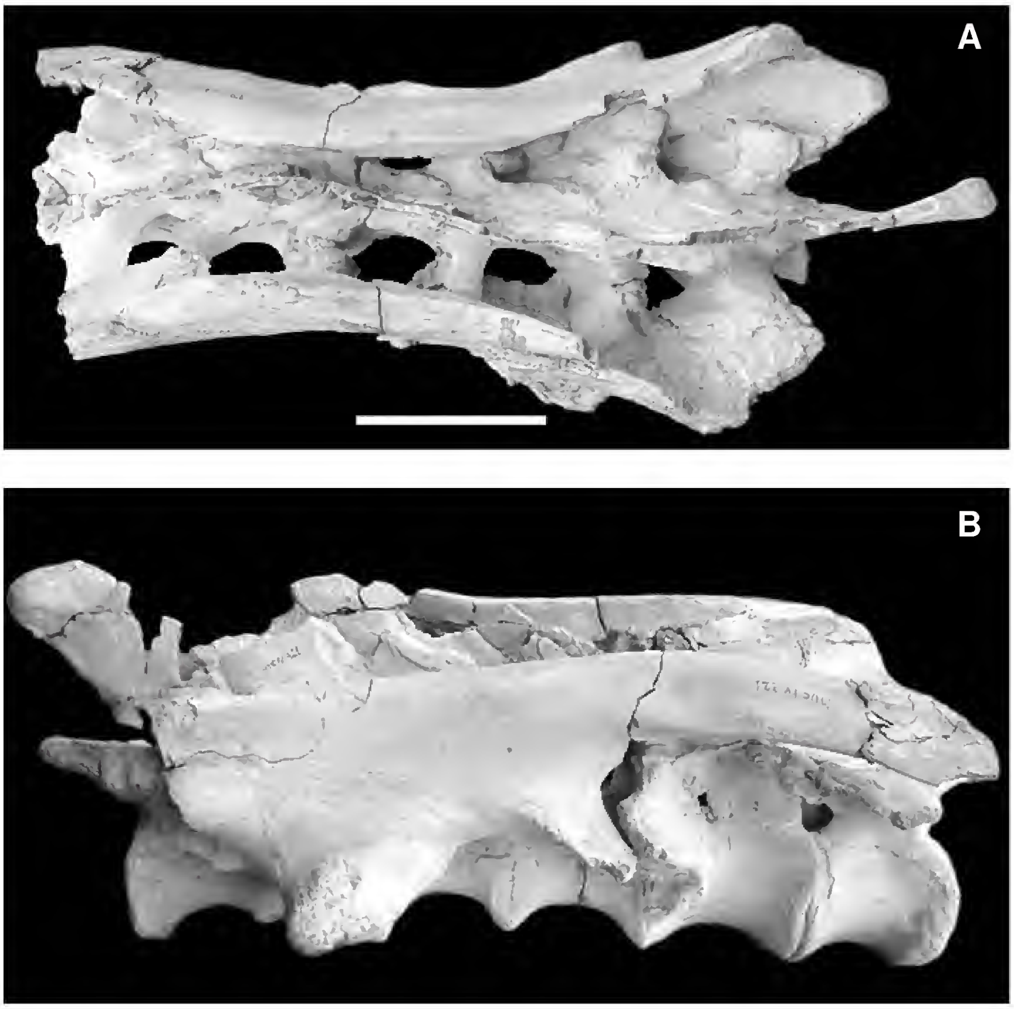


Fig.9- *Macrogryphosaurus gondwanicus* sp.nov. Sacrum, in (A) dorsal view, and (B) lateral view. Scale bar = 10cm.

The ischial peduncle has a rugose surface. It is laterally and ventrally flattened.

Ischium: Unconnected proximal, middle and distal portions of both ischia are available (Fig.12). The proximal end of ischium has two processes, one for ilium, and the other for the pubis. They are separated by a smooth acetabular embayment. The pubic process is subquadrangular in lateral view, and it ends in a flat, rectangular, rugose articular surface. The iliac process, instead, has an oval flat articular facet. The obturator process is not preserved. The ischial shaft was long, thin and curved. Taken at mid-length, the ischial shaft is twisted and has a suboval cross-section. Its distal end is slightly expanded and scarred on the medial side, indicating that left and right ischia were in contact to each other distally. Ischia bearing a small distal foot, and having a suboval or cross-section of the shaft, are also present in *Anabisetia* and Dryomorpha.

Pubis: The left pubis is almost complete (Fig.12), but the right one preserves just the pubic shaft. This bone forms the anteroventral margin of the acetabulum which is stout, concave and rugose. The prepubic process is short and flat, in contrast with the elongate and rod-like postpubic process. The length of the prepubic process is equivalent to 80% of the length of the "postpubic" process.

The presence of a higher angle (aproximatelly 150°) between pubic shaft and the prepubis is a plesiomorphic character retained in *Heterodontosaurus*. In *Macrogryphosaurus* gen.nov. this angle is lower than to 100° like that in *Camptosaurus, Thescelosaurus, Hypsilophodon, Tenontosaurus*, and *Dryosaurus*; therefore, considered a synapomorphy

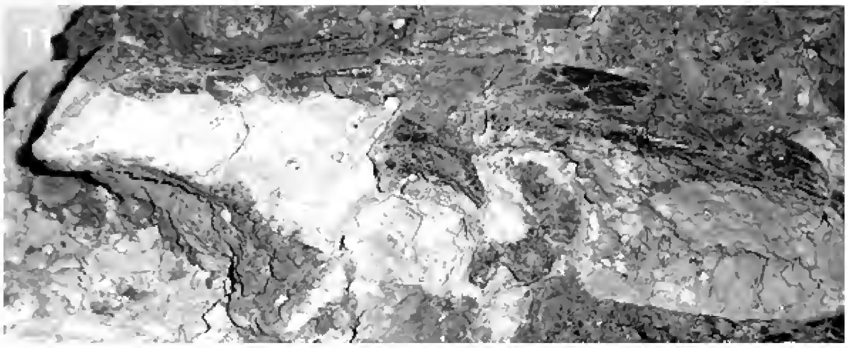


Fig.10- *Talenkauen santacrucensis*. Thoracic plate in lateral view; fig.11- *Talenkauen santacrucensis*. Ilium in lateral view; fig.12- *Macrogryphosaurus gondwanicus* sp.nov. Pubis and ischium: medial view: Scale bar = 10cm.

of Euornithopoda (WEISHAMPEL & HEINRICH, 1992). The prepubic process is lateromedially compressed and expanded dorso-ventrally, with its cranial end convex and slightly expanded. In *Macrogryphosaurus gondwanicus* gen.nov., sp.nov. the prepubis is lateromedially flat like that of *Heterodontosaurus*, *Dryosaurus*, and *Tenontosaurus*. By contrast, in *Gasparinisaura* and Hypsilophodontids, the prepubis has a rounded shape in cross section. The dorsal rim is concave in lateral view. Below the acetabulum, the postpubic process forms a narrow and curved rod. It curves backward and downward parallel to the ischium. The obturator foramen is closed, although there is a narrow notch placed dorsally. Below the obturator foramen the pubis is stout. A rugose area is developed for the attachment of the pubic head of ischium. The distal end of the pubis presents a small pubic foot resembling that of *Camptosaurus*.

DISCUSSION AND CONCLUSIONS

Cladistic analyses of ornithopods have been worked by many authors. (SERENO, 1986; WEISHAMPEL & HEINRICH, 1992; CORIA & SALGADO, 1996; NOVAS *et al.*, 2004; NORMAN *et al.*, 2004, etc). Initially *Gasparinisaura* was considered as an Euiguanodontia (CORIA & SALGADO, 1996; CORIA & CALVO, 2002; NOVAS *et al.*, 2004) but recently *Gasparinisaura* was included as a basal Ornithopoda without considering derived taxa (for instance Ankylopollexia) in the analysis (NORMAN *et al.*, 2004). In this paper we prefer to use a more complete analysis in order to assess the phylogenetic position of the Neuquén taxon. Therefore, we have used the comprehensive phylogenetic analysis of ornithopod relationships presented by NOVAS *et al.* (2004). We included the information available for *Macrogryphosaurus* gen.nov. (Fig.13) using the same data matrix from the 50 characters; we scored 14 for the new taxon (see Appendix 1). We added three new characters: (48) thin ossified plates in thoracic region; (49) third cervical with well-developed epipophyses, and (50) expanded distal end of chevron (*sensu*, CORIA & SALGADO, 1996).

This modified data set was run through PAUP 3.0 (DELTRAN). The resulting single tree is similar to that obtained by NOVAS *et al.* (2004), but two steps longer 88 steps (Fig.14). The resulting tree displayed essentially the same topology, and differed only by showing a monophyletic group formed by *Talenkauen santacrucensis* and *Macrogryphosaurus gondwanicus* gen.nov., sp.nov.; which is supported by two synapomorphies: (48) thin ossifed plates in thoracic region, and (49) third cervical with well-developed epipophyses. This new clade is named herein Elasmaria nov. The inclusion of *Macrogryphosaurus* gen.nov. in the data matrix (NOVAS *et al.*, 2004) improves the number of synapomorphies in Iguanodontia, adding character (22); in Euiguanodontia, adding characters (18, 26, 27), and in Dryomorpha adding characters (2, 4, 12, 19, 24, 25).

We recognize, for the first time, a Gondwanan clade of large sized basal euiguanodontians, Elasmaria nov., composed by *Talenkauen santacrucencis* and *Macrogryphosaurus gondwanicus* sp.nov..

Because the ossified plates of the thoracic region are very thin, devoid of external sculpturing; and also because they lie serially arranged on the sides of the thorax, staying connected with the caudal margin of the thoracic ribs, they were previously interpreted as uncinate processes (NOVAS *et al.*, 2004).

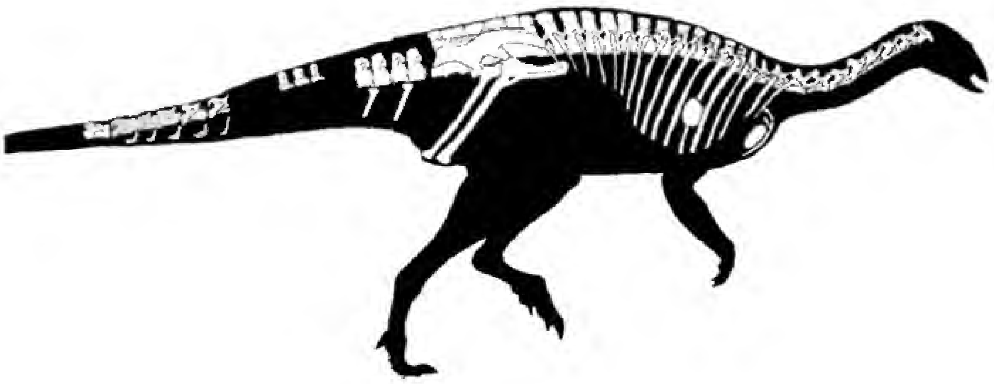


Fig.13- Reconstruction of *Macrogryphosaurus gondwanicus* sp.nov., including all preserved materials in white.

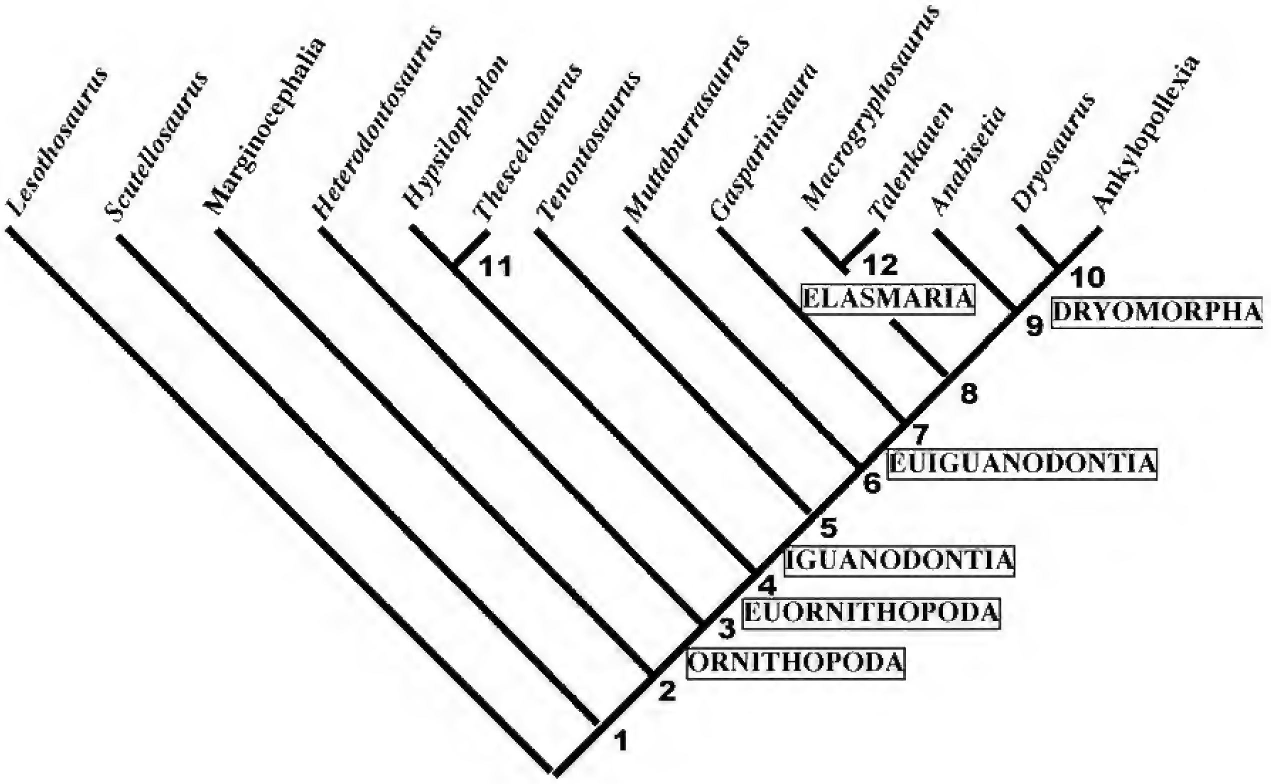


Fig.14- Cladogram depicting phylogenetic relationships of *Macrogryphosaurus gondwanicus* sp.nov. within ornithopoda, and the placement of Elasmaria. L = 88; CI = 0.625; RI = 0.742; RC = 0.463.

This made those authors hypothesize about their participation in the thoracic movements during respiration, as it occurs in living birds. These thin plates were found in *Macrogryphosaurus* gen.nov. below the thoracic ribs and between the thoracic ribs (Fig.7). Unique among Euiguanodontia, *Macrogryphosaurus gondwanicus* gen.nov., sp.nov. exhibits triradiate sternum with the anterior border tribranched, two laterally placed and outwardly directed and one smaller, centrally placed and forwardly directed. Sternal ribs flattened, twisted and distally expanded. Last dorsal with well-developed hyposphene. The thin plates plate-like located in front of the sterna. Together with these autapomorphies, this new species differs from *Talenkauen santacrucensis* by having the pubic peduncle of ilium less developed, more acute angle between the anterior process of ilium and the pubic peduncle, acetabular cavity slightly marked. Ten cervical vertebrae, 14 dorsal vertebrae, epipophyses on the 3rd cervical placed over the distal end of the postzygapophyses and posteriorly projected. Summing up, *Macrogryphosaurus gondwanicus* gen.nov., sp.nov. represents a new taxon of large sized ornithopod dinosaur from South America. It is the third example of an ornithischian dinosaur in which ossified plates on thorax are documented (Fig.10), the remaining two being the Euiguanodontia *Talenkauen santacrucensis,* from Santa Cruz and the hypsilophodontid *Thescelosaurus neglectus,* from the Maastrichtian of North America.

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APPENDIX

Character list and states were taken, with modification, from Novas *et al.* (2004). The data matrix was analyzed cladistically using the PAUP 3.0. One tree was obtained, which has the following values: L = 88; CI = 0.625; RI = 0.742; RC = 0.464.

List of Characters

1. Contact of lacrimal / premaxilla: (0) absent; (1) present.
2. Premaxillary teeth: (0) present; (1) absent.
3. Eversion of premaxilla: (0) absent; (1) present.
4. Anterior processes on maxilla: (0) 1 process; (1) 2 processes.
5. Tooth ridges connected to denticles: (0) absent; (1) present.
6. Strong central ridge on maxillary teeth: (0) absent; (1) present.
7. Denticles on predentary: (0) absent; (1) present.
8. Ventral processes on predentary: (0) single; (1) double; (2) wedge-shaped.
9. Size of antorbital fenestra or fossa: (0) large; (1) small.
10. Quadratojugal size: (0) large; (1) reduced.
11. Ossified sternal ribs: (0) absent; (1) present.
12. Ossified hypaxial tendons: (0) present; (1) absent.
13. Humerus/scapula length ratio: (0) less than 1; (1) equal or more than 1.
14. Number of phalanges on manus of digit III: (0) 4; (1) 3.
15. Number of vertebrae in sacrum: (0) 5; (1) more than 5.
16. Prepubic process: (0) absent; (1) short; (2) long rod; (3) long shallow blade; (4) deep anteriorly.
17. Femur: distal anterior intercondylar groove: (0) absent, (1) present
18. Metatarsal V/III length ratio: (0) more than 0.3; (1) less than 0.3; (2) Metatarsal-V absent.
19. Relative size of the palpebral bone: (0) 80% or more of the maximal anteroposterior width of the orbit; (1) 70% or less of the maximal anteroposterior width of the orbit.
20. Antorbital fossa shape: (0) triangular; (1) circular or ovate.
21. Dorsal and ventral margins of the dentary: (0) rostrally converged; (1) parallel.
22. Dorsal margin of iliac blade: (0) convex; (1) sinuous.
23. Size of the external nares relative to the basal skull length: (0) less than 15%; (1) 20% or more.
24. Enamel of the lingual side of maxillary teeth: (0) present; (1) absent.
25. Participation of the jugal in the antorbital fenestra: (0) included; (1) excluded.
26. Jugal-postorbital articulation: (0) medially-faced; (1) laterally-faced.
27. Brevis shelf: (0) reduced; (1) well developed.
28. Metatarsal I: (0) present; (1) reduced or absent.
29. Maxillary tooth crowns: (0) low; (1) high.
30. Foot on the distal ischial shaft: (0) absent; (1) present.
31. Ischial shaft: (0) laterally flattened; (1) suboval in cross section.
32. Caudal process of jugal: (0) well developed; (1) reduced.
33. Relative position of the ventral margin of the infratemporal fenestra: (0) below the base of the orbit; (1) above the base of the orbit.
34. Position of the obturator process on the ischial shaft: (0) proximally; (1) distally placed.
35. Deltopectoral crest, form: (0) projecting from shaft; (1) or low or rounded in lateral or medial view of the humerus.
36. Premaxilla, orientation of lower rim: (0) ventrolateral; (1) lateral.
37. Quadrate, free portion of shaft: (0) 10% or less; or (1) 30% or more of quadrate height.
38. Maxillary crowns, anteroposterior width: (0) equal; or (1) narrower than dentary crowns.
39. Maxillary crowns, shape: (0) subtriangular; (1) diamond-shaped.
40. Maxillary primary ridge strength: (0) less; or (1) more prominent than dentary primary ridge.
41. Posterior cervicals, neural spine height: (0) prominent; (1) low.

42. Cervicals 4-9, form of central surfaces: (0) slightly amphicoelous; (1) slightly opisthocoelous; or (2) strongly opisthocoelous.
43. Manual digit I-ungual, length: (0) shorter; or (1) longer than manual digit II ungual.
44. Premaxilla-maxilla diastema: (0) absent; (1) present.
45. Ischial obturator process: (0) absent; (1) present.
46. Metatarsal II transversal compression: (0) absent; (1) present.
47. Deltopectoral crest, size: (0) well developed; (1) less developed.
48. Thin ossified plates in thoracic region: (0) absent; (1) present.
49. Third cervical with well-developed epipophyses: (0) absent; (1) present
50. Chevron shape: (0) paddle-shaped; (1) flag-shaped.

DATA MATRIX

	5	10	15	20	25	30	35	40	45	50
Lesothosaurus	00000	00000	00000	00000	00000	00000	000?0	0000?	00?00	0000?
Scutellosaurus	00000	00000	00000	000??	00?00	00000	000?0	0000?	00000	000??
Marginocephalia	00001	10001	0?001	31000	00000	00000	000?0	00000	00000	00000
Heterodontosaurus	1000?	00200	01001	10?00	00000	00000	00000	00000	00010	00000
Talenkauen	00101	111??	??1??	3????	01?0?	??00?	????1	1?100	10?1?	1111?
Macrogryphosaurus	?????	?????	10??1	3????	?1???	?1??1	1??0?	?????	10???	??111
Thescelosaurus	?0??1	0????	10100	2010?	01?0?	?0000	01011	??000	00?11	00100
Hypsilophodon	10000	00000	10100	20010	00001	?0000	01111	00000	00111	00000
Anabisetia	????0	1????	??1??	311??	11???	?1001	1??01	???11	????1	11???
Gasparinisaura	????1	1??11	????1	20101	11??1	11100	01000	?100?	1??11	10001
Muttaburrasaurus	1???1	1??11	????1	31??1	?1101	??00?	?00?1	1000?	00?11	000??
Tenontosaurus	10100	01010	00011	31011	11111	00000	00100	10000	01011	00000
Dryosaurus	11110	11111	01011	31111	11110	11111	10001	11111	01011	00000
Ankylopollexia	11110	11111	01011	31211	11110	11111	10001	11111	12111	00000

LIST OF DIAGNOSTIC CHARACTERS

The first number refers to the character on the list of the characters, and the derived state is given in brackets.

Ornithopoda 1 (1), 44 (1)
Euornithopoda 25 (1), 45 (1)
Iguanodontia 3 (1), 7 (1), 9 (1), 14 (1), 17 (1), 20 (1), 21 (1), 22 (1), 23 (1), 36 (1)
Euiguanodontia 18 (1), 26 (1), 27 (1), 37 (1), 41 (1), 46 (1)
Elasmaria 48 (1), 49(1)
Dryomorpha 2 (1), 4 (1), 12 (1), 19 (1), 24 (1), 25 (0), 28 (1), 29 (1), 46 (0)

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A NEW TITANOSAUR SAUROPOD
FROM THE LATE CRETACEOUS OF NEUQUÉN, PATAGONIA, ARGENTINA [1]

(With 14 figures)

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ABSTRACT: The discovery of *Muyelensaurus pecheni* gen. et sp.nov., a new slender titanosaurid, is relevant from anatomical and systematic viewpoints. The specimens come from the Upper Cretaceous strata of the Portezuelo Formation (Turonian-Early Coniacian) at Loma del Lindero, Rincón de los Sauces area, Neuquén Province, Argentina. The remains include a braincase, cervical, dorsal, sacral and caudal vertebrae, and numerous appendicular bones. It is characterized by the following association of autapomorphies: basal tubera diverge 70 degrees from each other; thin and concave lamina that unit basal tubera ventrally, basioccipital condyle wider than the proximal portion of the basal tubera; posterior dorsal neural spines with large prespinal lamina reinforced by two small accessory laminae, distal end of pubic blade rectangular and medially thick. A cladistic phylogenetic analysis placed *Muyelensaurus pecheni* gen. et sp.nov. and *Rinconsaurus caudamirus* in a new eutitanosaur clade named herein Rinconsauria. This new clade include middle-sized sauropods different from Aeolosaurini, Opisthocoelicaudiinae or Saltasaurinae taxa.

Key words: Sauropoda. Titanosauria. Rinconsauria. *Muyelensaurus pecheni* gen. et. sp.nov. Late Cretaceous.

RESUMEN: Un nuevo saurópodo Titanosaurio del Cretácico superior de Neuquén, Patagonia, Argentina.

El descubrimiento de *Muyelensaurus pecheni* gen. et. sp. nov., un nuevo y esbelto titanosaurio, es relevante tanto desde el punto de vista anatómico como sistemático. Los especimenes proceden de los estratos del Cretácico superior de la Formación Portezuelo (Turoniano-Coniaciano temprano) de Loma del Lindero, en la zona de Rincón de los Sauces, Provincia del Neuquén, Argentina. Los restos incluyen un basicráneo, vértebras cervicales, dorsales, sacras y caudales y numerosos huesos apendiculares. Esta caracterizado por la siguiente asociación de autopomorfías: tubera basal diverge 70 grados una de otra; tubera basal unida ventralmente por una lámina delgada y cóncava; cóndilo basioccipital mas ancho que la porción proximal de la tubera basal; espinas neurales en la vértebras dorsales posteriores con una lámina preespinal larga y reforzada por dos pequeñas láminas accesorias; extremo distal de la lámina púbica de forma rectangular y gruesa medialmente. El análisis filogenético cladístico ubica a *Muyelensaurus pecheni* gen. et sp. nov. y a *Rinconsaurus caudamirus* en un nuevo clado de Eutitanosaurio que denominamos aquí como Rinconsauria. Este clado incluye a saurópdos de mediano tamaño diferentes de otros taxa de Aeolosaurini, Opisthocoelicaudiinae o Saltasaurinae.

Palabras clave: Sauropoda. Titanosauria. Rinconsauria. *Muyelensaurus pecheni* gen. et. sp.nov. Cretácico Superior.

INTRODUCTION

Titanosauria is the most diverse and geographically widespread Cretaceous sauropod clade. In spite of that, most of titanosaurs are represented by incomplete skeletal elements lacking well-preserved cranial remains. In this context, the discovery of a new genus and species represented by a braincase associated with numerous axial and appendicular bones is relevant from anatomical and systematic viewpoints.

In Argentina, only the titanosaurids *Antarctosaurus wichmannianus* (HUENE, 1929), *Saltasaurus loricatus* (BONAPARTE & POWELL, 1980), *Bonitasaura salgadoi* (APESTEGUÍA, 2004), *Bonatitan reigi* (MARTINELLI & FORASIEPI, 2004), and an unnamed specimen from Bajo de Añelo, Neuquén Province (CALVO & KELLNER, 2006) include descriptions of braincase. In contrast, well-preserved

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titanosaurids recently recovered in Patagonia that include cranial remains (Calvo *et al.,* 1997; Coria & Salgado, 1998) have not been described yet.

In Northwestern Patagonia, the Neuquén Group is the richest dinosaur bearing unit. It comprises a thick continental succession (maximum thickness 1,300m) deposited between Early Cenomanian to Early Campanian (Leanza & Hugo, 2001). The Neuquén Group has given since 1882 numerous titanosaur species (Huene, 1929; Powell, 1986; Calvo & Bonaparte, 1991; Bonaparte & Coria, 1993; González Riga, 2003; 2005).

In the last years, extraordinary titanosaur fossils were found in Rincón de los Sauces area, Northern Neuquén Province, Patagonia. *Rinconsaurus caudamirus* (Calvo & González Riga, 2003) is the first species described from this locality. Moreover, other discoveries carried out in Rincón de los Sauces include articulated specimens that have not been described yet (Calvo *et al.*, 1997; Coria & Salgado, 1998).

The objective of this work is to describe a new and slender titanosaur from the Late Cretaceous, and to analyze their phylogenetic relationships. The study of this taxon, the second species described in Rincón de los Sauces, is a new evidence of the morphologic diversity of the South American titanosaurs.

MATERIAL AND METHODS

The fossils had been found at Loma del Lindero site, 10km west to Rincón de los Sauces Town (Fig.1). This site was excavated during four years (1998-2001) under the direction of the first author (J.O.C.). The first fossil remains from Loma del Lindero site were found by Marcelino Palomo and communicated to authors by Salvador Palomo in 1997. At Loma del Lindero locality, numerous titanosaur remains (~ 300 bones) associated with a turtle specimen and theropods have been found (Calvo & González Riga, 1999; de la Fuente *et al.*, 2007). Fossil remains are housed at the Laboratory of Rincón de los Sauces Museum.

Geological Setting

In the last years, well-preserved titanosaur sauropods were found in Rincón de los Sauces area, Northern Neuquén Province, Patagonia. In the Río Seco site, located 2km South to Rincón de los Sauces Town, a slender eutitanosaur named *Rinconsaurus caudamirus* (Calvo & González Riga, 2003) and a basal sebecosuchian crocodyliform named *Pehuenchesuchus enderi* (Turner & Calvo, 2005) were found in strata tentatively assigned to Río Neuquén Subgroup (Late Turonian-Coniacian).

In Loma del Lindero site, 10km West to Rincón de los Sauces Town, numerous sauropod bones were collected in fluvial facies assigned to the Portezuelo Formation, base of the Río Neuquén Subgroup (Late Turonian-Early Coniacian after Leanza & Hugo, 2001). The fossils come from reddish pelites and yellowish sandstones of overbank facies. A partially similar sedimentary context is also present in Cerro Guillermo area (Mendoza Province) (González Riga & Astini, 2007), where the titanosaur *Mendozasaurus neguyelap* was found (González Riga, 2003; 2005).

Institutional abbreviation – FMNH PR, Field Museum of Natural History, Chicago, USA; MRS-Pv, Museo de Rincón de los Sauces, Neuquén, Argentina; MUCPv. Museo de Paleontología de la Universidad Nacional del Comahue, Neuquén, Argentina.

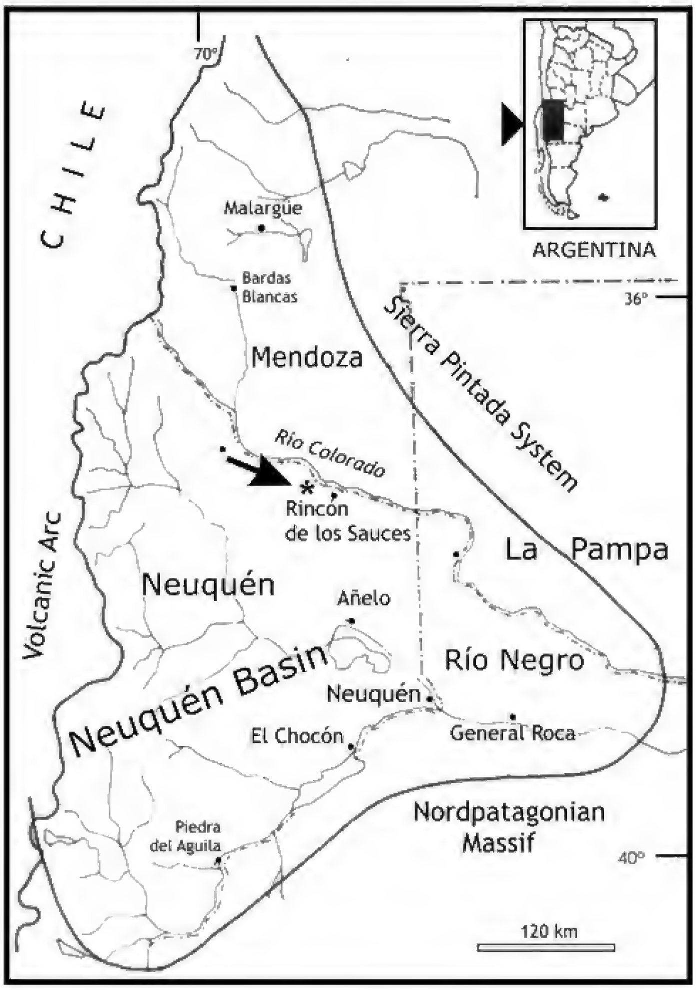

Fig.1- Map of Neuquén basin (Patagonia, Argentina) showing the locality where the holotype of *Muyelensaurus pecheni* gen. et sp.nov. was found.

SYSTEMATIC PALEONTOLOGY

SAURISCHIA Seeley, 1887
SAUROPODA Marsh, 1878
TITANOSAURIA Bonaparte & Coria, 1993
TITANOSAURIDAE Lydekker, 1893
RINCONSAURIA new taxon

Etymology – In reference to Rincón de los Sauces area, Neuquén Province, Patagonia, Argentina.

Definition – *Muyelensaurus*, *Rinconsaurus*, their most recent common ancestor and all of its descendants.

Diagnosis – Titanosaurids with the following association of characters: suboval teeth with labial and lingual faces well differentiated by crests, bony processes that support the postzygapophyseal facets in middle caudal vertebrae, and posterior caudal centra depressed posteriorly.

Included species – *Rinconsaurus caudamirus* Calvo & González Riga, 2003, and *Muyelensaurus pecheni* gen. et sp.nov.

Muyelensaurus gen.nov.

Etymology – From *Muyelen*, one of the names of the Colorado river after the Mapuche indigenous language (Erize, 1988); *saurus* (Greek), lizard.

Type-species – *Muyelensaurus pecheni* sp.nov.

Diagnosis – Slender Rinconsauria characterized by the following association of autapomorphies: basal tubera diverge 70 degree from each other; extensive, thin and concave medial lamina that unit basal tubera ventrally, basioccipital condyle wider than the proximal portion of the basal tubera; posterior dorsal neural spines with large prespinal lamina reinforced by two small accessory laminae, distal end of pubic blade rectangular and medially thick. In contrast to *Rinconsaurus, Muyelensaurus* gen.nov has anterior dorsals with neural spines posteriorly directed less than 45 degree with respect to the vertical, posterior dorsals with large and deep infradiapophyseal fossa and ventral face of posterior cervical centra narrow and strongly concave at level of the parapophysis. Moreover, different from *Rinconsaurus*, *Muyelensurus* gen.nov. lacks an accessory centroparapophyseal lamina in posterior dorsals, anterior caudals with postzygapophyseal process, and amphicoelous-biconvex or amphicoelous-opisthocoelous-biconvex caudal centra.

Muyelensaurus pecheni sp.nov.

Etymology – In honor of Dra. Ana María Pechen, Main head of the National University of Comahue (2002-2006), who supported the study of dinosaur fossils in Neuquén Province, Patagonia.

Holotype – MRS-PV 207, a braincase including partial frontal and parietal, basioccipital, incomplete basipterigoid process, supraoccipital, exoccipital, basisphenoidals tubers, orbitosphenoids, and incomplete parasphenoids.

Paratype – The following bones associated with the holotype are included: represented by a premaxilar (MRS-Pv 59, 60, 337), cervical vertebrae (MRS-Pv 65, 66,121, 122, 204, 230, 232, 229, 279, 391, 392, 420, 422, 428), dorsal vertebrae (MRS-Pv 67, 68, 224, 404, 412, 421), sacrum (MRS-Pv 355), caudal vertebrae (MRS-Pv 135, 137, 164,170, 171, 173, 174, 189, 190, 193, 200, 209, 214, 252, 377, 408), scapula (MRS-Pv 396, 397, 259), sternal plate (MRS-Pv 125), humerus (MRS-Pv 70, 132, 212, 352, 357, 387), ulnae (MRS-Pv 72, 243, 353, 182), radio (MRS-Pv 71, 139) metacarpals (MRS-Pv 127, 152, 157, 181, 198, 231, 235, 236), ischia (MRS-Pv 87, 199, 247, 251), ilia (MRS-Pv 131, 134, 202, 399), pubes (MRS-Pv 88, 154, 204, 371), femora (MRS-Pv 89, 91, 352, 356, 358, 389, 429), tibiae (MRS-Pv 161, 162, 257, 266), fibulae (MRS-Pv 90, 245, 246, 258, 271, 369, 375), astragalus (MRS-Pv 187), metatarsals (MRS-Pv 50-54, 128, 141, 142, 166, 168, 242, 273, 274, 378, 379), and phalanges (MRS-Pv 55, 56, 57, 58, 143, 144-147, 165, 237).

Referred material – posterior dorsal vertebrae (MRS-Pv 123, 203, 419 and 431).

Specimens – The holotype and paratypes of *Muyelensaurus pecheni* sp.nov. correspond to four adult and one juvenile individuals. All fossil remains were found disarticulated but associated in the same site and include cranial remains, cervical, dorsal, sacral, and caudal vertebrae, and appendicular bones (Fig.2). Duplicate bones represented by appendicular bones exhibit the same morphological characters. This evidences the presence of a monospecific assemblage.

Horizon, age and locality: Portezuelo Formation, Río Neuquén Subgroup, Neuquén Group, Late Cretaceous, Late Turonian-Early Coniacian (after Leanza & Hugo, 2001). The fossils come from Loma del Lindero site, 10km West to Rincón de los Sauces City, Neuquén Province, Patagonia, Argentina.

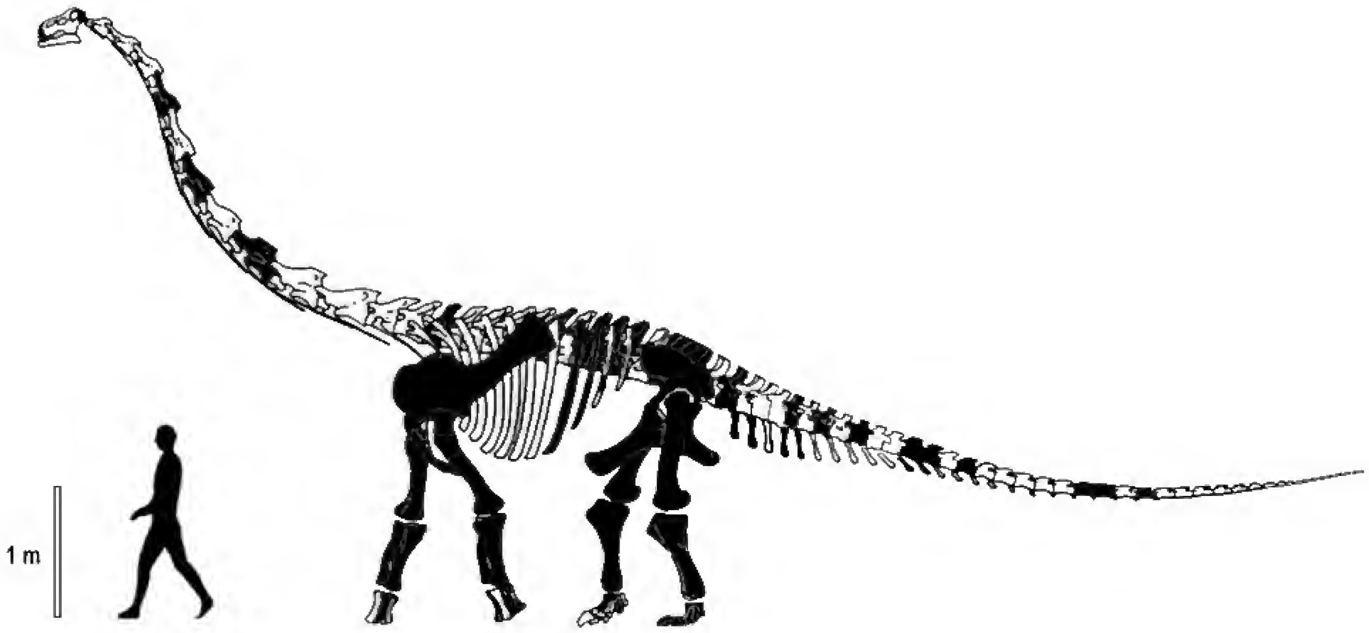

Fig.2- *Muyelensaurus pecheni* gen. et sp.nov., preserved bones (in black) shown in a titanosaur skeletal reconstruction of Lehman & Coulson (2002).

DESCRIPTION

Skull – Premaxilar fragments with teeth (Fig.3), and an incomplete braincase (Fig.4) were recovered. Suboval teeth are characterized by the presence of labial and lingual faces well differentiated by crests, like in *Rinconsaurus caudamirus* (Calvo & González Riga, 2003). The braincase is slightly crushed. It preserves a fragment of the left parietal and frontal, a fragment parietal, complete supraoccipital, the right paraoccipital process, basioccipital condyle, basal tubera, a fragment of the rigth basipterygoid process, and partially preserved orbitosphenoid, crista prootica, and parasphenoid.

The frontal, represented by a small fragment, forms the posterior rim of the orbit. In anterior view, it is fused to the orbitosphenoid. The parietal is robust and axially elongated. The supratemporal fenestrae are relatively reduced, transversely orientated and laterally directed, as in the titanosaur *Saltasaurus* and some other sauropods (Wilson & Sereno, 1998; Curry Rogers & Forster, 2001). The preserved medial border of the supratemporal fenestra is formed by the parietal. On the anterior rim of the supratemporal fenestra participates the frontal, like in *Rapetosaurus* (Curry Rogers & Forster, 2004), *Nemegtosaurus* and *Saltasaurus* (*contra* Wilson, 2002), and *Bonatitan* (Martinelli & Forasiepi, 2004).

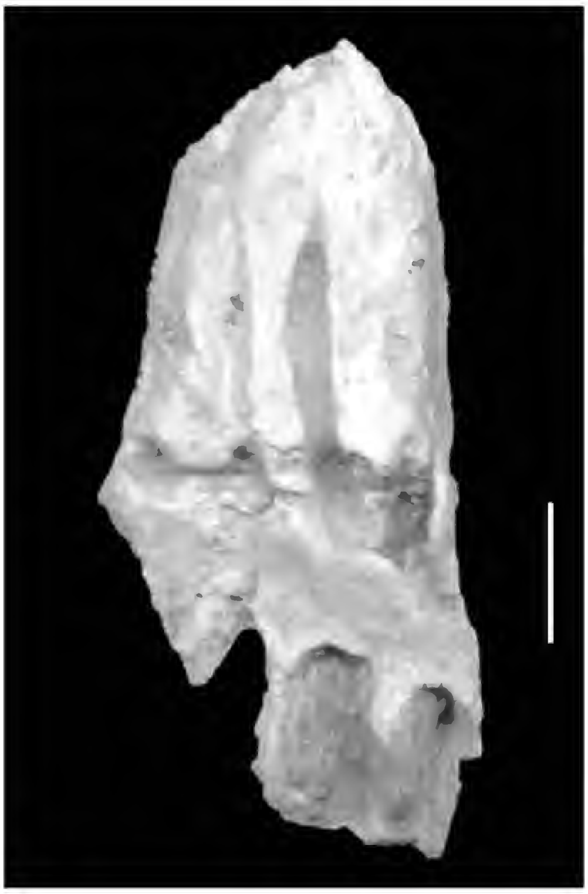

Fig.3- *Muyelensaurus pecheni* gen. et sp.nov., a fragment of premaxilar with teeth (MRS-Pv 59) in lateral view. Scale bar = 1cm.

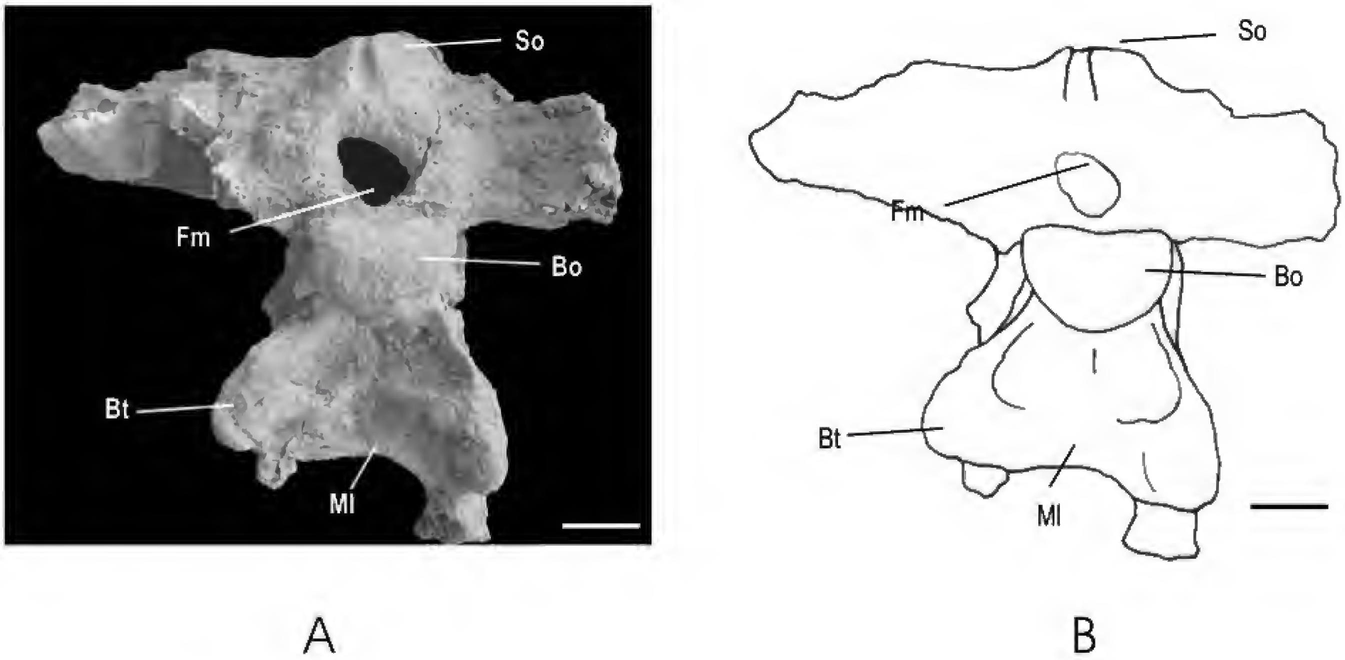

Fig.4- *Muyelensaurus pecheni* gen. et sp.nov., braincase (MRS-Pv 207) in occipital view (A, picture; B, drawing). (Bo) basioccipital, (Bt), basitubera, (Fm), foramen magnum, (Ml), medial lamina, (So) supraoccipital. Scale bar = 2cm.

The proximal portion of the supraoccipital has a subquadrangular shape. In spite of that the distal end is not preserved. There is a small process that shows that it was directed ventrally as in *Saltasaurus*.

The basioccipital is slightly deformed by compression. In posteroventral view, it is subtriangular with its dorsal border slightly concave and their lateroventral sides convex. The neck is constricted transversely and concave anteroposteriorly; therefore, the condyle has a mushroom shape, an unusual morphology among sauropods.

The basisphenoid is formed by the tubera and the basipterygoid processes. The first ones are complete but the second ones are missing except by the proximal portion of the right process. Basal tubera are well separated by an extended and thin medial lamina (see Ml in Fig.4) that has a concave ventral contour in a posterior view. Basal tubera diverge 70 degree from each other (Fig.4). A lateral ridge connects each basal tubera with the condylar neck on its external side; and a small ridge unites each tubera with the midline. In between these ridges, a wide depression is developed opened only on the ventral side. The proximal portion of the right basipterygoid process is preserved. According to the evidence they are well separated and were directed almost parallel.

Cervical vertebrae – An almost complete middle cervical vertebra and numerous incomplete remains were collected (Fig.5; MRS-Pv 65). This cervical has an opisthocoelous centrum as wide as high in posterior view and relatively long (ratio: total length / height of cotyle more than 4.0). In contrast to *Rinconsaurus caudamirus* (Calvo & González Riga, 2003), the lateral faces have a deep concavity, but lack a true pleurocoels. The posterior centrodiapophyseal and postzygodiapophyseal laminae are well defined, as in other titanosaurs like *Rapetosaurus krausei* (Curry Rogers & Forster, 2001). The neural spine is formed by the fusion of spinoprezygapophyseal and spinopostzygapophyseal laminae. It has a triangular contour in lateral view and is thinner distally than those of titanosaur specimen "Series A" from Peirópolis, Brazil (Powell, 1987). Prezygapohysis process surpasses the anterior border of the centrum, but in contrast to *Rinconsaurus*, the postzygapophyses do not extend beyond the posterior border. The prezygapophyseal facets are slightly oriented dorsomedially. The diapophysis is reinforced by the posterior centrodiapophyseal, prezygodiapophyseal and postzygodiapophyseal laminae. Likewise some titanosaurs (*Saltasaurus*, *Rapetosaurus*), these laminae form a supradiapophyseal concavity lacking well-defined borders (González Riga, 2005).

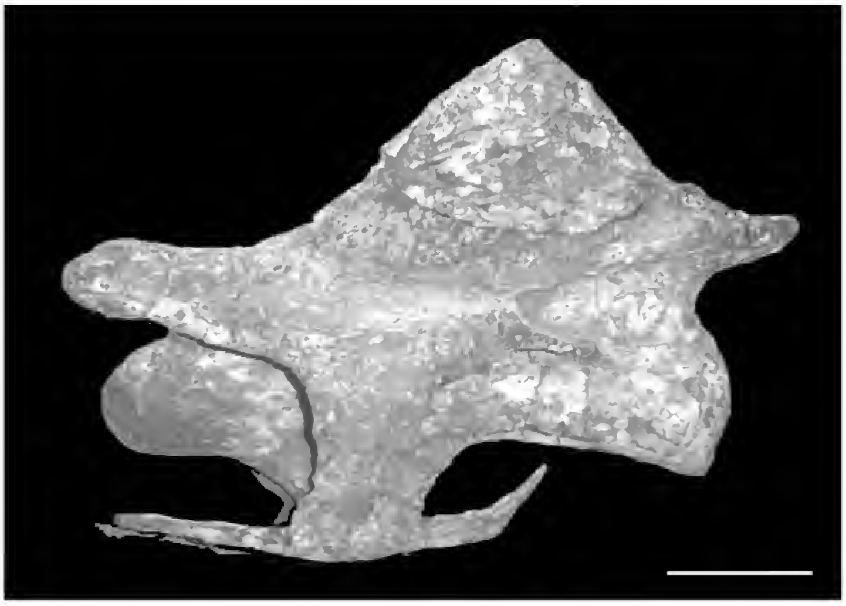

Fig.5- *Muyelensaurus pecheni* gen. et sp.nov., middle cervical vertebra (MRS-Pv 65) in lateral view. Scale bar = 5cm.

The parapophyses, located in the anterior half of the vertebral body, are laminar and subtriangular in shape. In contrast to *Rinconsaurus*, the ventral face is narrow and strongly concave at level of the parapophysis. Other cervicals (MRS-Pv 121, 391, 392, 420, 422, 229, 428, and 279) are crusted and damaged, but have a similar size to the cervical vertebra described. In contrast, one cervical (MRS-Pv 122) is assigned to a larger specimen (centrum length: 43cm). It shows a tall neural spine that have a subtriangular contour in lateral view. Other cervicals of large size, but fragmentary preserved, have been recovered (MRS-Pv 204, 230, 232, and 66).

Anterior dorsal vertebra – One complete anterior dorsal vertebra have been recovered (Fig.6; MRS-Pv 404). The neural arch is three times higher than the centrum and is placed anteriorly. The centrum has a deep pleurocoel that occupies the half of the length. The parapophysis is placed on the top of the centrum. The prezygapophysis are wide and have an oval shape. They are well separated from the midline. The centroprezygapophyseal and diapoprezygapophyseal lamina are robust. The diapophysis is connected to the neural spine by a robust spinodiapophyseal lamina. Ventrally, the diapophysis is reinforced by a paradiapophyseal lamina and a centrodiapophyseal lamina. In contrast to this taxon, the centroprezygapophyseal laminae are absent in *Rinconsaurus*. Small accessory centrodiapophyseal laminae are born on the base of the diapoparapophyseal laminae and are connected to the centrodiapophyseal laminae. Therefore two deep depressions are developed below the diapophysis. In posterior view a centropostzygapophyseal lamina is present. The single neural spine is directed posteriorly around 45 degree with respect to the vertical, in contrast to *Rinconsaurus* that reaches 60 degree. The prespinal lamina is present and transverse processes are directed dorsolaterally.

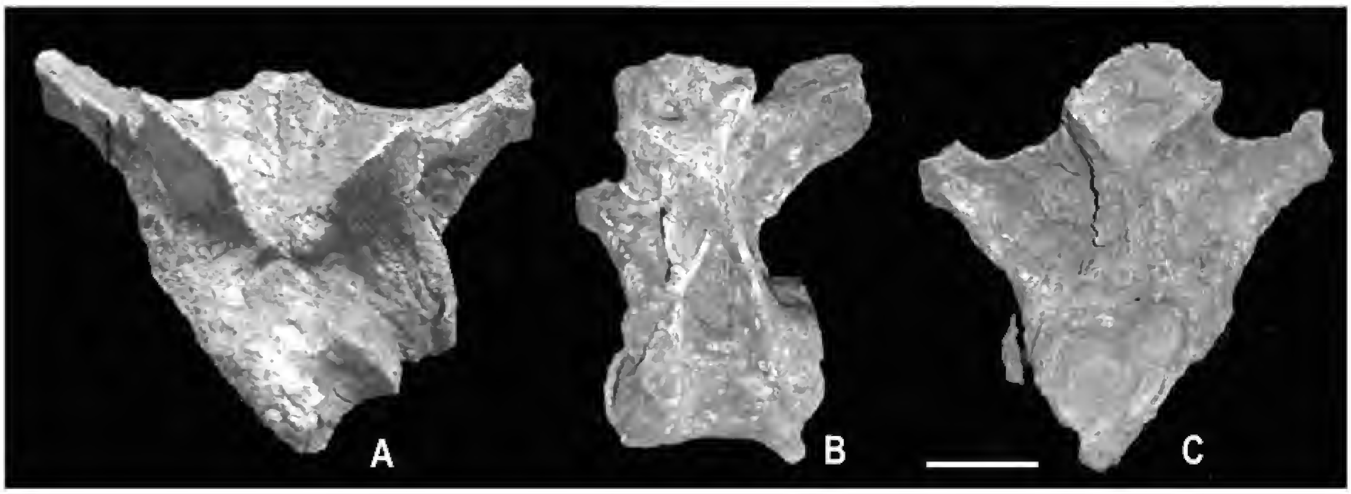

Fig.6- *Muyelensaurus pecheni* gen. et sp.nov., anterior dorsal vertebra (MRS-Pv 404) in anterior (A), lateral (B), and posterior (C) views. Scale bar = 5cm.

Posterior dorsal vertebrae – Several disarticulated posterior dorsal vertebrae (MRS-Pv 67, 68, 412, and 224) and incomplete posterior dorsal arch (MRS-Pv 421) were preserved. The posterior dorsals have opisthocoelous and subcircular centra, as wide as high (Fig.7). The lateral and ventral faces are anteroposteriorly concave. The lateral faces of the centrum (Fig.8A) show deep eye-shaped pleurocoels with acuminate posterior contour, a synapomorphy of Titanosauria (*sensu* Salgado *et al.,* 1997a). They lack hyposphene-hypantrum articulations. Postzygapophyseal facets are elongated, narrow, relativelly small and directed ventromedially (Fig.8B).

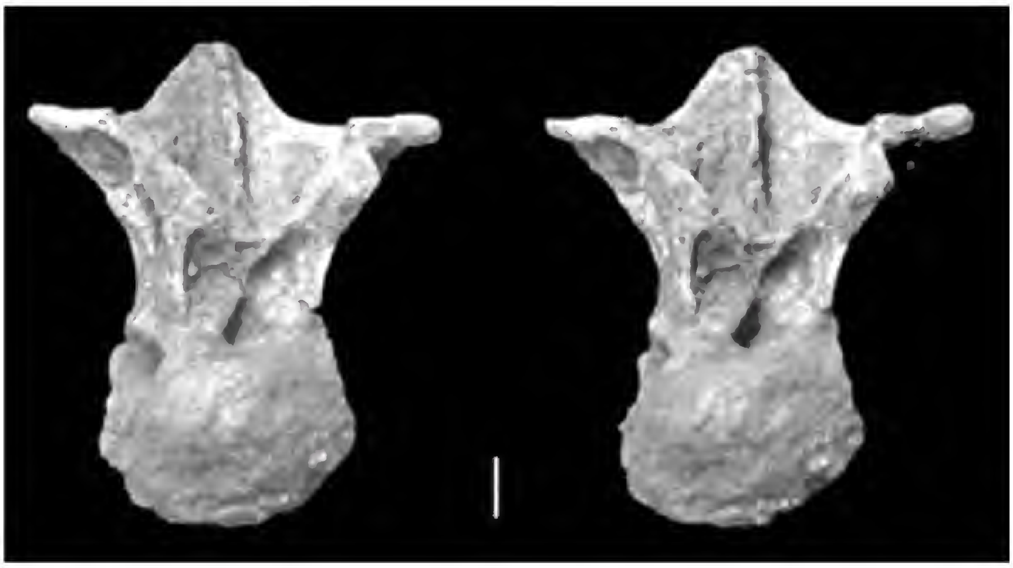

Fig.7- *Muyelensaurus pecheni* gen. et sp.nov., stereophotographs of the posterior dorsal vertebra (MRS-Pv 412) in anterior view. Scale bar = 5cm.

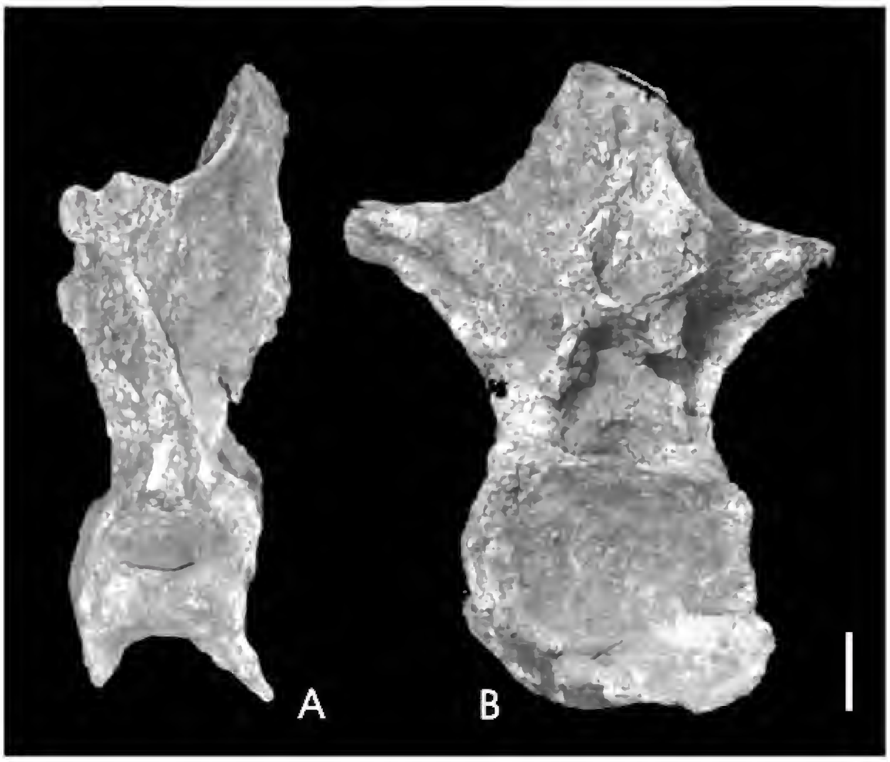

Fig.8- *Muyelensaurus pecheni* gen. et sp.nov., posterior dorsal vertebra (MRS-Pv 412) in lateral (B) and posterior (B) views. Scale bar = 5cm.

They are connected to the centropostzygapophyseal laminae. In contrast to *Rinconsaurus caudamirus* (MRS-Pv 17, 18), the most posterior dorsals lack postzygodiapophyseal lamina. The diapophyses are supported by posterior and anterior centro diapophyseal laminae. These laminae delimit a subtriangular infradiapophyseal depression in some dorsals (MRS-Pv 67 and 68) and a true infradiapophyseal fossa in the dorsal MRS-Pv 412. A less developed infradiapophyseal depression is present in posterior dorsal of *Rinconsaurus caudamirus* (MRS-Pv 13). The prespinal lamina is large anteroposteriorly and reaches the base of the neural arch. There are two small accessory prespinal laminae bifurcated close to the base of the neural arch (Fig.7). This character has not been described in any other posterior dorsal vertebrae of titanosaurs and is considered herein as a probable autapomorphy of *Muyelensaurus*. In *Mendozasaurus*, anterior dorsals have a similar structure but they are small spinoprezy gapophyseal laminae that are directed to the prezygapophysis (González Riga, 2003). Other peculiar character of the dorsals is the presence of accessory spinodiapophyseal lamina. This lamina exhibits a variable morphology: it is extensive in some dorsals (MRS-Pv 67 and 68) whereas it is reduced or absent in other dorsals. Accessory spinodiapophyseal laminae, but with less development, are also present in *Argentinosaurus huinculensis* (Bonaparte & Coria, 1993). The neural canal is reduced and shows a subtriangular contour. Over the neural canal, there is a deep fossa divided by a medial septum. The neural spines are less posteriorly directed toward the posterior section of the series. The neural spines have lanceolate anterior and posterior contours due to the development of lateral process of the spinodiapophyseal lamina. Other middle and posterior dorsal vertebrae recovered are distorted and considered as refereed material (MRS-Pv 123, 203, 419, and 431). They exhibit a large and very deep infradiapophyseal fossa limited by the anterior and posterior centrodiapophyseal laminae. Finally, in contrast to *Muyelensaurus*, the posterior dorsal vertebrae of *Rinconsaurus* have an accessory centroparapophyseal lamina, which is extended from the base of the parapophysis to the base of centrodiapophyseal lamina (MRS-Pv 17 and 18). This structure is absent in other titanosaurs and can be interpreted as an autapomorphy of *Rinconsaurus*.

Sacrum – Five sacral vertebrae partially preserved have been collected (MRS-Pv 355). They are fused and have neural spines united each other by an interspinal medial lamina. The sacral ribs are laminar and dorsally expanded reaching the level of the neural spines.

Caudal vertebrae – Numerous caudal vertebrae corresponding to several individuals of different sizes were recovered. All caudals have strongly procoelous centra, in contrast to *Rinconsaurus* that is characterized by the intercalation of amphicoelous-biconvex or amphicoelous-opisthocoelous-biconvex centra.

The most anterior caudal recovered (Fig.9; MRS-Pv 200) is large and have a centrum slightly inclined anteriorly less than *Gondwanatitan* (Kellner & Azevedo, 1999) and *Aeolosaurus* Powell, 1986. The anterior face of the centrum is as wide as high. The neural arch is located over the anterior border of the centrum, like Aeolosaurini species. The neural spine is ticker distally, and has a quadrangular contour in dorsal view. It is supported by the prespinal and postspinal laminae.

Fig.9- *Muyelensaurus pecheni* gen. et sp.nov., anterior caudal vertebra (MRS-Pv 200) in lateral view. Scale bar = 5cm.

In *Rinconsaurus* the neural spines of the anterior caudals are less thick than they are distally. The partially preserved transverse processes are wide and posteriorly directed. The characteristic process of the postzygapophyseal facets, present in *Rinconsaurus caudamirus* (MRS-Pv 23), is absent in *Muyelensaurus*.

Other anterior and middle caudal vertebrae correspond to a middle-sized specimen (MRS-Pv 377, 137, 174, 408, 214, 252, and 173) or to a juvenile specimen (MRS-Pv 164 and 193). In anterior caudals (MRS-Pv 137) the centra are slightly inclined anteriorly, but this character disappears toward the middle section of the tail.

All anterior caudals lack the postzygapophyseal process that is present in *Rinconsaurus*. In contrast, middle and middle-posterior caudals (MRS-Pv 193, 164, and 135) share with *Rinconsaurus* the presence of a postzygapophyseal process (Figs.10-11). The neural spines are incomplete, but the preserved portion indicates an elongate morphology axially extended, and posterior caudal centra are depressed posteriorly. The distal caudals (MRS-Pv 170, 171, 190, 189, and 209) are similar to those of *Rinconsaurus*. They have very reduced neural spines slightly inclined anteriorly that become horizontal toward the distal end of the tail. In contrast to *Rinconsaurus*, the neural arch of the distal caudal are reduced anteroposteriorly since they never reach the half of the centrum length.

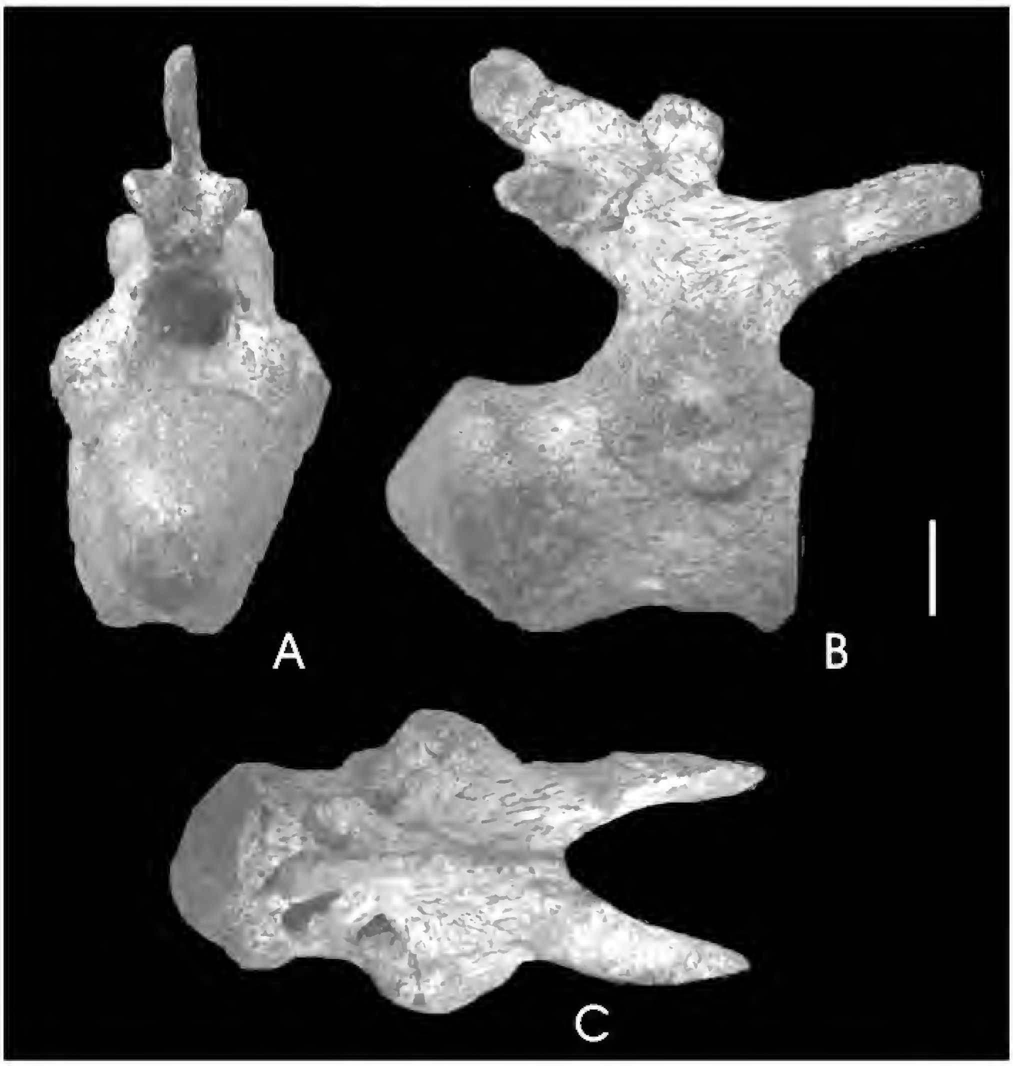

Fig.10- *Muyelensaurus pecheni* gen. et sp.nov., middle caudal vertebra (MRS-Pv 164) in anterior (A), lateral (B) and dorsal (C) views. Scale bar = 2cm.

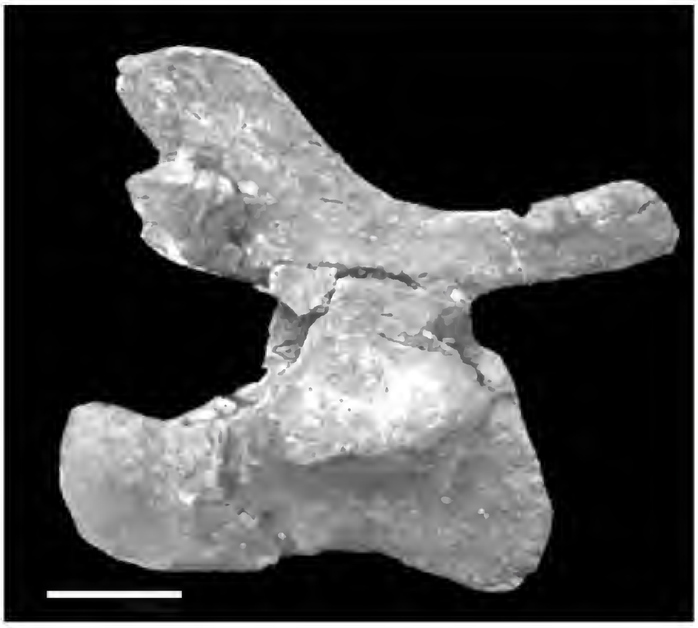

Fig.11- *Muyelensaurus pecheni* gen. et sp.nov., posterior caudal vertebra (MRS-Pv 135) in lateral view. Scale bar = 2cm.

Appendicular bones – The abundant bones recovered are similar to those of *Rinconsaurus* and other titanosaurs, but show some differences. They will be described in detail elsewhere. The sternal plate (MRS-Pv 125) exhibits a typical semilunar contour, and its posterior border is not straight as that present in some titanosaurs, like *Mendozasaurus* and *Malawisaurus* (González Riga, 2003).

A complete right scapula (Fig.12.A; MRS-Pv 259) and two partial scapular blades (MRS-Pv 396 and 397) were recovered. The scapula, a long and laminar bone, has a thin and slender scapular blade. The distal end is expanded, the diagonal acromion is thin and the supracoracoideus fossa is very prominent. The ventral border is slightly concave up to its union with the proximal end, where begins a new concave border.

Six humeri were collected (MRS-Pv 70, 132, 212, 352, 357, and 387). One left humerus (Fig.12B; MRS-Pv 70) is the best preserved. It is relatively slender, since the proximal width reaches the 25 percent of the total length.

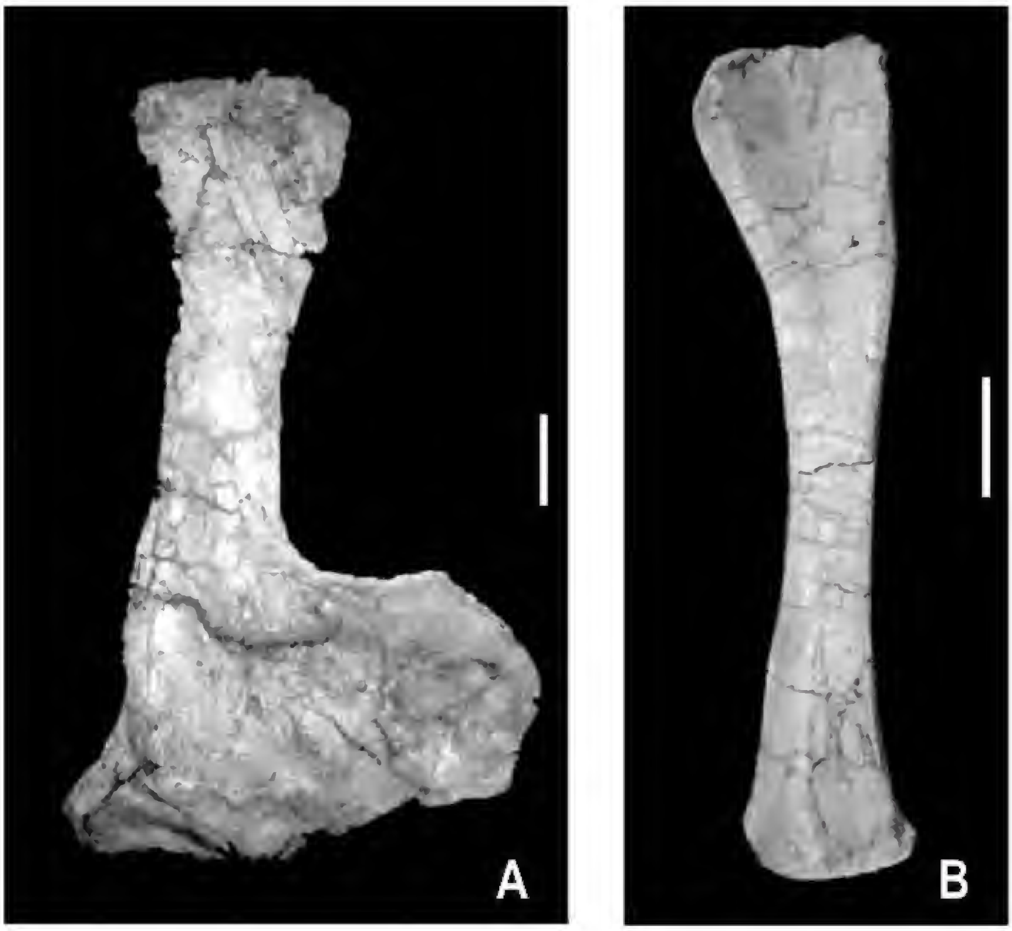

Fig.12- *Muyelensaurus pecheni* gen. et sp.nov., right scapula (MRS-Pv 259) in lateral view (A), left humerus (MRS-Pv-70) in anterior view (B). Scale bar = 10cm.

The proximal end is straight and the humeral head is small, prominent and acute; morphology has not been described in other titanosaurs. In the anterior face, the deltopectoral crest is thin, well developed and extend more than a half of the proximal portion. In posterior view, the distal end shows the radial condyle greater than the ulnar condyle.

The ulna, radius and metacarpals are similar to those of *Rinconsaurus*. In particular, the metacarpals exhibit expanded ends, reduced diaphyses and have not convex phalangeal articular facets, like in all Titanosauria (Salgado *et al.,* 1997a; Calvo & González Riga, 2003).

The ilium, ischium and pubis are similar (Fig.13), in general lines, to those of *Rinconsaurus*. However, the pubis has an open foramen and a quadrangular and thicker medially distal end, in contrast to *Rinconsaurus* that shows a more rounded and thin end.

The femora and tibiae remains suggest the presence of five specimens. The femur is long and straight. It has a lateral bulge poor developed comparing to others titanosaurs and in anterior view it has a convex border less acute than *Rinconsaurus*. The femoral head is small and it extends dorsally surpassing the greater trochanter. The fourth trochanter is placed at over the midhalf of the total length. The tibial condyle is slightly smaller than the fibular one.

The tibia is a slender bone wider on proximal end than on the distal end. The cnemial crest is curved and anterolaterally directed. The fibulae are long and of sigmoidal shape. In lateral view, the proximal end has the dorsal border convex and it is more expanded than the distal one. The distal border is straight. The anterior border is concave except on the distal end where it is inclined posteriorly. The left astragalus has been preserved (MRS-Pv 187). It is subtriangular and robust. The ascending process is a small ridge. There is a smooth longitudinal depression below the ascending process for articulation of the fibula. In posterior view, the posterior astragalar fossa is small and it is restricted to the upper portion. The entire astragalar surface displays rugosities of cartilaginous insertion. Several metatarsals corresponding to two specimens, a smaller (MRS-Pv 142, 54, and 50) and one larger (MRS-Pv 168,166, 52, 51, 128, and 141) have been recovered. The phalanges are similar, in general lines, to those of *Mendozasaurus* (González Riga, 2003) and *Epachthosaurus* (Martínez *et al.* 2004).

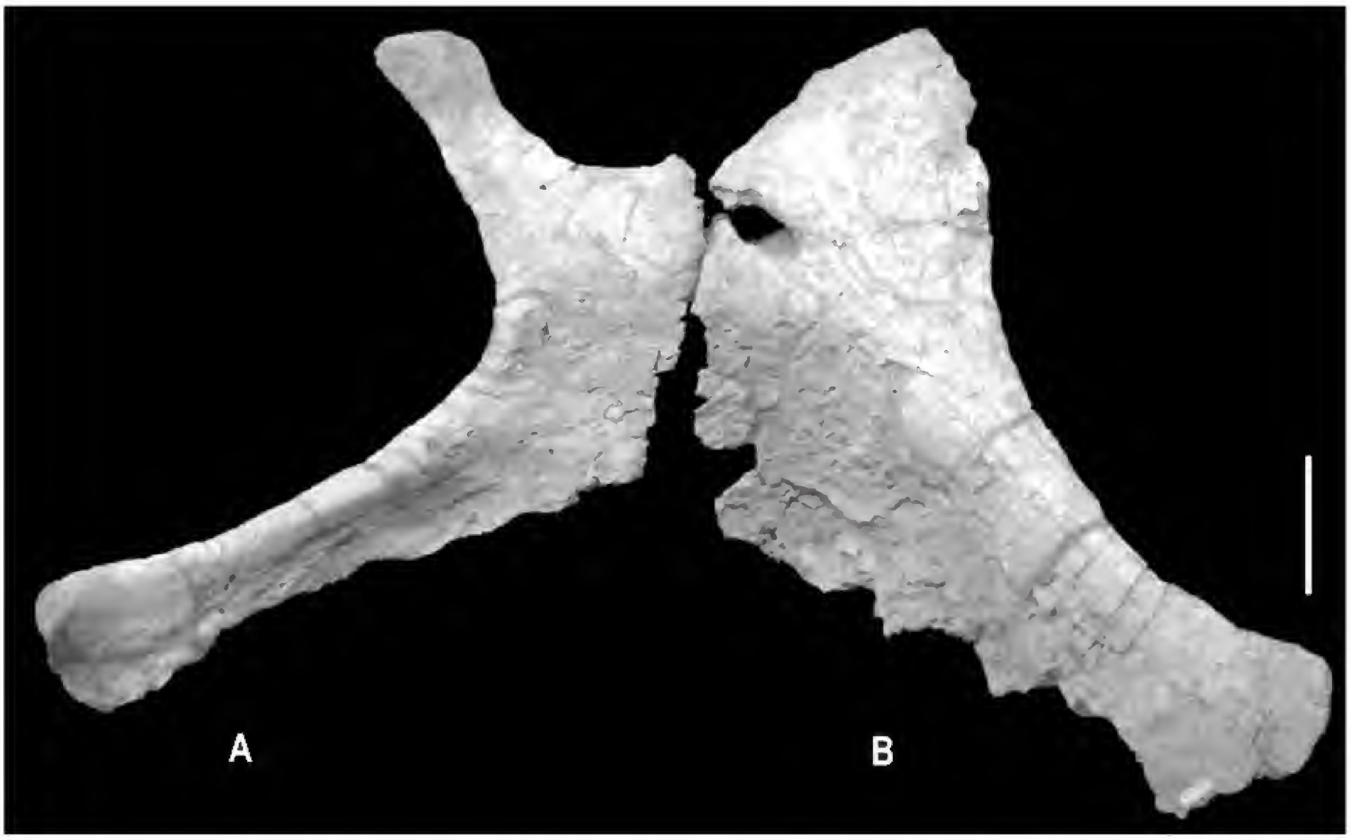

Fig.13- *Muyelensaurus pecheni* gen. et sp.nov., pubis and ischium (MRS-Pv 88) in lateral view. Scale bar = 10cm.

COMPARISON AND DISCUSSION

Cladistic analyses of Titanosauria have been worked by several authors since 1995 (Salgado *et al.,* 1997a; Wilson & Sereno, 1998; Upchurch, 1998; Wilson & Upchurch, 2003). In most of these analyses few titanosaur taxa were included because the objective was to support the higher level of the Sauropoda phylogeny. Then, it was used similar titanosaurid taxa choosing different characters; therefore, taxon names have changed as well as node names in the different published trees. In order to improve the phylogenetic position of taxa inside the Titanosauria, in this paper, we have used the data matrix and characters proposed by Salgado *et al.* (1997a), Wilson & Sereno (1998), Upchurch (1998), Wilson (2002), Wilson & Upchurch (2003) González Riga (2003), Calvo & González Riga (2003) and we have evaluated all them adding new ones.

The phylogenetic relationships of *Muyelensaurus pecheni* plus 17 other taxa were analyzed through a parsimony cladistic analysis based on 65 characters (see Appendix, Tab.1).

Camarasaurus grandis (Cope, 1877) was considered as outgroup, and *Brachiosaurus brancai* (Janensch, 1950), *Chubutisaurus insignis* (Del Corro, 1975; Salgado, 1993), *Andesaurus delgadoi* (Calvo & Bonaparte, 1991), *Malawisaurus dixeyi* (Jacobs *et al.* 1993), *Mendozasaurus neguyelap* (González Riga, 2003; 2005), *Epachthosaurus sciuttoi* (Powell, 1990; Martínez *et al.*, 2004), *Aeolosaurus rionegrinus* (Powell, 1986; Salgado & Coria, 1993; Salgado *et al.*, 1997b), *Gondwanatitan faustoi* (Kellner & AZevedo, 1999), *Rinconsaurus caudamirus* (Calvo & González Riga, 2003), *Rapetosaurus krausei* (Curry Rogers & Forster, 2001, 2004), *Lirainosaurus astibiae* (Sanz *et al.*, 1999), *Alamosaurus sanjuanensis* (Gilmore, 1946), *Neuquensaurus australis* (Huene, 1929; Powell, 1986; Salgado *et al.,* 2005), *Opisthocoelicaudia skarzynskii* (Borsuk-Bialynicka, 1977), *Saltasaurus loricatus* (Bonaparte & Powell, 1980; Powell, 1992), *Rocasaurus muniozi* (Salgado & Azpilicueta, 2000), and *Muyelensaurus pecheni* gen. et sp.nov. formed the ingroup.

The data matrix was analyzed with Nona, version 2.0 (Goloboff, 1993). The application of the heuristic method produced one most parsimonious tree with a length of 105 steps and high consistency and retention indices (C.I. = 0.76; R.I. = 0.78). The multistate characters were considered unordered. The cladogram obtained (Fig.14) is similar, in general lines, to previous studies (Salgado *et al.,* 1997a; Wilson, 2002; González Riga, 2003; Calvo & González Riga, 2003) but presents differences due to the inclusion of new taxa and characters.

Titanosauria, proposed originally by Bonaparte & Coria (1993), was defined as the most recent common ancestor of *Andesaurus delgadoi* and Titanosauridae, and all of its descendants (Salgado *et al.,* 1997a). This node-based group, was redefined by different criteria or replaced by other names, but in a recent analysis, Wilson & Upchurch (2003) follow the original definition of Salgado *et al.* (1997a). In our analysis, Titanosauria (Fig.14, node 3) is supported by seven synapomorphies obtained by delayed optimization: centroparapophyseal lamina in posterior dorsal vertebrae (26.1), ventrally widened or slightly forked centrodiapophyseal laminae in posterior dorsal vertebrae (27.1), posteriorly acuminate pleurocoels in dorsal vertebrae (29.1), laminated and anteroposteriorly elongated neural spine in middle caudal vertebrae (43.1), absence of distal phalangeal articular facets in metacarpals (55.1), pubis longer than ischium (56.1), and posterior process of the ischium less than the twice of the length of pubis articulation (57.1).

Titanosauridae was defined originally by Salgado *et al.* (1997a) as the clade including the most recent common ancestor of *Malawisaurus, Epachthosaurus, Argentinosaurus, Opisthocoelicaudia, Aeolosaurus, Alamosaurus,* Saltasaurinae, and all of its descendants. In posterior analyses, Sereno (1998) and Wilson & Upchurch (2003) claimed that Titanosauridae must be abandoned due to the type species of *Titanosaurus indicus* that is invalid. However, Salgado (2003) indicated that the name Titanosauridae, according the Phylocode, should not necessarily be abandoned, and redefined this clade again. During this controversial positions, diverse authors avoided the use of Tinanosauridae and it was replaced by others (*e.g.* Titanosauria, Titanosauroidea, Saltasauridae) (see Salgado, 2003). In this confusing context, it is important to remark that:

1) Several authors propose to replace Titanosauridae for Saltasauridae, but this last clade is less inclusive (Sereno, 1998; Wilson & Upchurch, 2003); in other words, Saltasauridae and Titanosauridae are not equivalent groups such as claimed by Salgado (2003). Saltasauridae *sensu* Sereno (1998) exclude *Malawisaurus, Mendozasaurus,* and other taxa that lack strongly procoelous middle caudals. Summing-up, all these hypothesis include few titanosaurid taxa, excluding important species like *Aeolosaurus.*

2) Tinosauridae *sensu* Salgado *et al.* (1997a) has nomenclatural priority in relation to the clade Lithostrotia proposed by Wilson & Upchurch (2003) because it was defined in the same way.
3) The new definition of Titanosauridae of Salgado (2003) excludes *Malawisaurus* because this taxon lacks strongly procoelous middle caudals. However, *Opisthocoelicaudia* has not this character and is included within Titanosauridae. In this context, we think that the definition of a clade must be founded in a group of characters supported by cladistic analyses. Moreover, the procoely of the caudal series is a variable character in titanosaurs. For example, *Rinconsaurus* shows a typical strongly procoelous caudal sequence discontinued by amphicoelous, opisthocoelous, and biconvex centra (Calvo & González Riga, 2003). On the other hand, *Mendozasaurus* has slightly procoelous middle caudal centra with reduced posterior condyles, associated with typical strongly procoelous anterior caudal vertebrae (González Riga, 2003). A particular case is observed in *Malawisaurus*, from the Lower Cretaceous of Africa. It has strongly procoelous anterior caudal centra apparently associated with gently amphicoelous or platycoelous middle and posterior caudals (Jacobs *et al.*, 1993; Gomani, 1999).

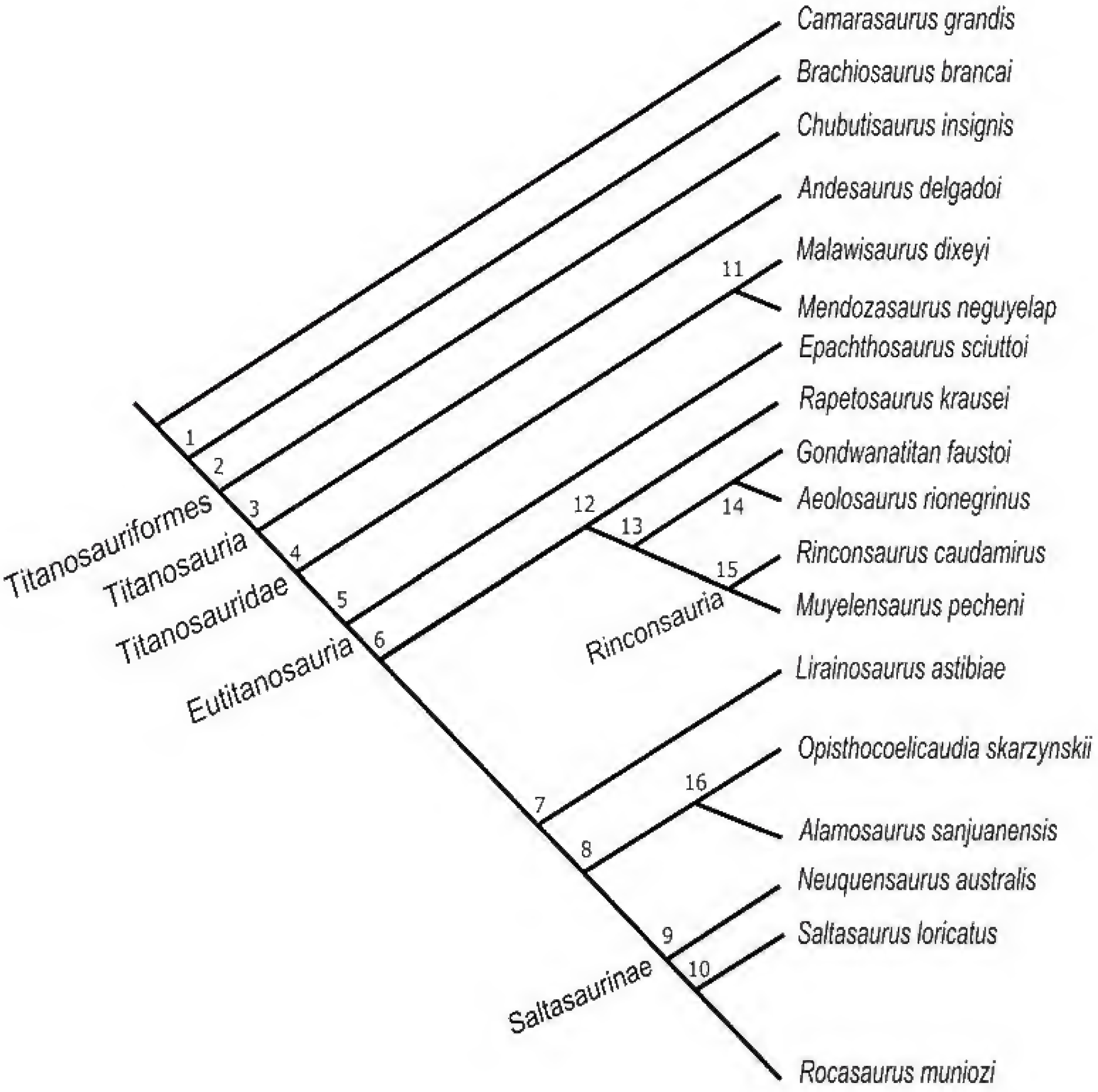

Fig.14- A most parsimonious tree determined by cladistic analysis (105 steps; CI 0.76; RI 0. 78; see matrix in Appendix) showing the phylogenetic relationships of *Muyelensaurus pecheni* gen. et sp.nov. References: Aeolosaurini (node 14), Rinconsauria (node 15), Opisthocoelicaudinae (node 16) and Saltasaurinae (node 9).

In this context, we prefer to use the original phylogenetic definition of Titanosauridae *sensu* SALGADO *et al.* (1997a), since this name has a long usage, it is compatible with the PhyloCode (CANTINO & QUEIROZ, 2000) and it is supported by a cladistic analysis of many Titanosauridae taxa.

In our phylogenetic analysis, we use 14 Titanosauridae taxa. Herein, Titanosauridae (Fig.14, node 4) is supported by 10 synapomorphies defined by delayed optimization: pencil chisel-like (8.1), absence of cervical pleurocoels divided by septa (13.1), procoelous first caudal vertebra (31.1), strongly procoelous anterior caudal centra, with prominent condyles (37.2), prezygapophyses length between 40 to 50 percent with respect to the centrum length in middle caudal vertebrae (44.1), scapular glenoid strongly beveled medially (48.1), humerus with straight or slightly curved proximal border (50.1), prominent ulnar olecranon process (51.1), semilunar sternal plates (52.1), and presence of osteoderms (65.1).

This phylogenetic analysis confirms the hypothesis proposed by GONZÁLEZ RIGA (2003) that *Malawisaurus* is the sister group of *Mendozasaurus* and these two taxa are considered basal titanosaurids.

Muyelensaurus, a more derived titanosaurid, can be clearly diagnosed as an Eutitanosauria SANZ *et al.*, 1999, but following the new phylogenetic definition of SALGADO (2003): "all titanosaurs closer to *Saltasaurus* than to *Epachthosaurus*". Within Eutitanosauria, we recognize two different clades: Aeolosaurini (FRANCO-ROSAS *et al.,* 2004) and Rinconsauria *nov.* (Fig.14, node 15).

Aeolosaurini FRANCO-ROSAS *et al.* (2004) was diagnosed by having: 1) anterior and middle caudal centra with the anterior faces inclined forward, 2) neural arches located over the anterior border in middle caudal centra, 3) middle caudal neural spines forward directed, 4) elongated prezygapophysis in middle caudals with respect to the displacement of the neural arch forward, 5) prezygapophyseal and postzygapophyseal facets elongated anteroposteriorly, at least in anterior and middle caudals. They include *Aeolosaurus, Gondwanatitan,* and *Rinconsaurus*, but they did not support it by a cladistic analysis. However, *Rinconsaurus* lacks characters 1, 2 and 3, and the 4 and 5 are difficult to evaluate; for this reason *Rinconsaurus* should be excluded.

The most important aspect of our analysis is the definition of a new clade named herein Rinconsauria (node 15) that includes *Rinconsaurus* and *Muyelensaurus*. Both taxa are relatively slender and middle-sized Eutitanosauria that have suboval teeth with labial and lingual faces well differentiated by crests, bony processes that support the postzygapophyseal facets in middle caudal vertebrae, and posterior caudal centra depressed posteriorly. The robustness of the Rinconsauria node was valued by bootstrap and jackknife indices that reach values of 90 and 74, respectively.

The finding of *Muyelensaurus* allows us to improve the diagnosis of *Rinconsaurus caudamirus* (CALVO & GONZÁLEZ RIGA, 2003) as the following association of features: neural spines in mid-anterior dorsal vertebrae inclined posteriorly more than 60 degree with respect to the vertical; anterior caudal vertebrae with bony processes that support the postzygapophyseal facets; accessory centroparapophyseal lamina extended from the base of the parapophysis to the base of centrodiapophyseal lamina in posterior dorsal vertebrae; procoelous posterior caudal centra with intercalation of a series of amphycoelous-biconvex centra.

Muyelensaurus pecheni gen. et sp.nov. is characterized by the following autapomorphies: basal tubera diverge 70 degree from each other; extensive, thin and concave lamina that unites basal tubera ventrally, basioccipital condyle wider than the proximal portion of the basal tubera; posterior dorsal neural spines with large prespinal lamina reinforced by two small accessory laminae. With respect to the basal tubera, we recognized a diverse morphology. For example, the basal tubera of *Rapaetosaurus* (FMNH PR 2197; CURRY ROGERS & FORSTER, 2004) diverge 55 degree and lacks a concave ventral lamina. *Nemegtosaurus* (NOWINSKI, 1971) shows basal tubera that diverge less than 30 degree and they have not an extensive ventral lamina. In similar way, *Quaesitosaurus orientalis* (KURZANOV & BANNIKOV, 1983) shows basal tubera that diverges 45 degree and have a fossa under the basioccipital. Moroever, the basal tubera are not well differenciated to robust basipterygoid processes. In an unnamed titanosaurid from Patagonia (MUCPv 334; CALVO & KELLNER, 2006), the basal tubera diverge 50 degree, and are united ventrally by a thick bony bridge. In *Antarctosaurus septentrionalis* (CHATTERJEE & RUDRA, 1996), the basal tubera are very separated from each other, but not diverge from the basioccipital. Moreover, the basal tubera are not united by a slightly concave ventral lamina, and show facets divided ventrally in two small processes. In unnamed titanosauriform from Texas (TIDWELL & CARPENTER, 2003), the basal tubera diverge only 15 degree and are relatively short and robust, and lack the bony lamina. In *Bonatitan reigi* (MCN-PV RN 821; Martinelli & Forasiepi, 2004), the basal tubera diverge less than 60 degree and lack the ventral lamina. Finally, complete different are basal tubera present in *Titanosaurus indicus* (Chatterjee & Rudra, 1996) because they are subdued and completely fused with the basipterygoid process.

The discovery of *Muyelensaurus* shows that the eutitanosaurs from Patagonia form a new clade named herein Rinconsauria, that include small and middle-sized sauropods different from the Aeolosaurini taxa (*Aeolosaurus* and *Gondwanatitan*) as well as from more derived species belonging to the clade Opisthocoelicaudiinae (McIntosh, 1990) and Saltasaurinae (Salgado *et al.,* 1997a).

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APPENDIX:

TABLE 1

In the Character-Taxon Matrix is shown the distribution of 65 characters corresponding to 17 taxa of sauropods. Characters have been defined or modified by the authors cited in the list.

CHARACTER	TAXON MATRIX						
Camarasaurus grandis	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	00000
Brachiosaurus brancai	0001000110	1000001001	0100100000	0000000010	0000000000	0000000010	11100
Chubutisaurus insignis	??????????	??????????	????2?0001	?0??00001?	????0???00	????0?????	?111?
Andesaurus delgadoi	??????????	??????????	?1?0111011	?0?0001010	0010000?0?	????1110??	?01??
Malawisaurus dixeyi	???????210	?11000?00?	?1?0211111	??10002010	0?11000???	1110??10??	???11
Mendozasaurus neguyelap	??????????	??1010?122	?10?2??111	?110002110	0111000101	111?1?????	?0111
Epachthosaurus sciuttoi	??????????	??????????	?111211011	11?0002210	0011000101	11??11??11	1011?
Rapetosaurus krausei	1110111212	201000100?	1111211111	1?00002210	010?000101	110??11011	101?1
Lirainosaurus astibiae	???????21?	??????????	?1?1211111	?11?002210	0000000?01	?101??????	?01?1
Rinconsaurus caudamirus	???????211	?010001011	?111211111	1???002210	0101011101	1101111111	101??
Muyelensaurus pecheni	1110111211	?11000?011	?111211111	1?0?002210	0201011101	110?111111	1011?
Gondwanatitan faustoi	??????????	??????????	?111211111	11???12220	1002001?0?	??????0111	???1?
Aeolosaurus rionegrinus	???????212	??????????	?1??2?????	?30?012220	1102001?01	?10?1101??	??11?
Opisthocoelicaudia skarzynskii	??????????	??????????	1011210111	1211000010	0200000111	1101111111	1011?
Alamosaurus sanjuanensis	???????2?2	?010001001	?1?1200111	1311002210	0200000101	1111111211	1011?
Neuquensaurus australis	??????????	?011001012	?111211111	131?102211	0200000101	11011?1211	1?111
Saltasaurus loricatus	1?10010212	?001011012	?111211111	110?102211	0200100112	1101111211	10111
Rocasaurus muniozi	??????????	??????01?	?111211111	????102211	0?00100???	????11211	1?1??

LIST OF CHARACTERS

1. Frontal contribution to supratemporal fossa: absent (0); present (1) (WILSON & SERENO, 1998).
2. Parietal occipital process, dorsoventral height: deep, nearly twice the diameter of the foramen magnum (0); short, less than the diameter of the foramen magnum (1) (WILSON, 2002).
3. Parietal, contribution to post-temporal fenestra: absent (0); present (1) (WILSON, 2002).
4. Parietal, distance separating supratemporal fenestrae: less than (0); or twice (1); the long axis of supratemporal fenestra (WILSON, 2002).
5. Supraoccipital, height: twice (0); subequal (1); or less (2) than height of foramen magnum (WILSON, 2002).
6. Paroccipital process, ventral non-articular process: absent (0); present (1) (WILSON, 2002).
7. Longitudinal groove on the supraoccipital: absent (0); present (1) (CURRY ROGERS, 2005).
8. Tooth shape: spoon-like (0); compressed cone chisel-like (1); pencil chisel-like (2) (modified from CALVO, 1994 by CALVO & GONZÁLEZ RIGA, 2003).
9. Wear facets of teeth sharply inclined: absent (0); present (1) (SALGADO & CALVO, 1997).
10. Tooth crowns, cross-sectional shape at mid-crown: D-shaped (0); subcylindrical with smooth crest (1); cylindrical (2) (modified from WILSON & SERENO, 1998).
11. Cervical vertebrae, number: 12 (0); 13 (1); 14 o more (2) (UPCHURCH, 1998).
12. Pleurocoels in anterior and middle cervical vertebrae: present (0); absent (1) (modified from CALVO & SALGADO, 1995). 13. Cervical pleurocoel divided by lamina or septa: present (0); absent (1) (UPCHURCH, 1998).
14. Cervical prezygapophyses, relative length: articular facets that surpass (0); or not surpass (1) the centra (SALGADO *et al.*, 1997a).
15. Posterior cervical neural spines lateraly expanded and wider than the centra: absent (0); present (1) (GONZÁLEZ RIGA, 2005).
16. Neural spines in cervical vertebrae: tall (0); small (1) (modified from CALVO & SALGADO, 1995).
17. Anterior cervical neural spines: bifid (0); single (1) (UPCHURCH, 1998).
18. Posterior cervical vertebrae, proportions - ratio total height / centrum length: less (0); or more (1) than 1.5 (modified from CALVO & SALGADO, 1995 by GONZÁLEZ RIGA, 2005).

19. Supradiapophyseal fossa in posterior cervical vertebrae: absent (0); shallow or reduced (1); deep and extended (2) (González Riga, 2005).
20. Posterior cervical centra, proportions: ratio anteroposterior length / height of posterior face: >3 (0); between 2,5 and 1,5 (1); less than 1,5 (2) (modified from Wilson, 2002).
21. Dorsal vertebrae, number: 12 (0); 11 (1) (McIntosh, 1990).
22. Anterior dorsal neural spines, shape: bifid (0); single (1) (McIntosh, 1990).
23. Anterior dorsal neural spines inclined posteriorly more than 20 degree from vertical: absent (0); present (1) (modified from Wilson & Sereno, 1998).
24. Posterior dorsal neural spines, dorsal development: more (0); or less (1) than 20 percent of the total height of the vertebra (modified from Sanz *et al.*, 1999 from González Riga, 2003).
25. Prespinal lamina in dorsal vertebrae: absent (0); present in the distal end of neural spine (1); present all along the neural spine (2) (Salgado *et al.*, 1997a).
26. Centroparapophyseal lamina in posterior dorsal vertebrae: absent (0); present (1) Bonaparte & Coria, 1993).
27. Ventrally widened or slightly forked centrodiapophyseal laminae in posterior dorsal vertebrae: absent (0); present (1) (Salgado *et al.*, 1997a).
28. Hyposphene-hypantrum articulation in dorsal vertebrae: present (0); absent (1) (Salgado *et al.*, 1997a).
29. Pleurocoels in dorsal vertebrae, shape: circular or elliptical (0); posteriorly acuminate (1) (Salgado *et al.*, 1997a).
30. Camellate or somphospondylous types of internal structures of presacral vertebrae: absent (0); present (1) (modified from Wilson & Sereno, 1998 by González Riga, 2003).
31. Sacral vertebrae, number: five (0); six or more (1) (McIntosh, 1990).
32. First caudal vertebrae, type: platycoelous (0); procoelous (1); opisthocoelous (2); biconvex (3) (Salgado *et al.*, 1997a).
33. Wide and deep interzygapophyseal cavity in caudal vertebrae: absent (0); present (1).
34. Caudal transverse processes: disappear by caudal 15 (0); disappear by caudal 10 (1) (Wilson, 2002).
35. Anterior and middle caudal centra, proportions: as high as wide (0); depressed, wider than high (1) (Salgado *et al.*, 1997a).
36. Mid caudal centra with the anterior face strongly inclined anteriorly: absent (0); present (1) (Franco-Rosas *et al.*, 2004).
37. Articular face shape on anterior caudal centra: non-procoelous (0); slightly procoelous (1); strongly procoelous with prominent condyles (2) (modified from Salgado *et al.*, 1997a by González Riga, 2003).
38. Articular face shape on middle caudal centra: non-procoelous (0); slightly procoelous with reduced condyles (1); strongly procoelous with prominent condyles (2) (modified from Salgado *et al.*, 1997a by González Riga, 2003).
39. Neural arch in anterior caudal vertebrae: placed in the middle of the centrum (0); anteriorly (1); on the anterior border (2) (Salgado *et al.*, 1997a).
40. Anterodorsal border of neural spine in middle caudal vertebrae located posteriorly with respect to anterior border of the postzygapophyses: absent (0); present (1) (Salgado *et al.*, 1997a).
41. Anteriorly directed anterior caudal neural spine: absent (0); present (1).
42. Shape of the section of neural spines in most anterior caudal vertebrae in dorsal view: axially elongated (0); transversely elongated (1); quadrangular (2).
43. Neural spine in middle caudal vertebrae, shape: short anteroposteriorly (0); laminated and anteroposteriorly elongated (1) (modified from González Riga, 2003 by Bonaparte *et al.*, 2006).
44. Length proportions of prezygapophyses with respect to the centrum length in middle caudal vertebrae: shorter than 50 %(0); between 40 to 50% (1); longer than 50 % (2) (modified from González Riga, 2003).
45. Ventral depression divided by a longitudinal septum in anterior and middle caudal vertebrae: absent (0); present (1) (Salgado & Azpilicueta, 2000).
46. Postzygapophyseal process in middle caudal vertebra: absent (0); present (1).
47. Well developed interprezygapophyseal lamina in middle caudal vertebrae: absent (0); present (1).
48. Scapular glenoid orientation: relatively flat (0); strongly beveled medially (1) (Wilson and Sereno, 1998).
49. Humerus, breadth of proximal end with respect to the total length: less (0); or more (1) than the 50 percent (González Riga, 2003). 50. Humerus, type of proximal border: strongly curved (0); straight or slightly curved (1); sigmoidal (2) (modified from Upchurch, 1998 by González Riga, 2002).
51. Ulnar olecranon process, development: prominent, projecting above proximal articulation (0); rudimentary, level with proximal articulation (1) (Wilson and Sereno, 1998).
52. Sternal plates, shape: suboval (0); semilunar (1) (Salgado *et al.*, 1997a).
53. Semilular sternal plate with straight posterior border: absent (0); present (1) (González Riga, 2003).
54. Coracoid, shape: suboval (0); quadrangular (1) (Salgado *et al.*, 1997a).
55. Metacarpals, distal phalangeal articular facets: present (0); absent (1) (Salgado *et al.*, 1997a).
56. Pubis, length with respect to ischium length: shorter or equal (0); longer (1) (Salgado *et al.*, 1997a).
57. Ischium, posterior process twice or more the length of pubis articulation: present (0); absent (1) (modified from Salgado *et al.*, 1997a by Calvo & González Riga, 2003).

58. Ischium, iliac pedicel: short and poorly developed (0); slender and well developed (1); wide and well developed (2) (Calvo & González Riga, 2003).
59. Shape of preacetabular lobe of ilium: moderately expanded (0); broadly expanded and directed upward (1) (Salgado *et al.*, 1997a). 60. Orientation of preacetabular lobe of ilium: nearly vertical (0); nearly horizontal and laterally projected (1) (Salgado *et al.*, 1997a).
61. Relative orientation of the pubic peduncle of ilium: angled (0); perpendicular with respect to the sacral axis (1) (Salgado *et al.*, 1997a).
62. Humerus / femoral ratio of 0.90 or more: absent (0); present (1) (McIntosh, 1990).
63. Lateral bulge of femur, below the greater trochanter: absent (0); present (1) (McIntosh, 1990).
64. Distal end of tibia broader transversely than anteroposteriorly: absent (0); present (1) (Salgado *et al.*, 1997a).
65. Osteoderms: absent (0); present (1) (Sanz *et al.*, 1999).

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A PRESUMED TITANOSAURIAN VERTEBRA FROM THE LATE CRETACEOUS OF NORTH ISLAND, NEW ZEALAND [1]

(With 2 figures)

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ABSTRACT: A bone recovered from the Upper Cretaceous Maungataniwha Sandstone of North Island, New Zealand, appears to be an incomplete titanosaurian caudal centrum. The proportions of the apparently procoelous centrum suggest that it is a middle caudal. This indicates the presence of a titanosaurian sauropod in Campanian-Maastrichtian New Zealand. At this time, titanosaurians are known from South America, Africa, India, Laurasian Asia, Europe, and North America. Palaeozoogeographic considerations suggest that titanosaurians were also present in Antarctica.

Key words: Sauropoda. Titanosauria. New Zealand. Cretaceous. Maungataniwha Sandstone.

RESUMO: Uma possível vértebra de titanossauro do Cretáceo Superior de North Island, Nova Zelândia.
Um osso procedente do Arenito Maungataniwha do Cretáceo Superior de North Island, Nova Zelândia, parece ser um centro caudal incompleto de titanossauro. As proporções dessa vértebra caudal, aparentemente procélica sugerem tratar-se de uma caudal média. Isso indica a ocorrência de um saurópode titanossauro do Campaniano-Maastrichtiano da Nova Zelândia. Durante esse espaço de tempo, titanossauros habitaram a América do Sul, África, Índia, Laurásia asiática e América do Norte. Inferências paleozoogeográricas sugerem que titanossauros também viveram na Antártica.

Palavras-chave: Sauropoda. Titanosauria. Nova Zelândia. Cretáceo. Arenito Maungataniwha.

INTRODUCTION

In 1999, the junior author prepared a piece of bone found when splitting a calcareous concretion from the Upper Cretaceous Maungataniwha Sandstone, of North Island, New Zealand. It was found at the Mangahouanga Str. site Map Ref. V19 420-469, by J. Wiffen on 23 October 1999. The specimen, CD.586, is held in the New Zealand Geological & Nuclear Sciences Collections, Lower Hutt. This bone seems to be part of a procoelous or opisthocoelous vertebral centrum. We believe that it is probably an incomplete procoelous sauropod middle caudal centrum. Thus, this is the first sauropod material from New Zealand that can be identified to a level below Sauropoda and the first report of a titanosaurian from New Zealand.

RESULTS AND DISCUSSION

Occurrence

The concretion was collected from the Maungataniwha Sandstone, exposed in the valley of Mangahouanga Stream, near Hawke's Bay, North Island (Fig.1A). The Maungataniwha Sandstone appears to have been an estuarine deposit (Isaac *et al.*, 1991; Moore, 1991) on the eastern coast of Late Cretaceous New Zealand. The sandstone is Piripauan-Haumurian (Campanian-Maastrichtian) in age, but only the lower quarter is definitely Piripauan (approximately Campanian) in age, the higher levels being Piripauan or Haumurian (Moore, 1987).

From a study of the dinoflagellates at the site the age is estimated to be 73 million years (Wilson & Moore 1988; Young, 1999). Thus we consider the specimen to date from approximately the Campanian-Maastrichtian boundary.

This unit yields both a near-shore marine vertebrate fauna (Wiffen, 1981; 1983; Wiffen & Moisley, 1986) and bones of terrestrial vertebrates (Wiffen, 1996, and citations therein), as well as a few insects (Craw & Watts, 1987; Wiffen, 1996). The terrestrial vertebrate fauna includes pterosaurs (Wiffen & Molnar, 1988), non-avian theropods (Molnar & Wiffen, 1994), possibly an avian (Scarlett & Molnar, 1984), an ornithopod (Wiffen & Molnar, 1989), a nodosaur

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(MOLNAR & WIFFEN, 1994), a sauropod (MOLNAR & WIFFEN, 1994) and, possibly, a freshwater turtle (WIFFEN, 1996) – none of these identifiable more exactly.

The report of a sauropod rests on a single incomplete bone, a piece of rib 380mm long, and probably deriving from a bone a meter or more in length. The size, degree of curvature and form and position of a flange-like shelf along the lateral margin of the bone all more closely match the situation seen in some sauropod dinosaurs (MOLNAR & WIFFEN, 1994), than in any other large Cretaceous tetrapods.

COMPLETENESS

In order to facilitate describing the completeness of this element, the conclusion that it represents a sauropod caudal will be assumed. The posterior articular face, a small part of the dorsal region and much of the left side are preserved (Fig.2A-2D). Most of the surficial bone is missing, revealing a coarse spongy texture, but in two places, both on the left side of the bone, small patches (of at most 10 by 25mm) of lamellar bone are exposed. The posterior face, although worn, shows lamellar bone over at least 75% of the surface, indicating that this region preserves its original form. A concave surface anteriorly may represent part of the anterior articular face.

TAPHONOMY

The bone was completely enclosed in the concretion and was severely worn when exposed during acid preparation, indicating that the breakage and wear occurred prior to burial, or at least lithification of the sediments. Bones of marine saurians found at this site do not show comparable wear (unless exposed at the surface of a concretion). The condition of the caudal suggests that it was exposed subaerially for some time prior to its transport into the area where it was preserved, and hence that it probably derived from a land-dwelling, rather than a marine, animal.

DESCRIPTION

The form of the bone as preserved is basically that of a low, truncate cone, the condyle, from which projects a thick, flattened shelf with a mildly concave face at the end away from the condyle (Fig.2A-2D).

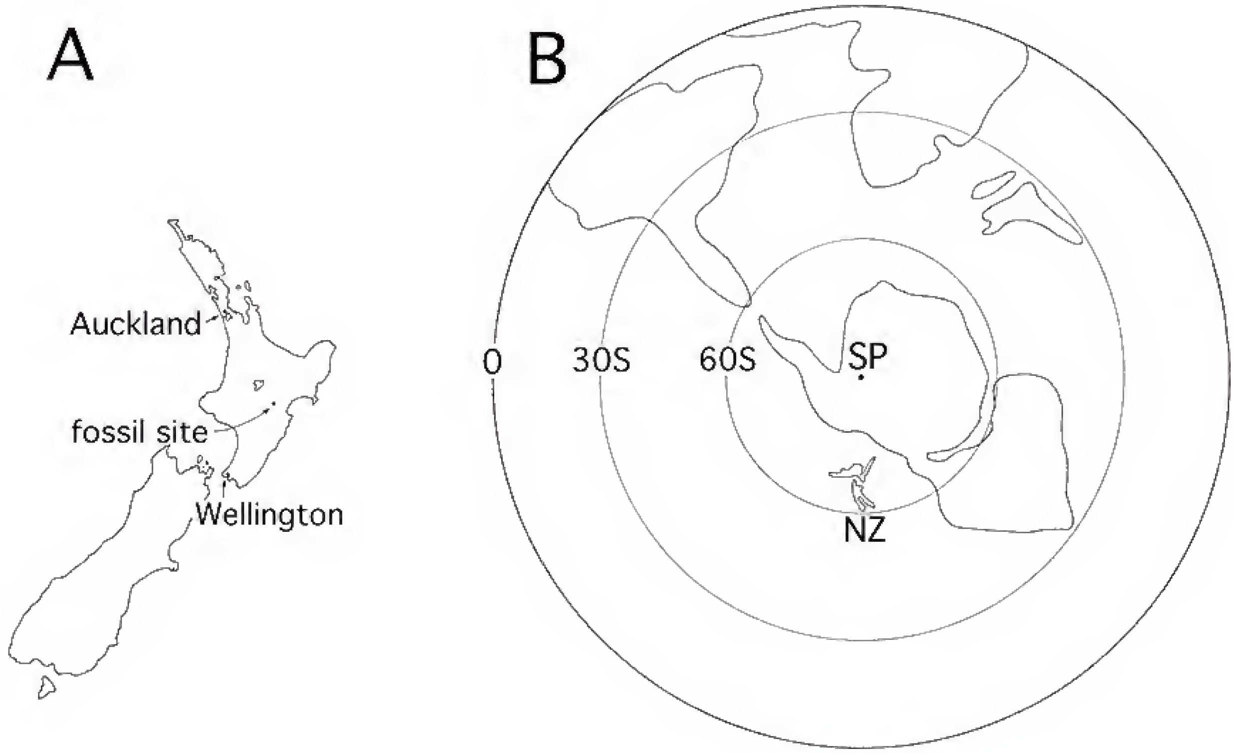

Fig.1. (A) New Zealand, showing the location of the exposures of the Maungataniwha Sandstone, at Mangahouanga Stream, North island. (B) The palaeoposition of New Zealand (NZ) during the Maastrichtian, in south polar projection, based on COOPER *et al.* (1982). SP: South Pole. (After MOLNAR & WIFFEN, 1994).

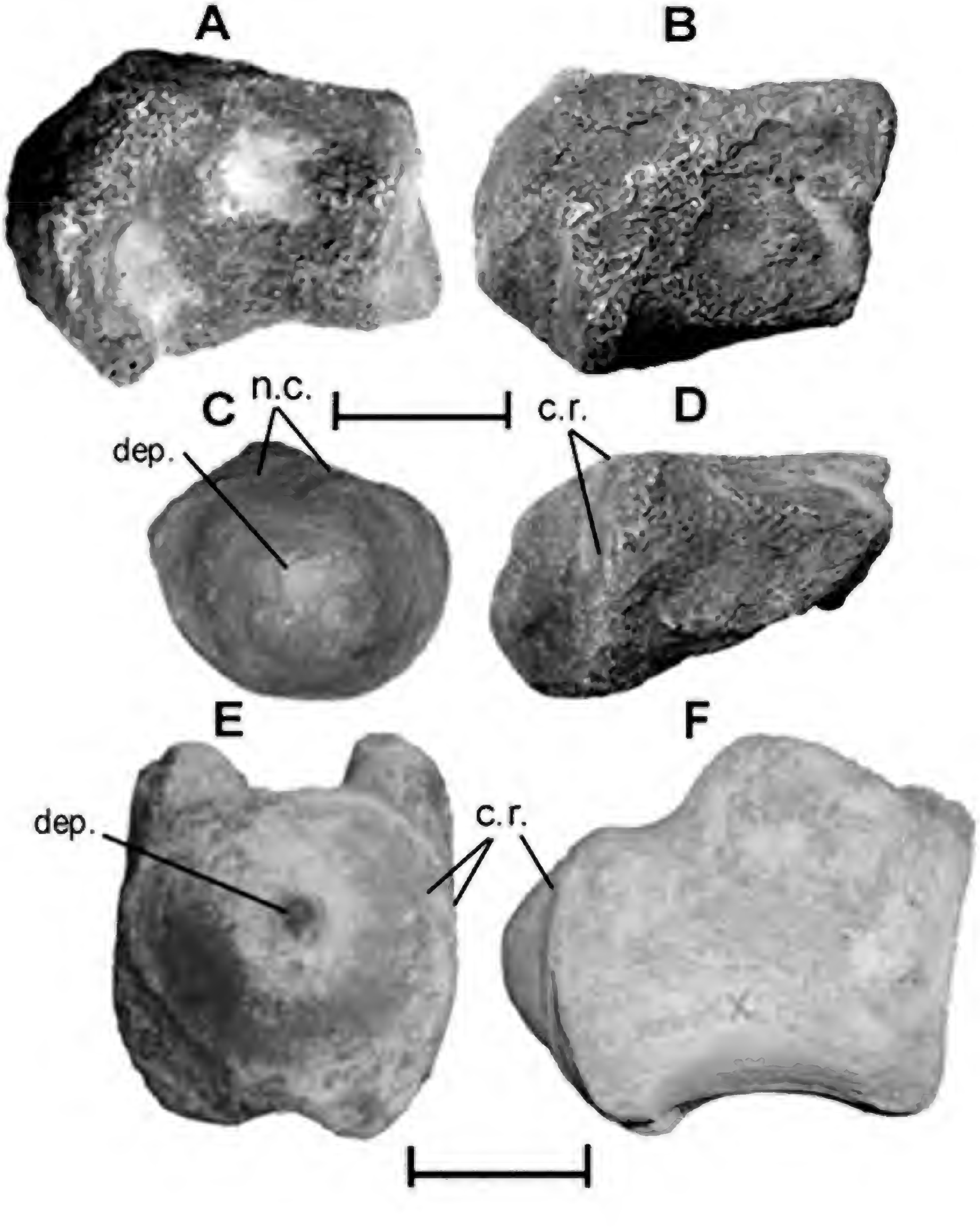

Fig.2. The fossil titanosaurian caudal centrum (CD.586) from Mangahouanga Stream (A-D) compared with an unidentified titanosaurian caudal (MACN unnumbered) from Argentina (E-F). (A) Ventral view, showing two cavities (light regions) in the centrum; (B) dorsal view; (C) posterior view; (D) right lateral view; (E) posterior view; (F) left lateral view, reversed for comparison. The conical forms of the condyles can be seen in outline in A, B, D, and F. The depression at the apex of the condyle of CD.586 retains some matrix and hence is light in color, but that of the MACN caudal is dark from shadow. The photos are of a cast of the specimen. Abbreviations: (c.r.) circumferential rim; (dep.) apical depression; (n.c.) base of neural canal. Scale bars = 50mm.

As mentioned above, this shelf is composed of spongy bone, and the condyle is surfaced with lamellar bone. The condyle is almost conical in form, with a small, but distinct, depression of 17 by 16mm at the apex. One segment of the edge of the condyle is indented by a shallow groove. Unlike the rest of the edge, spongy bone is exposed here. This presumably indicates the posterior termination of the neural canal, and is the basis for identifying the dorsal direction of the bone (Fig.2C). In two places around its circumference, the condyle retains a kind of flange or rim 14mm wide (measured radially parallel to its surface), altogether circumscribing about half of the circumference (Fig.2D). Viewed from above or below, the slopes of the condyle are straight and make an angle of about 85°. From the side, the dorsal slope is straight, and the ventral slightly rounded, but this is due to erosion along the ventral edge, where spongy bone is exposed. These slopes make an angle of 90º.

The articular face is about 91mm broad, and was at least 70mm deep. If the rim continued all around the condyle with the same width, the height would have been approximately 95mm. If the smoothly concave surface represents part of the anterior articular face, then the length of the centrum would have been approximately 122mm, and the proportions those of a middle caudal centrum.

The broken surface of the body of the centrum suggests that two internal cavities were present, or perhaps a single subdivided cavity (Fig.2A). If the groove mentioned above indicates the neural canal, then the septum between the two chambers would be orientated almost in the sagittal plane (deviating by about 10º).

IDENTIFICATION

The Maungataniwha Sandstone is a marine unit that has yielded sauropterygian, mosasaurian, and turtle remains: could this specimen represent one of these? This seems unlikely. Cretaceous sauropterygians are not known to have had procoelous or opisthocoelous vertebrae. The only well-preserved part of the specimen is the condyle, so only condylar characters can be used in the comparisons. In mosasaur vertebrae generally the condyle is more nearly hemispherical in form, and the central depression and rim are absent (see, for example, figures in LINGHAM-SOLIAR, 1994a, 1994b; WIFFEN, 1980, 1990).

The specimen seems quite large for a turtle, although giant marine turtles (e.g., *Archelon* and *Cratochelone*) were present during the Cretaceous. Turtles may have procoelous or opisthocoelous cervicals or caudals (ROMER, 1956). The cervicals of marine turtles lack the condylar rim and central depression (e.g., plates 31-33 of ZANGERL, 1960). Cretaceous marine turtle caudals in the collections of the Museum of Northern Arizona suggest that the condyles were substantially less projecting, and bordered ventrally by a more extensive flat face of the centrum. Furthermore, we feel that the great size of the animal to be inferred if this bone represents a cervical or caudal vertebra of a marine turtle, makes identification as dinosaurian the more parsimonious.

The size of this piece alone suggests that it might be dinosaurian. Of dinosaurs, only sauropods exhibit procoelous vertebrae, but some theropods and ornithopods, as well as sauropods, have opisthocoelous vertebrae. Small, basal ornithopods have weakly opisthocoelous (or non-opisthocoelous) centra (NORMAN *et al.*, 2004) and hence differ from that described here. Large ornithopods such as *Iguanodon* (NORMAN, 1980, 1986), *Ouranosaurus* (TAQUET, 1976), *Muttaburrasaurus* (MOLNAR, 1996), and hadrosaurs (LULL & WRIGHT, 1942) have opisthocoelous cervicals and anterior dorsals, although those of *Muttaburrasaurus* are but mildly opisthocoelous. Again, as with the forms previously considered, the condyle is not conical, but rounded, and lacks the circumferential rim and central depression.

Large theropods also have opisthocoelous cervicals (HOLTZ *et al.*, 2004), but again the condyles differ in form, and lack the rim and central depression. Sauropod cervicals lack the circumferential rim and central depression of the condyle, although some cervicals (e.g., those of *Rhoetosaurus brownei*) may have a central condylar projection, and they often have more extensive internal chambers than seen here. Anterior dorsals may be opisthocoelous, and although some may have conical condyles (*Saltasaurus loricatus*, Pl.26, POWELL, 2003) or appear to have circumferential rims (*Neuquensaurus australis*, Lam. 3, HUENE, 1929), these characters do not seem to occur together, and none show a central depression of the condyle. As far as we can determine from the literature, conical condyles and rims (or apparent rims), occur only in titanosaurians.

The opisthocoelous caudals of *Opisthocoelicaudia skarzynskii* lack the circumferential rim, although they do seem to have a conical, rather than rounded, condyle (BORSUK-BIALYNICKA, 1977). Published figures suggest that procoelous titanosaurian vertebrae may exhibit rounded or conical condyles. For example, viewed from the side the condyles of at least some middle caudals of *Iuticosaurus valdensis* (Fig.19 of

Wilson & Upchurch, 2003), *N. australis* (Pl.58 of Powell, 2003) and *S. loricatus* (Pls.52-53 of Powell, 2003) appear hemispherical (or nearly so) in form, and at least some of *Iuticosaurus lydekkeri* (Fig.19 of Wilson & Upchurch, 2003), *Laplatasaurus araukanicus* (Figs.8-9 of Lam.22 of Huene, 1929), *Aeolosaurus rionegrinus* (Pl.11 of Powell, 2003) and *Magyarosaurus dacus* (Fig.19 of Wilson & Upchurch, 2003) appear to be conical. So far as we have been able to determine conical condyles, circumferential rims and central depressions are found together only in titanosaurian caudals. Circumferential rims may be seen in *Magyarosaurus dacus* (Fig.19 of Wilson & Upchurch, 2003), *S. loricatus* (Powell, 2003), and *N. australis* (Powell, 2003), and a central depression in a caudal referred to *Magyarosaurus hungaricus* (Huene, 1932).

Some titanosaurian caudals in the Museo Argentino de Ciencias Naturales (MACN), particularly MACN-RN147 (attributed to *Aeolosaurus*) and MACN 15131 (*Laplatasaurus*), show conical or nearly conical condyles. Those of MACN-RN147 lack apical depressions, but one of MACN 15131 shows such a depression, as do several others, including the middle caudal of MACN 15084 and one designated 'Los Alamitos 89' (both unidentified titanosaurians). This vertebra, as well as an unnumbered centrum from the old collections (Fig.2E-F), show both a conical condyle and circumferential rim. It is this similarity that suggests to us that the Maungataniwha bone most likely represents an incomplete titanosaurian middle caudal vertebra.

Significance

The presence of titanosaurians in Cretaceous New Zealand is not especially surprising, although actually finding a (likely) specimen is gratifying. During most of the Cretaceous, New Zealand was part of what is now Antarctica, separating from it at approximately the beginning of the Campanian (Cooper & Millener, 1993). Thus the Maungataniwha tetrapods lived after the separation, and represent an insular fauna from high southern latitudes (Fig.1B) (Molnar & Wiffen, 1994). Late Cretaceous titanosaurians are known from central and western Europe, the U.S.A., China, Mongolia, India, north Africa, Madagascar, South America (Wilson & Upchurch, 2003), and Australia (Molnar, 2001). So, their appearance in New Zealand (then part of Antarctica) between the African and South American regions of Gondwanaland on the one hand, and the Australian on the other, is not unexpected.

Of more local interest is that this is only the second dinosaurian specimen from New Zealand that can be identified to a lower systematic level than Sauropoda. In view of the lack of knowledge of the details of the distribution among titanosaurians of the characters used here to identify the bone, no special relationship to forms such as *Aeolosaurus* and *Laplatasaurus* can be proposed without the discovery of further material.

Furthermore, Wilson & Upchurch (2003) indicate that the distributions of supposedly widespread titanosaurian taxa (e.g., *Laplatasaurus* and *Titanosaurus*) were much less broad than previously believed. However, the occurrence in New Zealand makes the habitation of Antarctica by related sauropods in the Late Cretaceous nearly certain.

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We wish to thank Dr. José Bonaparte for his kind permission to study and photograph titanosaurian caudals in the collections of the Museo Argentino de Ciencias Naturales. Alexander W. A. Kellner helpfully arranged access to titanosaur caudals in the Museu Nacional, Rio de Janeiro. Janet Whitmore Gillette kindly provided access to the marine turtle material in the Museum of Northern Arizona. We also appreciate the assistance of J. Calvo, D. Riff and two anonymous referees. And finally our thanks to Carter, Holt Harvey for continued access to the fossil site.

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ANATOMY OF *FUTALOGNKOSAURUS DUKEI* CALVO, PORFIRI, GONZÁLEZ RIGA & KELLNER, 2007 (DINOSAURIA, TITANOSAURIDAE) FROM THE NEUQUÉN GROUP (LATE CRETACEOUS), PATAGONIA, ARGENTINA [1]

(With 20 figures)

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ABSTRACT: Titanosaurs are among the largest dinosaurs known to date. Here we describe the anatomy of *Futalognkosaurus dukei*, the most complete giant sauropod ever found. It comes from outcrops of the Portezuelo Formation at the Barreales lake, some 90 km northwest of Neuquén city (Patagonia). The specimen consists of a complete neck, dorsal vertebrae with ribs, pelvis, and one caudal vertebra. *Futalognkosaurus dukei* is a member of the Titanosauridae and belongs to the Lognkosauria, a clade that includes *Mendozasaurus neguyelap* and probably also the giant *Puertasaurus reuili*.

Key words: Dinosauria. Titanosauridae. Lognkosauria. Neuquén Basin. Patagonia. Argentina.

RESUMO: Anatomia de *Futalognkosaurus dukei* Calvo, Porfiri, González Riga & Kellner, 2007 (Dinosauria, Titanosauridae) do Grupo Neuquén (Cretaceous Superior), Patagônia, Argentina

Titanossauros são alguns dos maiores dinossauros conhecidos. Neste trabalho descrevemos a anatomia de *Futalognkosaurus dukei*, o mais completo dos saurópodes de grande porte encontrado até a presente data. O material é procedente de afloramentos da Formação Portezuelo situados no lago Barreales, situado aproximadamente a 90 km noroeste da cidade de Neuquén (Patagônia). O espécime consiste da série cervical completa, vértebras dorsais e costelas, a pélvis e uma vértebra caudal. *Futalognkosaurus dukei* é um membro de Titanosauridae e pertence ao clado Lognkosauria que inclui *Mendozasaurus neguyelap* e provavelmente também o gigantesco *Puertasaurus reuili*.

Palavras-chave: Dinosauria. Titanosauridae. Lognkosauria. Bacia de Neuquén. Patagônia. Argentina.

INTRODUCTION

During the last years, extensive field works have been carried out at the North coast of the Barreales Lake, Neuquén Province, Argentina (Fig.1). This site, named Futalognko, is located in the region known as the Proyecto Dino and has yielded a large quantity of fossils making it one of the most important dinosaur localities in South America (Calvo *et al.*, 2002a; Porfiri & Calvo, 2004, Calvo *et al.*, 2007). Among the material recovered are sauropod postcranial elements, several sauropod teeth (Calvo & Grill, 2003), indeterminate ornithopods (Porfiri & Calvo, 2002; Calvo & Porfiri, 2003), and new specimens of the theropods *Megaraptor namunhuaiquii* (Calvo *et al.*, 2002b; 2004b; Porfiri & Calvo, 2003) and *Unenlagia paynemili* (Calvo *et al.*, 2003; Calvo *et al.*, 2004a). Theropod teeth assigned to dromaeosaurids (Poblete & Calvo, 2003) and carcharodontosaurids (Veralli & Calvo, 2004) were also found. The fossil record of this site includes also fish specimens (Gallo *et al.*, 2003), crocodylomorphs (Poblete & Calvo, 2005), pterosaurs (Kellner *et al.*, 2004; 2007), angiosperms and gymnosperms (Prámparo *et al.*, 2003; Passalia *et al.*, in press). Among the most spectacular finds at the Futalognko site is a partial skeleton of the giant titanosaur sauropod *Futalognkosaurus dukei* (Calvo *et al.*, 2007) which was collected between 2000 and 2005 (Calvo,

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2000, 2006; CALVO *et al.,* 2001). The aim of this paper is to describe in detail the anatomy of this giant sauropod.

GEOLOGICAL SETTING

The Neuquén Group, of Late Cretaceous age (DIGREGORIO, 1972; CAZAU & ULIANA, 1973), includes continental deposits formed in a restricted environment. The stratigraphic sequence is composed by alternating successions of sandstones, mudstones, conglomerates, and conglomeratic sandstones (Fig.2). The Neuquén Group is divided into the following subgroups: Río Limay, Río Neuquén, and Río Colorado (RAMOS, 1981). The outcrops in the area of the Dino Project correspond to the Rio Neuquén Subgroup (SÁNCHEZ *et al.*, 2003) and the sauropod described here comes from Portezuelo Formation (Late Turonian-Lower Coniacian, after LEANZA & HUGO, 2001). Outcrops are 20 meters thick and are covered by deposits assigned to the Plottier Formation. Both formations differ showing a notable change in the proportion between channels filling with respect to floodplains deposits, suggesting distinct paleoenvironmental conditions. Moreover, there is a well differentiated fluvial system represented in those units that changes from an intermediate to a high sinuosity system (SÁNCHEZ *et al.*, 2005).

Only the upper part of the Portezuelo Formation is exposed at the Futalognko site, representing a fluvial system characterized by several variations between channels and floodplain deposits, channel design, and spatial distribution, with slightly fining upward sequences. Facies associations allow us to postulate that the upper part of the Portezuelo Formation on the Barreales Lake shows three kinds of deposits. There are well developed sandy channels with mixed-loaded fluvial system, a second fluvial system of low to moderate sinuosity with predominance of lenticular channels, and architectural elements (*sensu* MIAL, 1996) like lateral accretion and overbank facies on the floodplain. Toward the top of the unity the subsidence rate increased slightly, resulting in the development of flooding areas with established bodies of water where the dinosaur described here and other fossils were preserved. Over this sequence, a highly sinuous meandering fluvial system was installed.

The Plottier Formation is superposed to the Portezuelo Formation, being almost horizontal and showing a gradual transition from the latter.

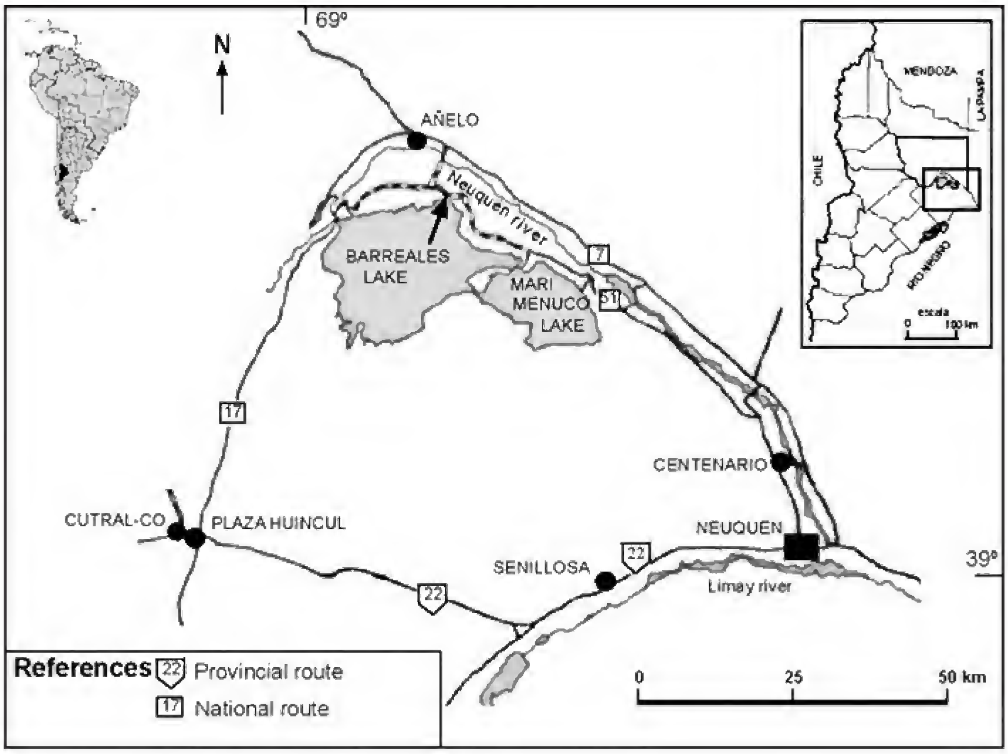

Fig.1- Map of Neuquén Province (northwest Patagonia) showing where *Futalognkosaurus dukei* was found.

A low rate between channels over floodplain deposits is found on the basal section with a high aggradational floodplain, indicating the development of an ephemeral fluvial system (Sánchez *et al.*, 2006). The restriction of the channel system may be related with the climatic conditions, probably combined with subsidence that would have temporarily controlled the system with strong aggradation of fine sediments in the floodplain, with periodic events of sheet flood and the development of shallow channels limited in their migration by the cohesiveness of the coast. Gradually, a braided fluvial system was developed, building *levees* and avulsion deposits associated with *crevasse* channels. Therefore, the Plottier Formation is characterized by a low sinuosity system and it is dominated by an intense aggradation of the floodplain (Sánchez *et al.,* 2006).

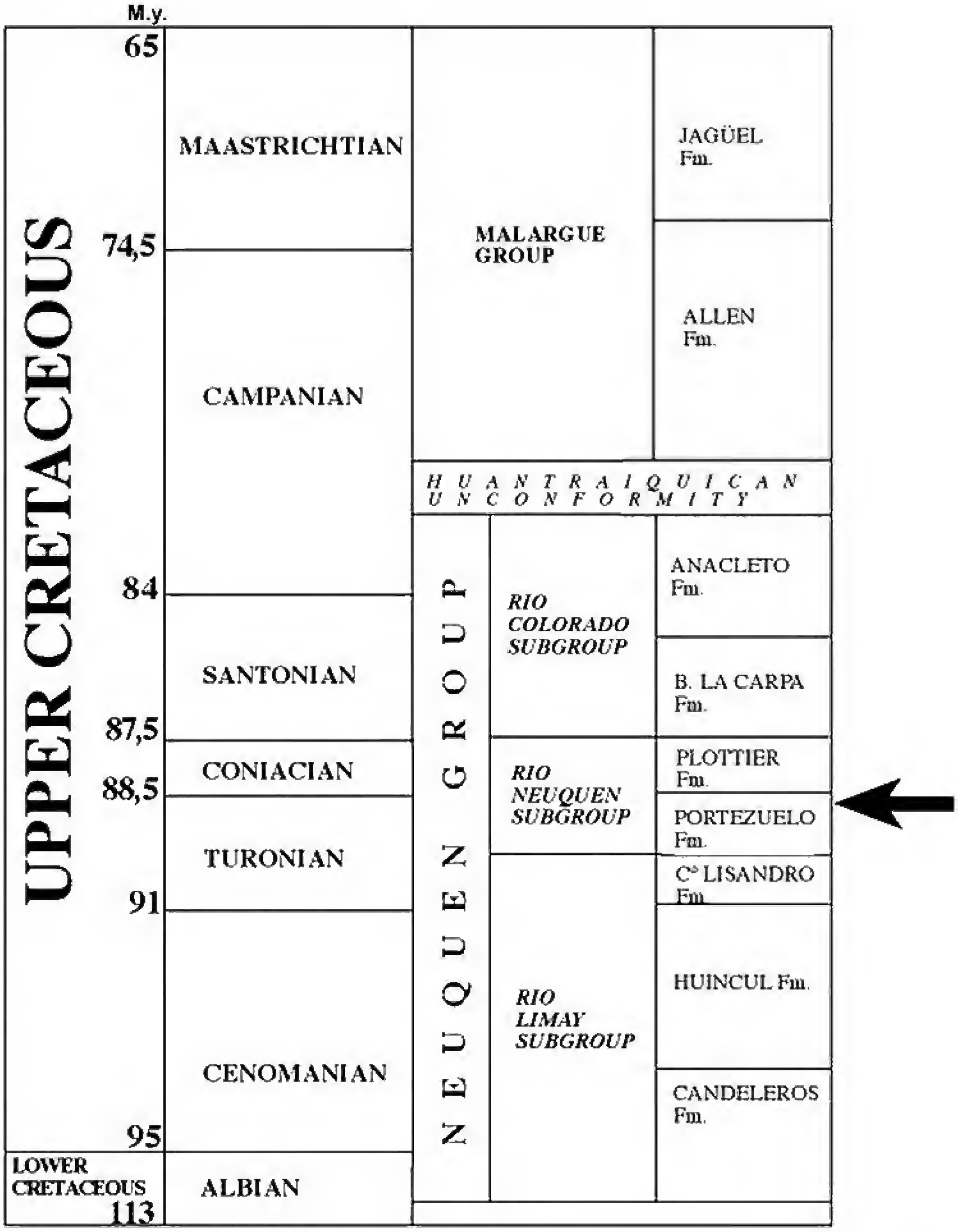

Fig.2- Stratigraphic column of the Neuquén Group (modified from Leanza & Hugo, 2001). Arrow indicates the stratigraphic position of the Futalognko site. (M.y.) millions of years.

SYSTEMATIC PALEONTOLOGY

Saurischia Seeley, 1887
Sauropodomorpha Huene, 1932
Sauropoda Marsh, 1878
Titanosauria Bonaparte & Coria, 1993
Titanosauridae Lydekker, 1893
Lognkosauria Calvo, Porfiri, González Riga & Kellner, 2007
Futalognkosaurus dukei Calvo, Porfiri, González Riga & Kellner, 2007

Holotype – Atlas, axis and five anterior, four middle and three posterior cervical vertebrae, 10 dorsal vertebrae, several ribs, complete sacrum, both ilia, right pubis and ischium, and one anterior caudal, housed at the Museo de Geologia y Paleontologia de la Universidad Nacional del Comahue under the number MUCPv-323.

Diagnosis – Neurapophyses of the atlas laminar and quadrangular, posteriorly directed; neural spine of the axis high, triangular; posterior border of the neural spine on middle cervical elements concave; ventral depression between parapophyses on middle cervical centra; anterior dorsal vertebrae with horizontal and aliform diapophysis; pre- and postzygapophyses of anterior dorsal vertebrae horizontal; first caudal vertebra with prespinal lamina bifurcated on its base forming two small infraprespinal laminae; supraspinal cavity in first caudal vertebra bordered by the prespinal and lateral laminae; 2nd and 3rd sacral ribs fused; wide and well developed iliac peduncle on ischia (Calvo *et al.*, 2007).

DESCRIPTIONS AND COMPARISONS

Cervical Vertebrae

The atlas is one of the best preserved of any known Titanosauria (Fig.3). The articulation with the occipital condyle is wider than high. In lateral view, the neural arch is displaced posteriorly (Fig.4). The neurapophyses is a thin quadrangular lamina that expands upward and curves medially, with the distal end directed posteriorly. There is no contact between both neurapophyses at the midline.

Fig.3- *Futalognkosaurus dukei*; atlas in anterior view. Scale bar =100mm. (NA) neurapophyses.

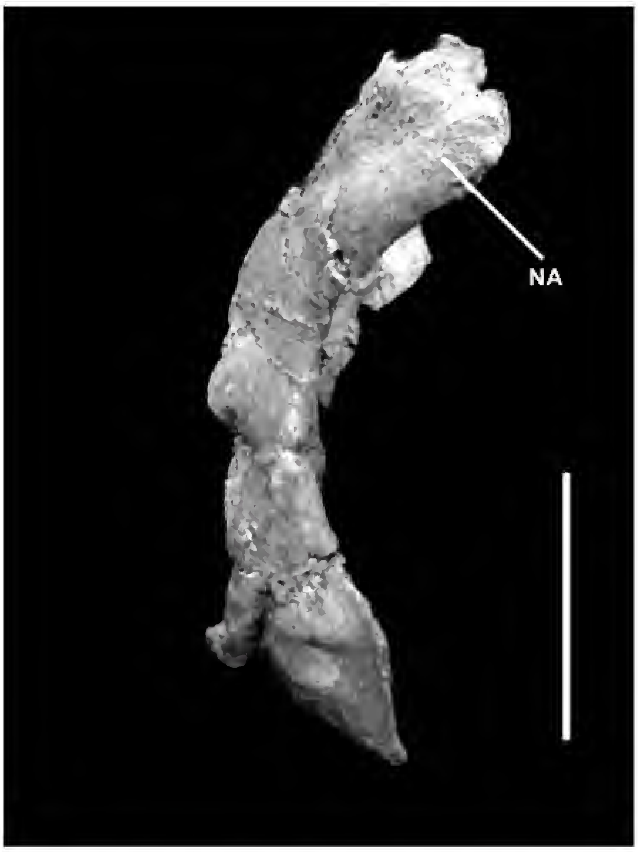

Fig.4- *Futalognkosaurus dukei*; atlas in lateral view. Scale bar =100mm. (NA) neurapophyses.

The axis has a short and high neural arch (Figs.5-6). It occupies 2/3 of the total height of this element. The odontoid process has not been preserved. The neural spine is high, robust, of triangular shape. The centrum is elongated without pleurocoels, differing from *Saltasaurus* (Powell, 1986) and *Alamosaurus* (Lehman & Coulson, 2002). Prezygapophyses were not preserved and postzygapophyses have a horizontal articulation.

All cervical vertebrae are opisthocoelous with the neural spines not bifurcated. Anterior cervical elements are longer than high (Fig.7). The triangular neural spine is robust and directed posteriorly. The third cervical vertebra has robust spinoprezygapophyseal and spinopostzygapophyseal laminae and a smooth channel is developed between them (Fig.8). On the fourth cervical, a deep channel between both spinoprezygapophyseal laminae is present, a feature observed in the following elements of the neck. This channel does not reach the top of the neural spine as observed in titanosaurid cervical sequence from Brazil known in the literature as the series A (Powell, 1987), that latter received the number MCT 1487-R (Campos & Kellner, 1999). The neural spine has a triangular shape, in lateral view, and it is compressed lateromedially but elongated anteroposteriorly as the rest of anterior cervical vertebrae.

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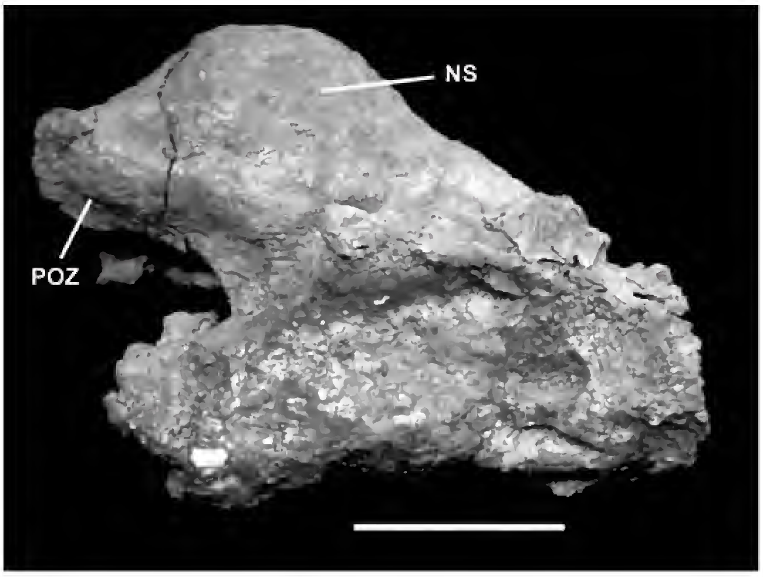

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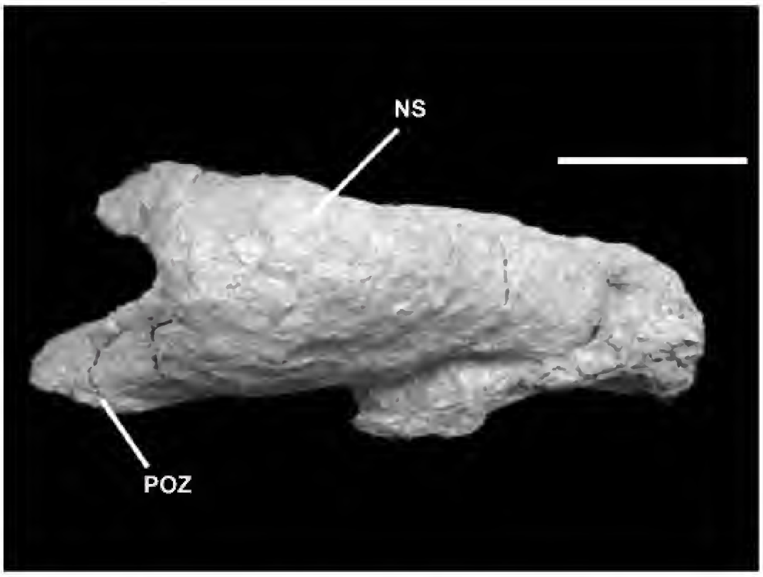
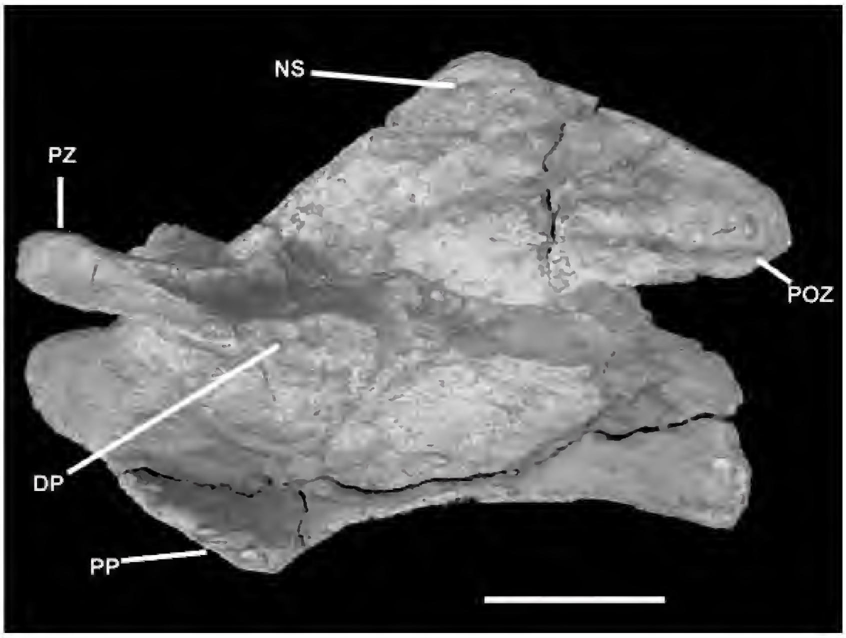


Futalognkosaurus dukei: fig.5- axis in lateral view; fig.6- axis in dorsal view. Scale bar =100mm. (POS) postspinal lamina, (NS) neural spines.

Pleurocoels are absent in all elements of the series, a feature observed in *Malawisaurus dixeyi* and in the sole cervical element known from *Gondwanatitan faustoi*, respectively from Malawi and Brazil (Jacobs *et al.*, 1993; Kellner & Azevedo, 1999). Parapophyses are laminar and restricted to the anterior portion of the centrum. The posterior centrodiapophyseal lamina is directed anterodorsally as in MCT 1487-R (Powell, 1987) and it is different to that present in *Saltasaurus loricatus* (Bonaparte & Powell, 1980). Anterior cervical vertebrae of Titanosauria are scarce in the fossil record, limiting further comparisons.

7



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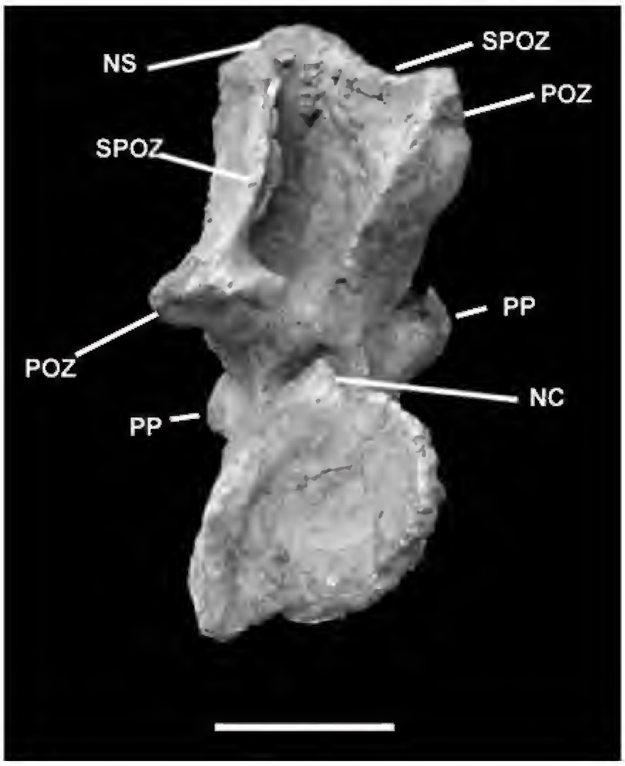

Futalognkosaurus dukei: fig.7- anterior cervical in lateral view; fig.8- anterior cervical in posterior view. Scale bar =100mm. (DP) diapophysis, (NC) neural canal, (NS) neural spines, (POZ) postzygapophysis, (PP) parapophysis, (PZ) prezygapophysis, (SPOZ) spinopostzygapophyseal lamina.

Middle cervical vertebrae are higher than long (Fig.9). The centrum lacks pleurocoels as in MCT 1487-R from Brazil, but differing from the condition reported in *Malawisaurus* and the shallow lateral pleurocoels reported by Curry Rogers & Forster (2001) in *Rapetosaurus krausei.* The prezygapophysis in *Futalognkosaurus* reaches the anterior border of the centrum, different from the condition present in MCT 1487-R and in the Saltasaurinae. The neural spine is very high and sail-shaped as in *Malawisaurus* and *Rapetosaurus*. *Futalognkosaurs* shares with *Rapetosaurus* higher neural arches in anterior and middle cervical vertebrae, three times higher than the centra. They extend over the complete length of the centra and are directed backwards. In lateral view, the spinoprezygapophyseal border is straight and the spinopostzygapophyseal margin is concave, a feature not observed in other members of the Titanosauria (Fig.9). The only taxa with similar sail-shaped neural spine is *Rapetosaurus* but it has the spinopostzygapophyseal border straight proximally and slightly concave distally. Moreover, in *Rapetosaurus* postzygapophyses are placed at middle height of the neural arch, as those present in *Rinconsaurus caudamirus* (Calvo & González Riga, 2003). In anterior view, the spinoprezygapophyseal laminae are fused on the distal end forming a deep suboval depression. This feature resembles, in some way, that present in middle cervicals of the titanosaurid MCT 1487-R from Brazil (Powell, 1987). However, in the latter, neural spines are very low with a rugose and wide distal end. Middle cervical vertebrae have a deep depression formed between the base of the neural spine and the diapopostzygapophyseal lamina (Fig.10). In ventral view, a deep depression is present on the proximal end of the centrum between the parapophyses. This depression is considered an autopomorphy of *Futalognkosaurus dukei.*

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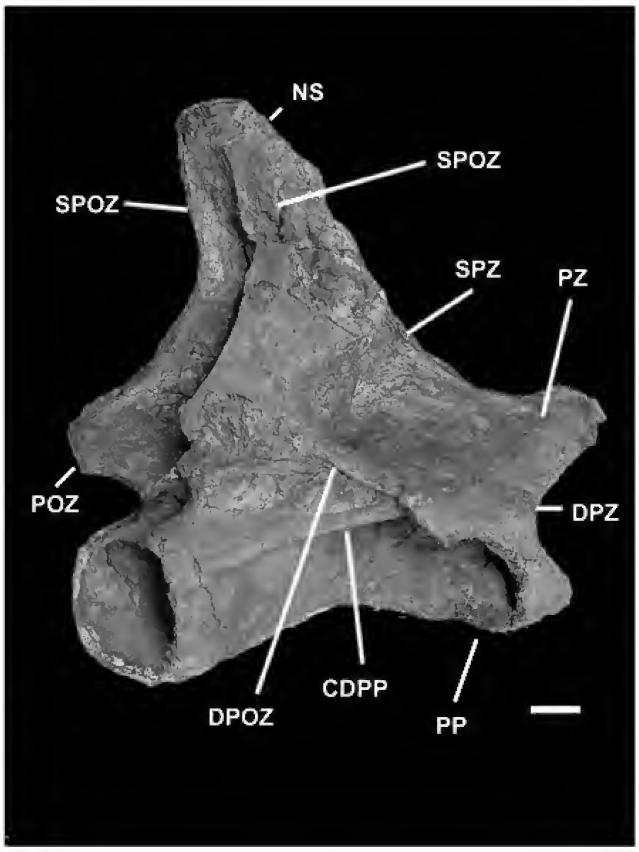

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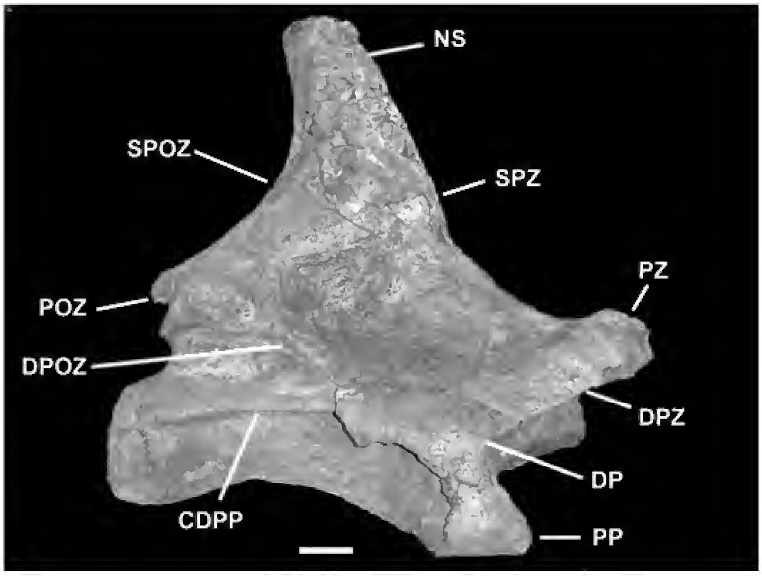

Futalognkosaurus dukei: fig 9- middle cervical in lateral view; fig.10- middle cervical in posterolateral view. Scale bar =100mm. (CDPP) centrodiapophyseal posterior lamina, (DP) diapophysis, (DPOZ) diapopostzygapophyseal lamina, (DPZ) diapoprezygapophyseal lamina, (NS) neural spines, (POZ) postzygapophysis, (PP) parapophysis, (PZ) prezygapophysis, (SPOZ) spinopostzygapophyseal lamina, (SPZ) spinoprezygapophyseal lamina..

Posterior cervicals are opisthocoelous with very elongated centra (Fig.11). Neural arches are high, being three or more times higher than the centrum, character only shared with *Mendozasaurus neguyelap* (González Riga, 2003). Neural spines are compressed proximodistally and expanded laterally as in *Puertasaurus reuili* (Novas *et al.*, 2005) and in *Mendozasaurus,* but to a lesser degree (Figs.11-12). This shape is completely different in all other titanosaurids such as *Saltasaurus*, MCT 1487-R from Brazil, and *Isisaurus colberti* (Jain & Bandyopadhyay, 1997). The neural spine is inclined slightly posteriorly, different from the condition reported in *Isisaurus colberti, Puertasaurus reuili*, and *Mendozasaurus neguyelap* that are perpendicular to the body axis. It displays an intraprezygapophyseal lamina and deep supradiapophyseal cavities as those present in *Isisaurus* and *Mendozasaurus*. In anterior view, no prespinal lamina is present (Fig.12). In *Isisaurus*, a true prespinal lamina is developed while in *Mendozasaurus* the prespinal lamina is restricted to the base of the neural arch (González Riga, 2005). Both spinoprezygapophyseal laminae in *Futalognkosaurus* are robust and reach almost the top of the neural spine (Fig.12). They are placed almost parallel to each other, leaving a slit-shaped depression between them. In *Mendozasaurus* and *Puertasaurus*, the spinoprezygapophyseal laminae are well separated and only reach the middle part of the neural spine. Other Titanosauridae such as Saltasaurinae (Powell, 1986) and Rinconsaurini (Calvo *et al.*, this volume), also show this feature, but the cavity is shallow. The last cervical vertebra (a cervicodorsal), shows a prespinal-like lamina but it does not reach the base of the neural arch. The supradiapophyseal cavity is separated by a septum from a lower depression placed on the diapophysis (Fig.13). *Futalognkosaurus dukei* differs from the giant titanosauriform *Sauroposeidon proteles* (Wedel *et al.*, 2000) which has extremely elongated cervical centra with a low neural arch, deep pleurocoels, and a deeply excavated neural spine.

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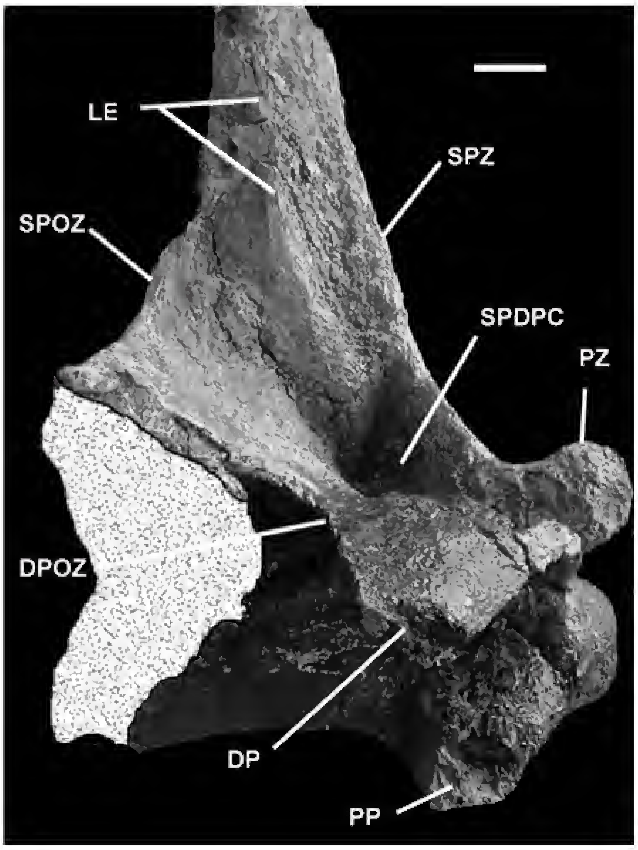

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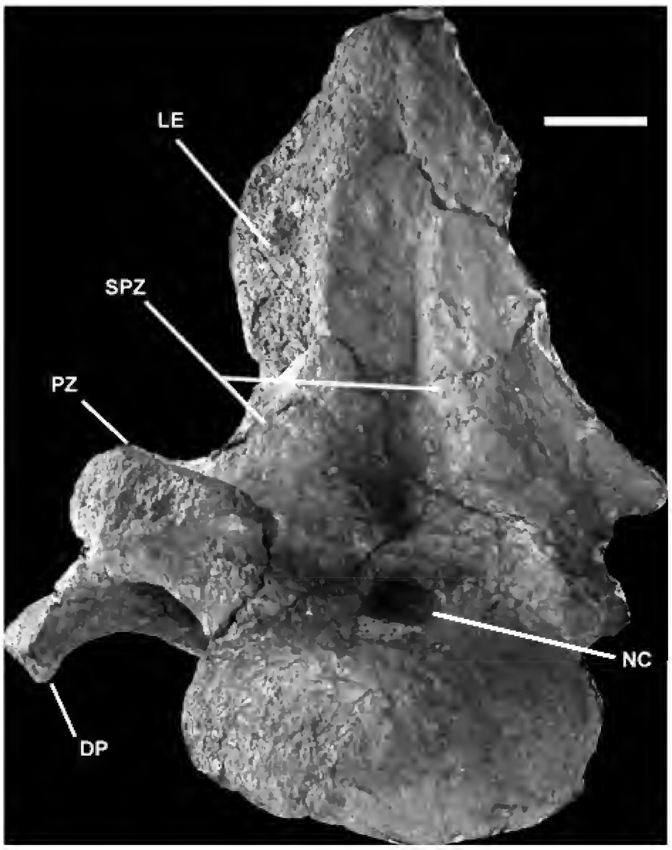

Futalognkosaurus dukei: fig.11- posterior cervical in lateral view; fig.12- posterior cervical in anterior view. Scale bar =100mm. (DP) diapophysis, (DPOZ) diapopostzygapophyseal lamina, (LE) lateral expansion, (LL) lateral laminae, (LR) longitudinal ridge, (NA) neurapophyses, (NC) neural canal, (NS) neural spines, (PC) pubis contact, (PF) pubic foramen, (POS) postspinal lamina, (POZ) postzygapophysis, (PP) parapophysis, (PS) prespinal lamina, (PZ) prezygapophysis, (SBD) spinobasaldiapophyseal lamina, (SC) supraspinal cavity, (SDP) spinodiapophyseal lamina, (SPDPC) supradiapophyseal cavity, (SPOZ) spinopostzygapophyseal lamina, (SPZ) spinoprezygapophyseal lamina, (SS) supraspinal lamina, (TP) transverse process

DORSAL VERTEBRAE

The ten articulated dorsal vertebrae are partially prepared, all being opisthocoelous (Fig.14). The most anterior dorsal has an elongated centrum and the second is 2/3 the length of the first. The centrum length gradually reduces in the more posterior elements of the sequence, with the first one being 43cm long and the last one 28cm (without considering the anterior ball). This pattern contrasts strongly with the cervical sequence of this species, where the length increases until the middle elements and then decreases slightly posteriorly. All dorsal vertebrae have eye-shaped pleurocoels. They lack hyposphene-hypantrum complex, differing from the condition observed in *Argentinosaurus huinculensis* (BONAPARTE & CORIA, 1993). All neural spines are undivided (Fig.14). Diapophyses are laminar, planar, and directed laterally, different from those of *Puertasaurus reuili* (NOVAS *et al.*, 2005) where they are dorsoventrally deep. The neural arch is transverselly width being approximately 100cm. Neural arches on the first and second dorsal vertebrae are similar to the last cervical, being slightly directed posteriorly and different to that of *Argentinosaurus* and *Puertasaurus*, that is vertically oriented. The neural spine is united with the proximal end of the diapophysis by a structure (here named spinobasaldiapophyseal lamina), and the spinopostzygapophyseal lamina (Fig.13). These laminae are directed more laterally than in the last cervical. The prespinal lamina is present along the neural spine and reaches the base of the neural arch, different from the condition observed in *Argentinosaurus*, which has a prespinal bump. A postspinal lamina is also present. The supradiapophyseal cavity is small, slit-like and placed on the neural spine (Fig.13). Starting at the third dorsal vertebra, the neural arches and neural spines are strongly inclined posteriorly (Figs. 13-14).

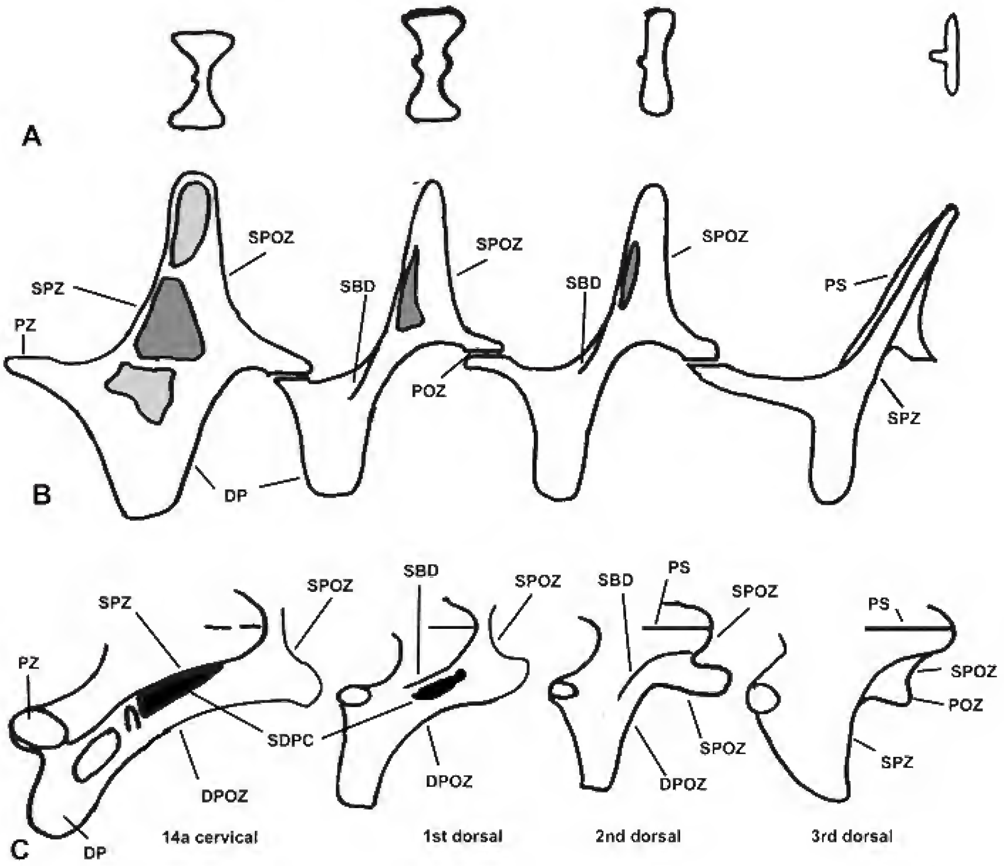

Fig.13- *Futalognkosaurus dukei*; sketch of the 14th cervical and 1st to 3rd dorsals. (A): cut section of the neural spine; (B): lateral view of the neural arches; (C) upper view of the half left neural arches. (CDPP) centrodiapophyseal posterior lamina, (DP) diapophysis, (DPOZ) diapopostzygapophyseal lamina, (POZ) postzygapophysis, (PS) prespinal lamina, (PZ) prezygapophysis, (SBD) spinobasaldiapophyseal lamina, (SPOZ) spinopostzygapophyseal lamina, (SPZ) spinoprezygapophyseal lamina.

Neural spines are reduced and not expanded distally, contrary to the condition of *Argentinosaurus*, and are narrower and more compressed anteroposteriorly than in *Mendozasaurus*. Prezygapophyses are placed almost horizontally, different from the inclined condition observed in *Mendozasaurus* and *Argentinosaurus*. In the posterior elements the spinoprezygapophyseal lamina is transformed in a spinodiapophyseal lamina (Fig.13). The supradiapophyseal cavity is reduced, placed on the neural spine and turns into a slit-like depression in dorsal 2. The well developed spinopostzygapophyseal and diapopostzygapophyseal laminae are preserved in all elements of the series. Dorsals 3 and 4 have the ventral surface of the centrum convex. From dorsal 5 to the end, the centrum has a ventral ridge, differing from the flattened condition observed in *Argentinosaurus*.

SACRUM

The sacrum is formed by six elements with a total length of 96cm (Fig.15). The width of the sixth sacral vertebra with ribs is 117cm, but including the ilium it reaches 136cm. The first sacral width, including ribs and the preacetabular laminae, is 255cm. The length of the first sacral rib from tip to tip is 200cm. They extend laterally over the upper border of the preacetabular laminae of the ilia. The centrum of the first sacral is 45cm wide and 38cm high. The sixth sacral vertebra is the longest element with the anterior surface 35cm wide and 27cm high. The first and second sacral vertebrae have the ventral surface flat, whereas in the remaining elements it is convex. *Futalognkosaurus* possesses the 2nd and 3rd sacral ribs fused, a featured not observed in any other Titanosauria (Fig.15). The last sacral has a convex posterior surface different from *Aeolosaurus rionegrinus* (POWELL, 1986), *Pellegrinisaurus powelli* (SALGADO, 1996), *Alamosaurus sanjuanensis* (GILMORE, 1946), *Neuquensaurus australis* (HUENE, 1929; POWELL, 1986), Titanosauridae indet. MCT 1536-R (CAMPOS & KELLNER, 1999), and *Opisthocoelicaudia skarzynskii* (BORSUK-BIALYNICKA, 1977).

CAUDAL VERTEBRA

Only one anterior caudal element, probably the 1st, was found so far (Figs. 16-17). It is strongly procoelous, with rounded posterior (40x40cm) and anterior (42x42cm) surfaces. The neural arch is inclined posteriorly and the transverse processes are wide, elongated dorsoventrally and directed laterally. The neural spine is distally expanded, a feature unique to *Futalognkosaurus* (Fig.16).

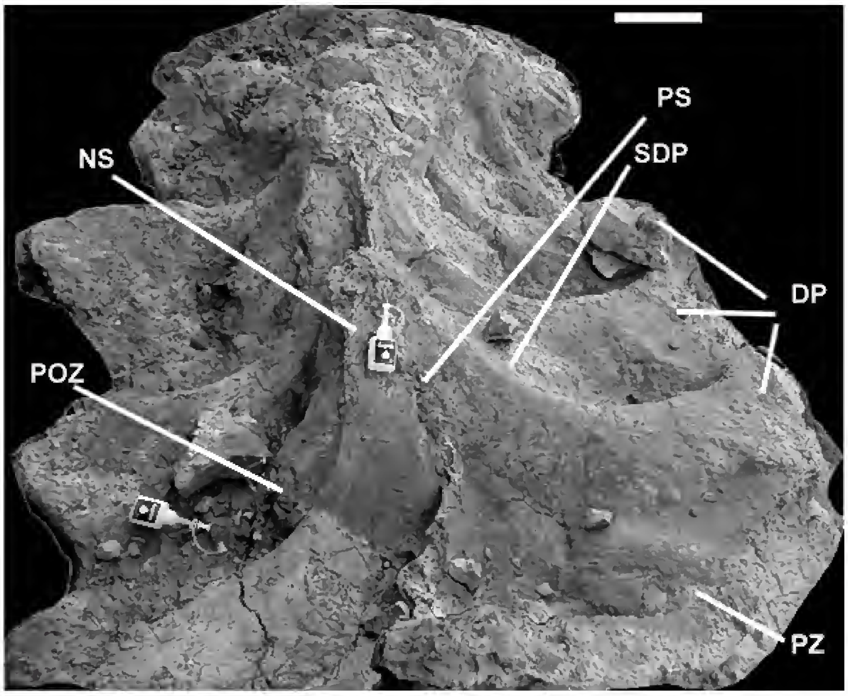

Fig.14- *Futalognkosaurus dukei*; anterior dorsals in anterior view. Scale bar =100mm. (DP) diapophysis, (NS) neural spines, (POZ) postzygapophysis, (PS) prespinal lamina, (PZ) prezygapophysis, (SDP) spinodiapophyseal lamina.

The prespinal lamina is strongly developed and joins the postspinal lamina by another lamina that crosses the distal end of the neural spine, here called supraspinal lamina (Figs.16-17). The prespinal lamina bifurcates on its base, forming two small infraprespinal laminae, another feature unique to this titanosaur (Fig.17). On anterior view, there are two deep "supraspinal" cavities on the neural spine, bordered by the prespinal and two lateral laminae (Fig.17). The lateral laminae start on the top of the prespinal lamina as spinoprezygapophyseal laminae and curve downwards to reach the base of the prespinal lamina at the level of the prezygapophysis. Those supraspinal cavities are considered an autopomorphic feature of *Futalognkosaurus dukei*.

PELVIS

The right pubis is a robust and laminar bone (Fig.18). The iliac articulation is the widest and the iliac process of the pubis is poorly defined. The external surface presents a longitudinal ridge as in *Aeolosaurus* and *Opisthocoelicaudia*, producing two concave surfaces, with the anterior one wider than the posterior. The distal end of the pubis is stout, slightly expanded in lateral view and has a suboval shape in posteroventral view. The distal end is 43,5cm wide. The oval pubic foramen is closed and placed near the puboischial contact. The shaft of the pubis is very long, reaching a total length of 137cm. The contact surface of the pubis with its counterpart is proximally thin and wide distally, where it shows a quadrangular shape.

The ischia are laminar and thin, having a well defined iliac process (Fig.19). The iliac articulation is long, well defined proximally and thinner on the distal end. The shaft is twisted medially. The contact with the pubis is long and curved. The contact surface with the other ischium is restricted only to the distal end; by contrast, in *Rinconsaurus* and *Opisthocoelicaudia* there is a complete contact between both ischia.

Both ilia are preserved, having a maximum height of 96cm. The preacetabular laminae are directed outward as in other Titanosauria. The separation of the iliac peduncles is 137cm. No particular feature that distinguishes those elements from other titanosaurs was observed.

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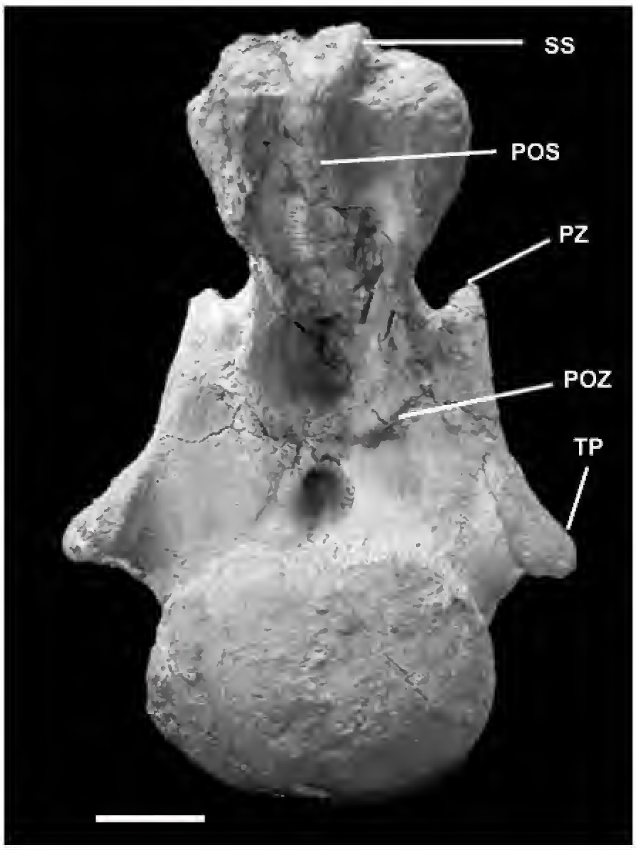

Futalognkosaurus dukei: fig.15- sacrum in a postero-ventral lateral view (field picture); fig.16- 1st caudal in posterior view, scale bar =100mm. (POS) postspinal lamina, (POZ) postzygapophysis, (PZ) prezygapophysis, (SS) supraspinal lamina, (TP) transverse process.

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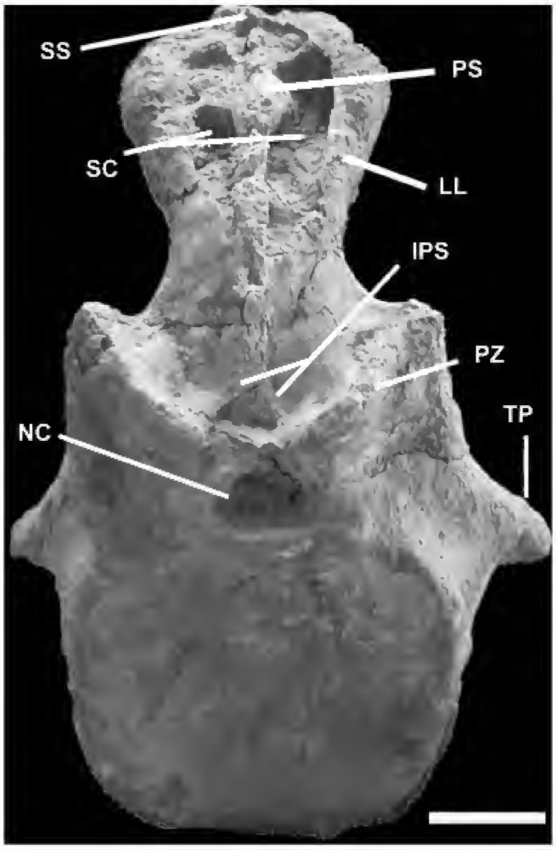

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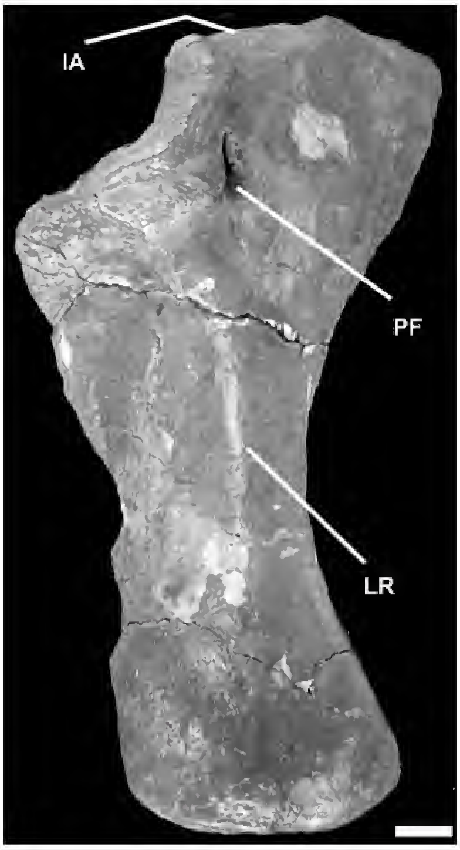

Futalognkosaurus dukei: fig.17- 1^{st} caudal in anterior view; fig.18- right pubis in lateral view. Scale bar =100mm. (IA) iliac articulation, (IPS) infraprespinal laminae, (LL) lateral laminae, (LR) longitudinal ridge, (NC) neural canal, (PF) pubic foramen, (PS) prespinal lamina, (PZ) prezygapophysis, (SC) supraspinal cavity, (SS) supraspinal lamina, (TP) transverse process.

DISCUSSION AND CONCLUSIONS

Titanosauria is one of the sauropod groups more extensively widespread, particularly in Gondwana. Recent cladistic analyses have improved the knowledge about the relationships of several titanosaurid taxa (Salgado *et al.*, 1997a,b; Wilson & Sereno, 1998; Upchurch, 1998; Wilson & Upchurch, 2003; Calvo *et al.*, 2007; Calvo *et al.*, this volume).

Calvo *et al.* (this volume) made a detailed analysis that supported the higher level grouping of Titanosauria (Bonaparte & Coria, 1993); moreover, the inclusion of *Futalognkosaurus* (Calvo *et al.*, 2007) in that analysis confirmed it as a Titanosauridae (*sensu* Salgado *et al.*, 1997a). *Mendozasaurus* and *Futalognkosaurus* form the clade Lognkosauria Calvo *et al.* (2007) (Fig.20), which is based on five synapomorphies: presence of a laterally expanded posterior cervical neural spines, wider than the centra, posterior cervical vertebrae with a height 1.5 the length of the centra, deep and extended supradiapophyseal cavity in posterior cervical vertebrae, posterior cervical centra proportions: ratio anteroposterior length / height of posterior face less than 1.5, and transversely elongated neural spines in dorsal view on most anterior caudal vertebrae. *Futalognkosaurus dukei* differs from other titanosaurids in the following unique combination of traits: quadrangular and laminar posteriorly directed neural apophysis in the axis, high and triangular neural spine of the atlas, concave posterior border on posterior cervical neural spine, horizontal aliform diapophysis on anterior dorsals, supradiapophyseal depression on posterior cervicals, horizontal pre- and postzygapophysis on anterior dorsals, two deep cavities aside the prespinal bordered by the spinoprezygapophyseal laminae, fusion of sacral ribs 2^{nd} and 3^{rd}.

Among the giant titanosaurid sauropods are *Argentinosaurus huinculensis* (Bonaparte & Coria, 1993), *Puertasaurus reuili* (Novas *et al.,* 2005), and

Futalognkosaurus dukei (Calvo *et al.,* 2007). *Argentinosaurus* is represented by only 10% of its skeleton and *Puertasaurus* by just 3% of the total elements. By contrast, *Futalognkosaurus* is represented by almost 70% of the total skeleton being the most complete giant sauropod ever found. *Puertasaurus* is represented by very poor material, but shares several characters with other members of the Lognkosauria (Calvo *et al.,* 2007), such as the absence of pleurocoels in cervical vertebra, transversely expanded neural spine in posterior cervicals, and anterior dorsal neural spines inclined less than 20 degree from vertical. Therefore, *Puertasaurus* can be considered as a basal member of Titanosauridae closely related to Lognkosauria.

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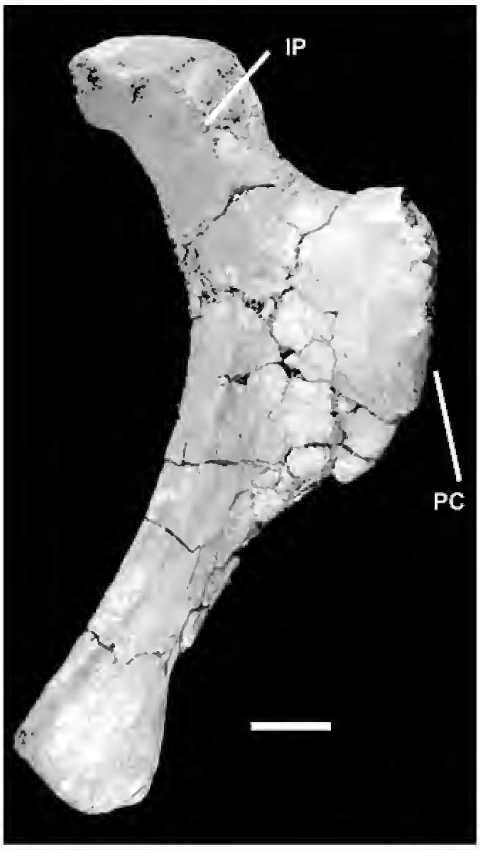

Fig.19- *Futalognkosaurus dukei*; right ischium in lateral view. Scale bar =100mm. (IP) iliac process, (PC) pubis contact.

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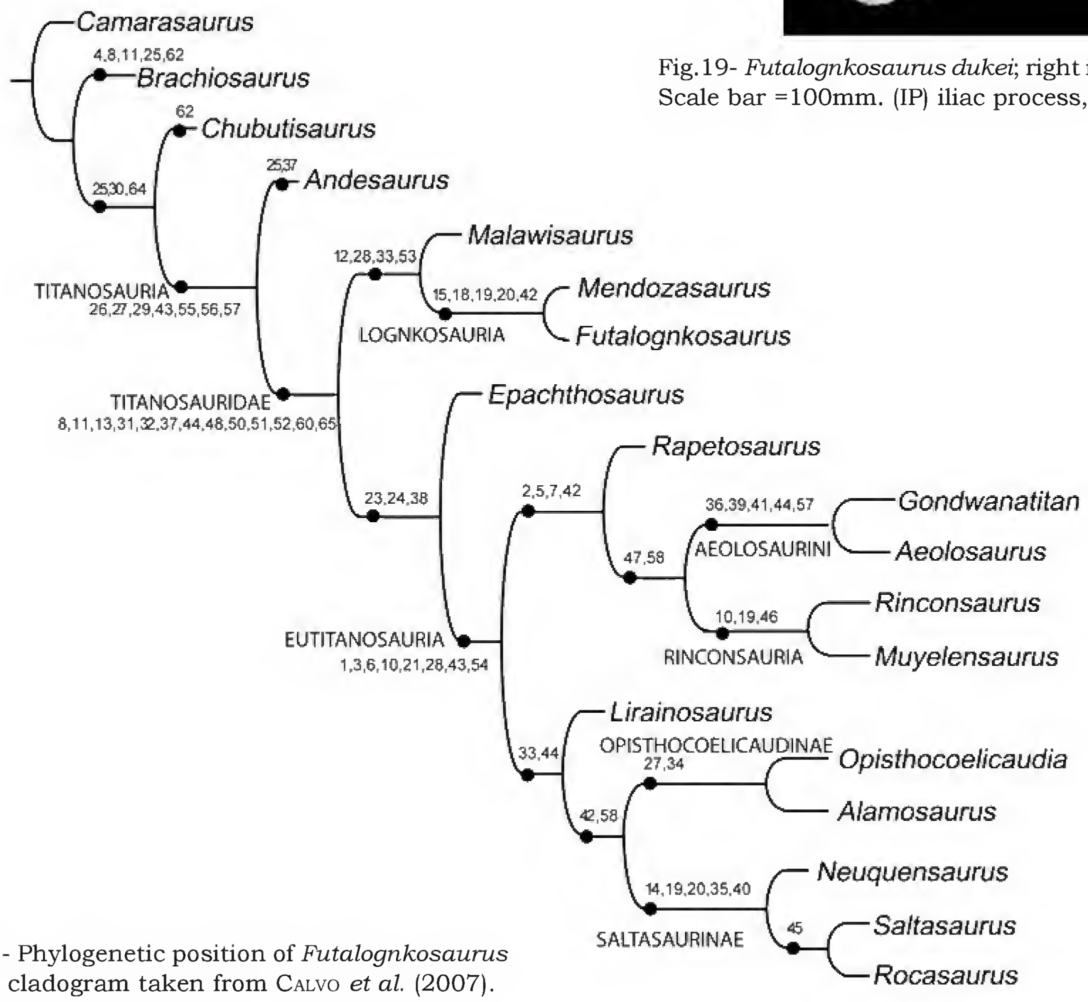

Fig.20- Phylogenetic position of *Futalognkosaurus dukei*; cladogram taken from Calvo *et al.* (2007).

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MORPHOLOGY OF A SPECIMEN OF *SUPERSAURUS* (DINOSAURIA, SAUROPODA) FROM THE MORRISON FORMATION OF WYOMING, AND A RE-EVALUATION OF DIPLODOCID PHYLOGENY [1]

(With 15 figures)

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ABSTRACT: A new specimen of *Supersaurus vivianae* is described, providing additional information about the osteology of *Supersaurus*. The single *Supersaurus* individual that the WDC quarry produced allows a re-examination of elements referred to *Supersaurus* from the Dry Mesa quarry. The osteology supports maintaining the generic distinction of *Supersaurus*. Phylogenetic evaluation finds a monophyletic Apatosaurinae containing [*Apatosaurus* + *Supersaurus*] + *Suuwassea,* and a monophyletic Diplodocinae containing [*Diplodocus* + *Seismosaurus*] + *Barosaurus*, although the generic distinction of *Seismosaurus* is not supported in the current analysis.

Key words: Dinosauria. Sauropoda. *Supersaurus*. Phylogeny. Morrison Formation.

RESUMO: Morfologia de um espécime de *Supersaurus* (Dinosauria, Sauropoda) da Formação Morrison de Wyoming e uma reavaliação da filogenia de diplodocídeos.

Um novo espécime de *Supersaurus vivianae* é descrito, acrescentando informações sobre a osteologia de *Supersaurus.* O único indivíduo de *Supersaurus* coletado no afloramento WDC permite o re-exame dos elementos referidos a *Supersaurus* do afloramento de Dry Mesa. A osteologia suporta a manutenção da distinção genérica de *Supersaurus*. Uma avaliação filogenética resultou em um grupo monofilético Apatosaurinae contendo [*Apatosaurus* + *Supersaurus*] + *Suuwassea,* e um grupo monofilético Diplodocinae contendo [*Diplodocus* + *Seismosaurus*] + *Barosaurus*, embora a distinção genérica de *Seismosaurus* não esteja suportada na presente análise.

Palavras-chave: Dinosauria. Sauropoda. *Supersaurus*. Filogenia. Formação Morrison.

INTRODUCTION

Diplodocoid taxa rank among the earliest described and best-known sauropods (Marsh, 1896; Hatcher, 1901; Holland, 1906; Lull, 1919; Gilmore, 1936), with new taxa continuing to be described, such as *Suuwassea* (Harris & Dodson, 2004) and *Dinheirosaurus* (Bonaparte & Mateus, 1999). Recent studies have provided needed attention to diplodocoid phylogenetic systematics (Upchurch *et al.*, 2004; Taylor & Naish, 2005; McIntosh, 2005; Harris, 2006), yet several diplodocid taxa have remained problematic due to their fragmentary nature, notably *Seismosaurus* and *Supersaurus*.

In 1985, J.A. Jensen erected three sauropod genera based on material collected from Dry Mesa Quarry: *Ultrasauros macintoshi*; *Dystylosaurus edwini*; and *Supersaurus vivianae*. All three have had complex nomenclatural histories (*e.g.*, Jensen, 1987; Curtice, 1995; Curtice *et al.*, 1996; Curtice & Stadtman, 2001), with the types of both *Ultrasauros* and *Dystylosaurus* eventually sunk into *Supersaurus vivianae* (Curtice, 1995; Curtice & Stadtman, 2001). In addition, some of the specimen numbers have changed in the last two decades.

The name *Supersaurus* was erected for a single scapulocoracoid, BYU 12962 (Jensen, 1985). Dozens of elements have been referred to this taxon since. Some referrals, such as the matching right scapulocoracoid, are unambiguous. Other elements have been referred based on quarry location, relative size, and hypotheses of phylogenetic

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position. The depositional circumstances and multiple disarticulated sauropod taxa in the Dry Mesa quarry made unambiguous referrals of other elements difficult. As a result, *Supersaurus* has largely been excluded from phylogenetic analyses, and opinion on its generic validity has been mixed. At one time J.S. McIntosh thought *S. vivianae* was a large species of *Barosaurus*, but more recently supported generic distinction (McIntosh, 2005; Glut, 1997). Alternately, it has been suggested that *Supersaurus* should be synonymized with *Seismosaurus*, or that the genus is a *nomen dubium* (Gillette, 1994).

A second specimen, a single individual from a quarry in Wyoming, makes it possible to evaluate the taxonomic status of referred supersaur skeletal elements in the BYU collection. Combined with morphological data from WDC DMJ-021 it is now possible to provide an emended diagnosis of the species, and to add *Supersaurus* to existing phylogenetic analyses. Approximately 30% of the skeleton has been recovered of WDC DMJ-021 which combined with the BYU specimen yields knowledge of 45-50% of the osteology of *Supersaurus*.

MATERIAL AND METHODS

Abbreviations: Institutional. AMNH, American Museum of Natural History, New York, New York; BYU, Brigham Young University, Provo, Utah; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; DMJ, Douglas Morrison Jimbo site; DMNH, Denver Museum of Nature and Science, Denver, Colorado; NMMNH, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico; NSMT, National Science Museum, Tokyo, Japan; UWGM, University of Wyoming Geological Museum, Laramie, Wyoming; WDC, Wyoming Dinosaur Center, Thermopolis, Wyoming; YPM, Yale Peabody Museum, New Haven, Connecticut.

Material

A single individual (WDC DMJ-021) with approximately 30% of the skeleton was discovered in the Morrison Formation near Douglas Wyoming. The specimen includes a relatively complete presacral column, sacral fragments, and incomplete caudal series. Remains of costal elements, fragmentary pelvic and femur, and complete tibiae and fibulae were also recovered. Elements previously referred to this taxon were also analysed. We follow Curtice *et al.* (1996) in using current BYU specimen numbers, with original numbers noted when necessary for continuity with earlier publications (Tab. 1).

A phylogenetic analysis was conducted using a modified version of Harris & Dodson's (2004) data matrix. The data set was modified by the addition of *Supersaurus* and *Seismosaurus* (see Appendix 1 for character scoring), as well as four new characters (Appendix 2), in part in an attempt to distinguish *Seismosaurus* from *Diplodocus*.

TAPHONOMY

WDC DMJ-021 was found in the Morrison Formation near Douglas Wyoming (Fig.1). Taphonomy of the Jimbo Quarry is interpreted as a debris-flow deposit that buried a single sauropod skeleton (Lovelace *et al.*, 2003, Lovelace, 2004; Lovelace, 2006). While allocthanous in nature, the debris flow appears to have preserved an autochthanous burial of the specimen, prior to the mass wasting event (Lovelace, 2006). The taphonomic interpretation of a single individual is backed up by relative size of preserved elements, and the absence of duplicate elements.

SYSTEMATIC PALEONTOLOGY

SAURISCHIA Seeley, 1887
SAUROPODA Marsh, 1878
DIPLODOCIDAE Marsh, 1884
APATOSAURINAE Janensch, 1929
Supersaurus vivianae Jensen, 1985

Holotype – BYU 12962 Jensen (1985), a large diplodocid left scapulocoracoid.

Referred specimens – BYU 4839, BYU 9024, BYU 9044, BYU 9045, BYU 9085, BYU 10612, BYU 12424, BYU 12555, BYU 12639, BYU 12819, BYU 12861, BYU 12946, BYU 12962, BYU 13016, BYU 13018, BYU 13981, BYU 16679, BYU 17462; Dry Mesa specimens likely pertaining to the type individual. Remains include a nearly complete pelvic girdle and sacrum, a right scapulocoracoid, several axial elements from the cervical, dorsal, and caudal region (see Tab.1 for element identification). WDC DMJ-021, a single associated specimen including a relatively complete presacral column (portions of 10 cervical vertebrae and 5 dorsal vertebrae), sacral fragments, and representative but incomplete caudal series. Several costal elements, fragmentary pelvic and femoral remains, and complete tibiae and fibulae. While a scapula is not known for WDC DMJ-021, other elements are identical to axial elements referred to the type individual of *Supersaurus*.

TABLE 1. Status of Dry Mesa Quarry specimens referred to *Supersaurus*. "Specimen #" column reflects current BYU ascension numbers; "Element" column provides a brief description of element; "Interpreted Referral Status" column provides current status on taxonomic referral.

Specimen #	Element	Interpreted Referral Status
BYU 9025[1]	left scapulocoracoid; (holotype)	N/A
BYU 12962[1]	right scapulocoracoid	Yes; mate to BYU 9025
BYU 12946[1]	right ischium	Yes; verified by WDC DMJ-021
BYU 12854[6]	distal proximal caudal	No; reassigned in this paper to Diplodocinae
BYU 12843[1,5]	distal proximal caudal	No; reassigned in this paper to Diplodocinae
BYU 9084[1]	12 articulated mid-caudals	No; reassigned in this paper to Diplodocinae
BYU 9077[1]	mid-caudal vertebra	No; reassigned in this paper to Diplodocinae
BYU 9024[2]	mid-cervical vertebra	Yes; verified by WDC DMJ-021
BYU 9045[3,5]	proximal caudal vertebra	Yes; verified by WDC DMJ-021
BYU 9044[3;4]	posterior dorsal vertebra	Yes; verified by WDC DMJ-021
BYU 12390[5]	Carpal	Indeterminate
BYU 9000[5]	Phalanx	Indeterminate
BYU 13744[5]	left ulna	No; 20-25% larger than predicted by length of tibia for WDC DMJ-021
BYU 12555[5]	left ischium	Yes; mate to BYU 12946
BYU 12424[5]	right pubis	Yes; verified by WDC DMJ-021
BYU 4839[5]	caudal vertebra	Fragmentary; Curtice (1996) suggests it is
BYU 12639[5]	caudal vertebra	Yes; not verified by WDC DMJ-021
BYU 12819[5]	caudal vertebra	Yes; verified by WDC DMJ-021
BYU 12814[5]	dorsal vertebra	Unable to confirm
BYU 9192	caudal vertebra	Unable to confirm
BYU 13018[5]	pelvis (left illium/four sacral vertebra)	Yes; not verified by WDC DMJ-021
BYU 13981	mid caudal vertebra	Referred to *Supersaurus* in the text
BYU 13016	mid caudal vertebra	Referred to *Supersaurus* in the text
BYU 12861	mid caudal vertebra	Referred to *Supersaurus* in the text
BYU 10612	mid caudal vertebra	Referred to *Supersaurus* in the text
BYU 9085	mid caudal vertebra	Referred to *Supersaurus* in the text
BYU 17462	anterior caudal vertebra	Referred to *Supersaurus* in the text
BYU 4503[5]	dorsal vertebra	Yes; verified by WDC DMJ-021
BYU 16679	caudal vertebra	Referred to *Supersaurus* in the text

([1] Jensen, 1985; [2] Jensen, 1987; [3] Curtice & Curtice, 1996; [4] Curtice *et al.*, 1996; [5] Curtice & Stadtman, 2001) – [6]Curtice, 1996.

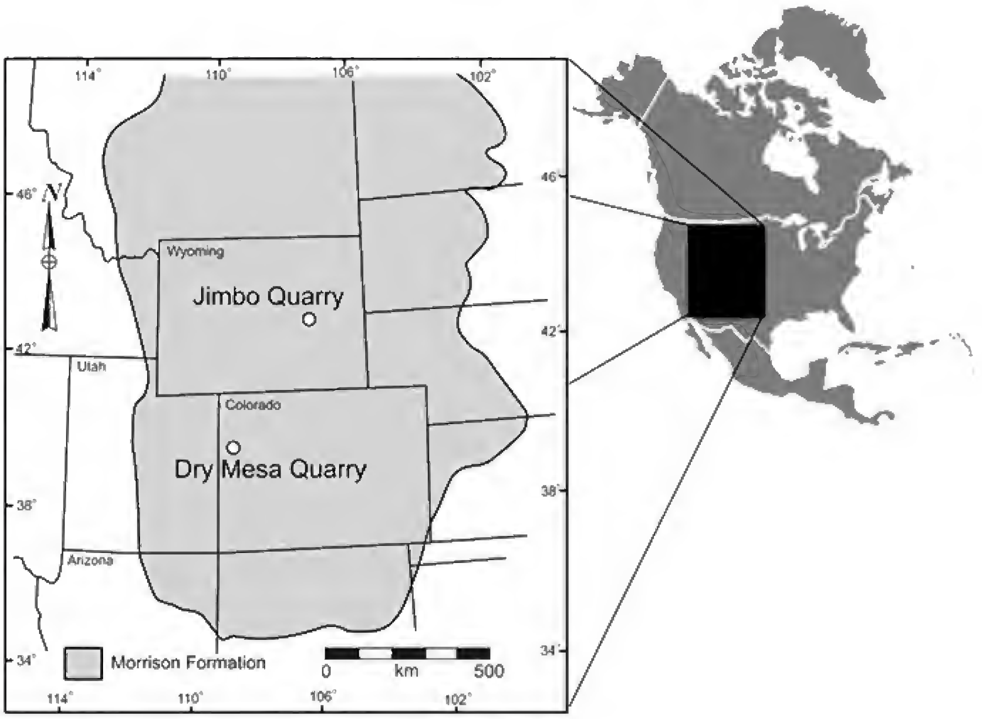

Fig.1- The range of Morrison Formation (shaded) exposed throughout the Rocky Mountain region of western North America. Modified after DUNAGAN & TURNER (2004).

Referral of all material is supported by relative position within their respective quarries (CURTICE & STADTMAN, 2001; LOVELACE, 2006), size of the skeletal elements, and congruence of phylogenetically significant diplodocid characters between the scapula and referred material (see below).

Emended Diagnosis – Large diplodocid sauropod with the following characteristics: elongate cervical vertebrae (elongation index ranging from 4-7) with an a extreme narrowing of the ventral surface of the vertebral body at midlength; well-developed parallel keels on the ventral surface of the cervical series; small ventral pleurocoel located between the parapophyses with dual pneumatopores divided by an anterior-posteriorly directed septa; lateral pleurocoels simple, shallow depressions with small pneumatopores; posterior dorsals with proportionately tall neural spines (> than 0.5 of vertebral height) and reduced neural arch height; anterior dorsals with dorsal vertebral bodies with moderate midline keel and shallow lateral sulci; posterior dorsals opisthocoelous; anterior caudal vertebrae with prominent ventral keel, and shallow pleurocoels; ribs pneumatized, with anterior-posteriorly expanded shafts; scapular blade expanded dorsally; deltoid ridge perpendicular to the acromian ridge.

RESULTS AND DISCUSSION

DESCRIPTION OF THE MATERIAL

Cervical vertebrae – The cervical vertebrae of *S. vivianae* are extremely elongate (length of centra for BYU 9024 is 1380mm). Centra length exceeds even those of *Sauroposeidon*, which was reported as having the longest cervical vertebrae of any known sauropod (WEDEL *et al.*, 2000); the greatest centra measurement of *Sauroposeidon* is 1250mm. While no cervical vertebra is complete, preserved elements are adequate for description and comparison. Supersaur cervical vertebral autapomorphies include a mediolaterally narrow ventral surface (5-8cm) of the middle centra. Cervical vertebrae lack elaborate pneumatic fossae (pleurocoels), a feature noted by JENSEN (1985) as differing greatly from the condition typically seen in the Diplodocidae. Cervical ribs are sub-equal in length to their respective centra, with some extending slightly beyond the posterior limit of the cotyle.

A mid-cervical vertebra (BYU 9024; Fig.2) originally assigned to *Ultrasauros* (JENSEN, 1985) was later referred to the type individual by JENSEN (1987). BYU 9024 compares favorably to preserved WDC cervical vertebrae, supporting its referral to the type individual. The WDC specimen includes substantial portions of ten cervical vertebrae, representing most of the cervical column. Seven of the cervical vertebrae contain nearly complete centra, each over a meter in length.

In cross section the form of the centra can be generalized as an I-beam (Fig.3E). The diameter of pneumatopores on the lateral surface of the centra are no more than 30-80mm. This condition is reduced in comparison to the pneumatopores in several *Apatosaurus*, and contrasts greatly with the elaborate pneumatic structures seen in the centra of *Diplodocus* and *Barosaurus* (Fig.3). On the ventral surface just posterior of the centroparapophyseal lamina there are two pneumatopores separated by a medial septum. This feature appears in all cervicals where this area is preserved (both anterior and posterior cervical vertebrae demonstrate this condition). Figure 4 shows this condition in cervical vertebrae (Cv.) 14 of *Apatosaurus ajax* as well as in Cv.13 of *Supersaurus*; however this feature is absent in *Barosaurus* (Lull, 1919) and *Diplodocus*. More work is needed to determine the distribution of this character in diplodocids.

Dorsal vertebrae – Five dorsal vertebrae have been recovered for WDC DMJ-021; four vertebrae preserve complete centra, one lacks only the transverse processes, while two preserve isolated neural spines. BYU 9044 exhibits features seen in several of WDC dorsal vertebrae, supporting Curtice *et al.*'s (1996) referral to the same individual as the type. WDC dorsal vertebra WDC DMJ-021-085 is extremely similar to mid-anterior dorsal vertebrae BYU 4503 (approximately number 4; Curtice & Stadtman, 2001), supporting BYU 4503's referral to the Dry Mesa *Supersaurus*.

Supersaurus dorsal vertebrae demonstrate several synapomorphic characters with *Apatosaurus*. The neural spines (measured from the junction between postzygapophyses to the top of the neural spine) of the posterior dorsal vertebrae make up more than half the height of the vertebra. This is similar to the condition seen in *Apatosaurus*. Both *Diplodocus* and *Barosaurus* exhibit posterior dorsal neural spine heights that contribute to less than half of the entire vertebrae (Fig.5). The bifed neural spines are lost prior to dorsal seven, and possibly as early as dorsal four or five (inferred from the merging of the spinoprezygapophyseal laminae with the prespinal lamina), unlike in *Diplodocus*. The cleft in the posterior dorsal neural spines of *Diplodocus* is absent in *Supersaurus*.

Preserved dorsal centra of *Supersaurus* exhibit a ventral keel on the centra, as observed in *Apatosaurus* (UWGM 15556). While the posterior dorsal vertebrae of all other diplodocids are amphiplatean (Gilmore, 1936; Hatcher, 1901; Lull, 1919), the posterior dorsals of both *Supersaurus* specimens are opisthocoelous, a probable autapomorphy of *Supersaurus*.

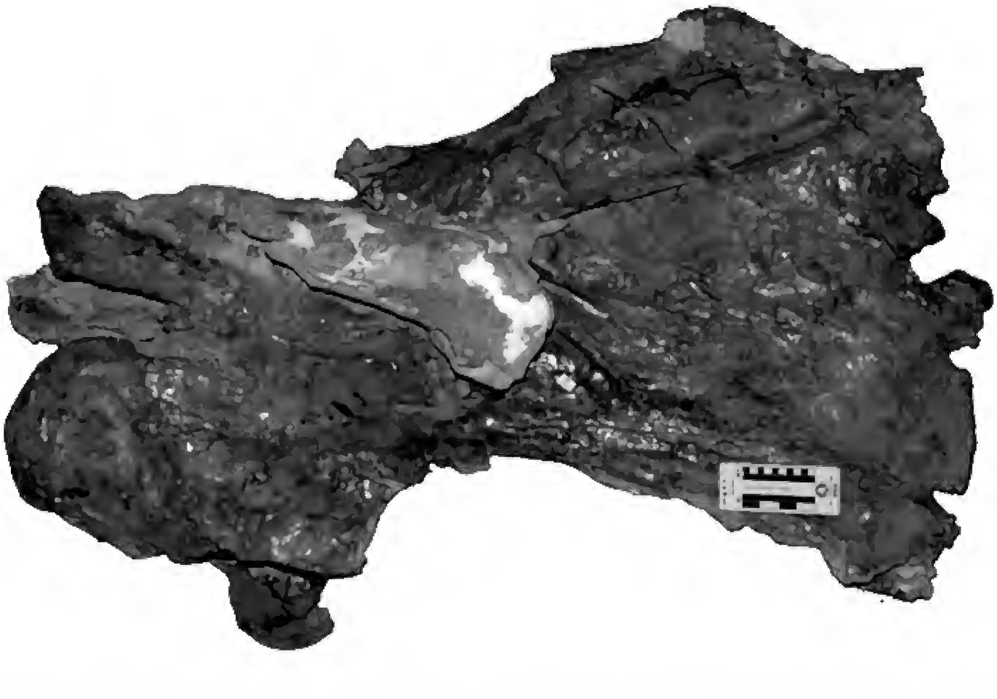

Fig.2- Cervical vertebrae 11 or 12, referred to type specimen of *Supersaurus vivianae* (BYU 9024).

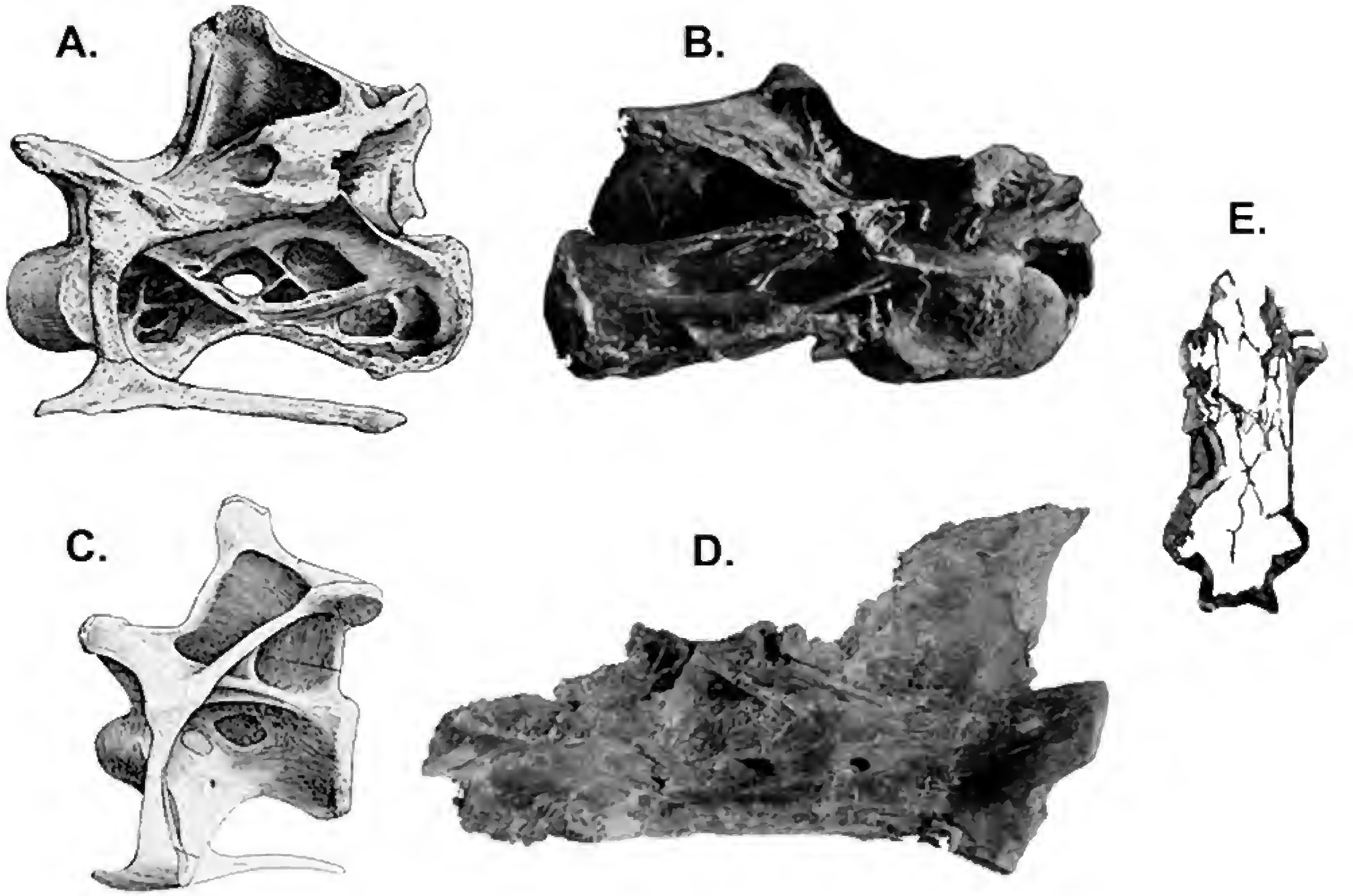

Fig.3- Lateral views of cervical vertebrae from A, *Diplodocus carnegii* (Hatcher, 1901); B, *Barosaurus lentus* (Lull, 1919); C, *Apatosaurus louisae* (Gilmore, 1936); D and E, *Supersaurus vivianae*; demonstrating pneumatic modifications of centra. *Supersaurus* has the least amount of modification with minimal size for pneumatopores. Internal structure is similar to that seen in other diplodocids (Janensch, 1947). Left lateral view of Cv.13 (D, missing the condyle, prezygapophyses and neural spine; length of incomplete centra 94cm). E, cross section through Cv.11, 5cm posterior of the diapophysis.

Caudal vertebrae – Curtice (1996) and MacIntosh (2005) suggest that diplodocid caudal vertebrae are a useful source of taxonomically significant characters. *Supersaurus* caudals share the presence of pneumatic fossae with *Barosaurus* and *Diplodocus*. Aside from this character, they exhibit numerous apatosaurine synapomorphies. Relative to diplodocines the anterior caudal vertebrae have short (less than twice the height of the centra) and distally expanded (rectangular box-like) neural spines (Fig.6) that lack a bifed cleft. The centra are heart-shaped in cross-section, have well-developed anterior cotyles and a platyean posterior surface, contrary to the condition reported by Curtice (1995) in which caudal vertebrae are reported as having a pronounced posterior ball. Inspection shows neither BYU 9045 nor WDC DMJ-021-083 exhibit a pronounced posterior ball, nor do any other caudals from either locality. We were unable to confirm the presence of a hyposphene/hypantrum complex on any of the BYU *Supersaurus* caudals, nor is one present on WDC DMJ-021.

Anterior caudal vertebrae centra exhibit a prominent ventral midline keel, as seen in *Apatosaurus excelsus* (Gilmore, 1936). The keel disappears by caudal vertebrae 12 or 13. Centra length is subequal over the first 30 caudal vertebrae, as in *Apatosaurus*. The height of the caudal neural spines decreases rapidly from anterior to posterior, a condition seen in both *Apatosaurus* and *Barosaurus*, but unlike the very slight decrease in anterior to posterior neural spine height seen in *Diplodocus* and *Seismosaurus* (see Figs.7-8).

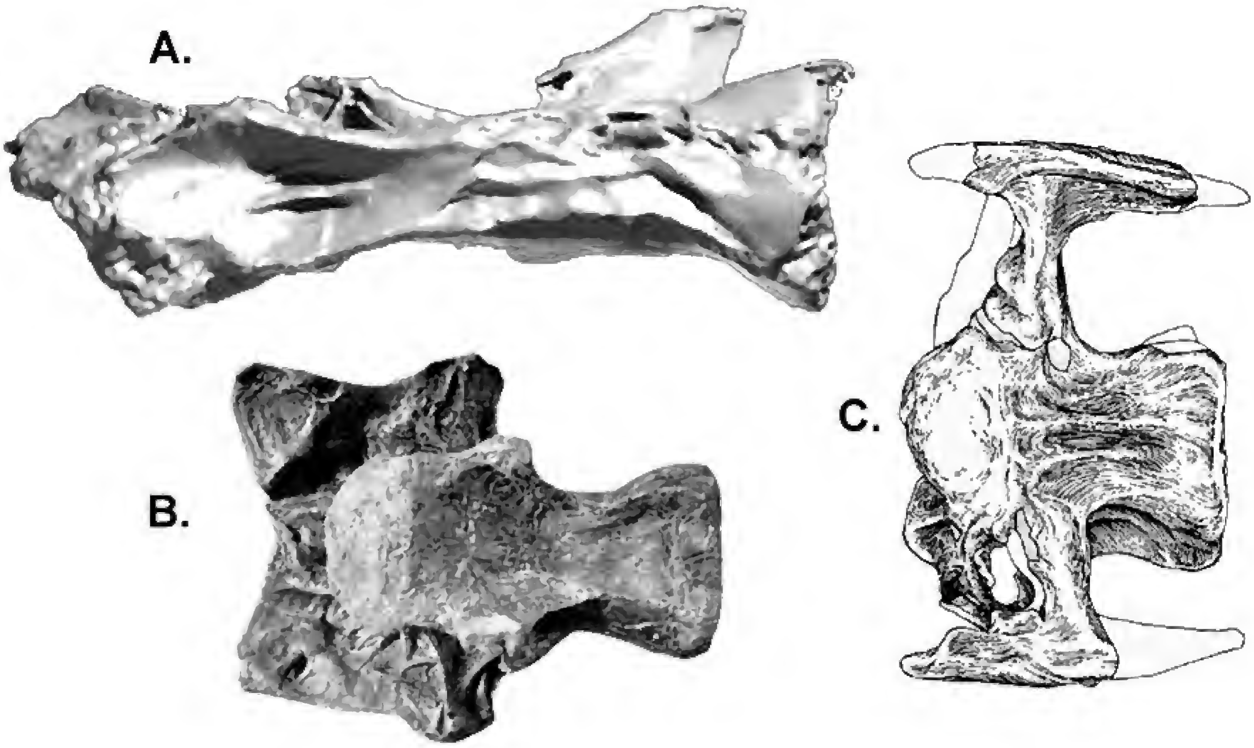

Fig.4- Ventral views of posterior cervical centra from A, *Supersaurus*; B, *Barosaurus lentus* (Lull, 1919); and C, *Apatosaurus ajax* (Upchurch *et al.*, 2004). There are two pneumatopores along the midline of the centra slightly posterior to the parapophyses, each pair separated by a sagital septum. This condition is seen in *A. ajax* as well as *Supersaurus*, but not observed in *Barosaurus* (Lull, 1919) or DMNH 1494 *Diplodocus*.

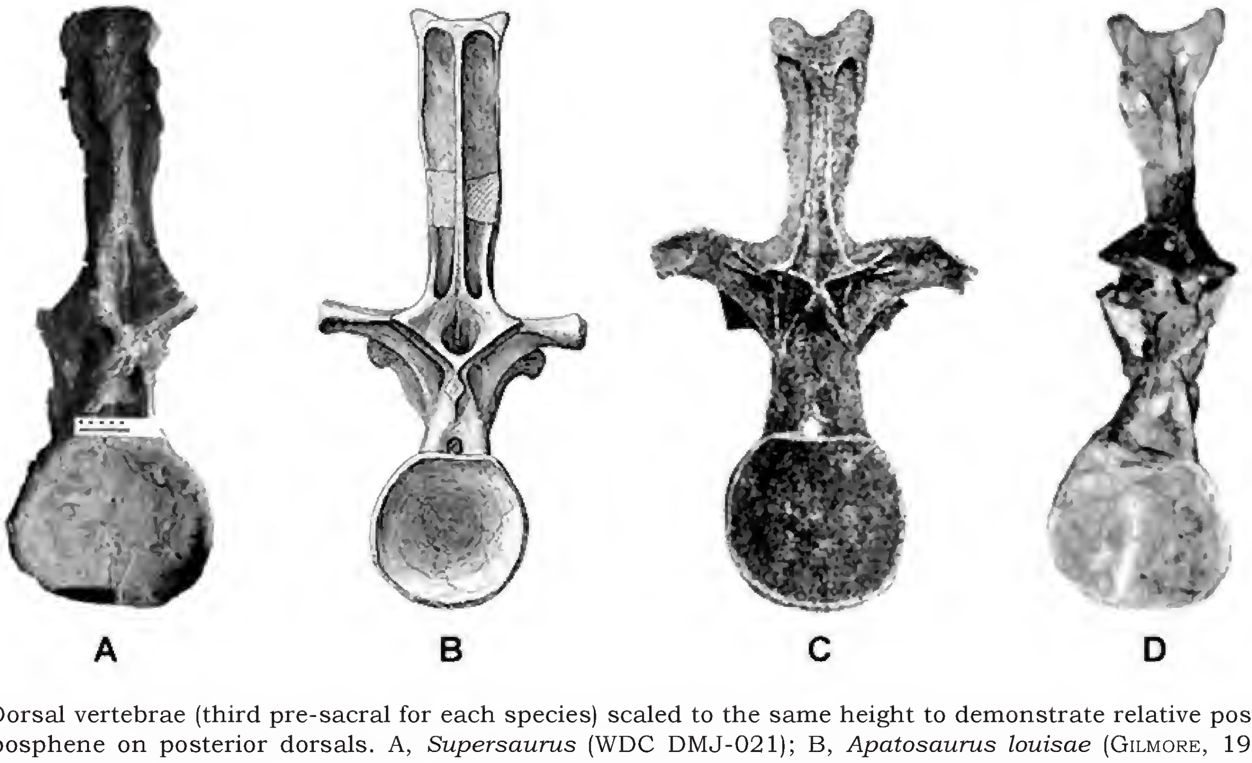

Fig.5- Dorsal vertebrae (third pre-sacral for each species) scaled to the same height to demonstrate relative position of the hyposphene on posterior dorsals. A, *Supersaurus* (WDC DMJ-021); B, *Apatosaurus louisae* (Gilmore, 1936); C, *Diplodocus* (Hatcher, 1901); D, *Barosaurus* (Lull, 1919). The ratios (relative height of centra and neural arch to the height of the neural spine) are 0.44, 0.40, 0.53, and 0.52 respectively, showing that diplodocines have a taller neural arch relative to *Supersaurus* and *Apatosaurus*.

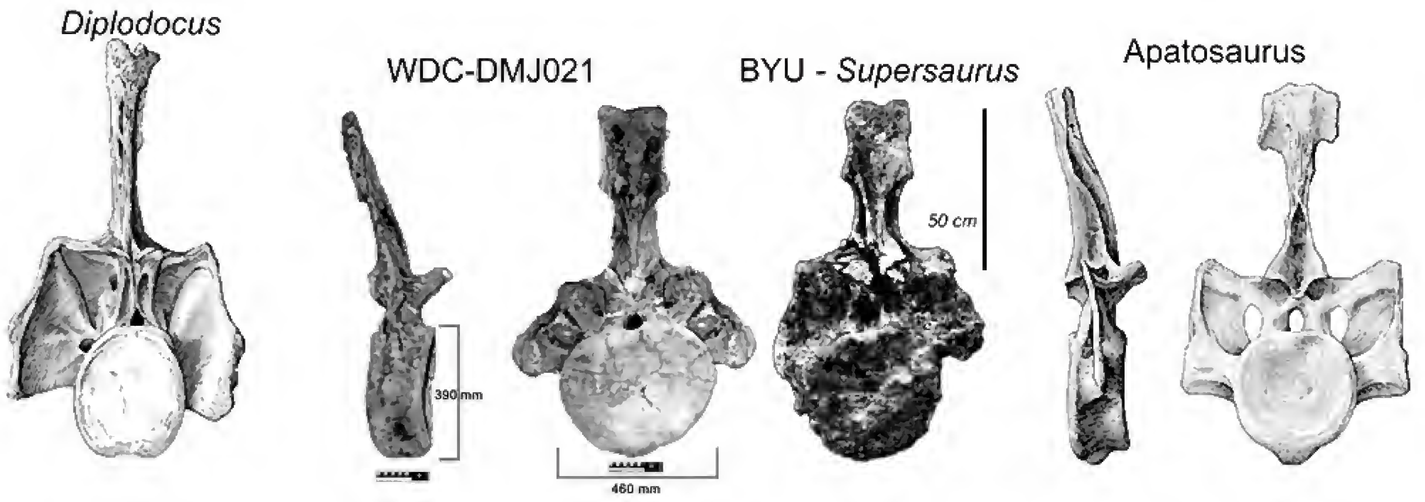

Fig.6- Caudal vertebrae of *Diplodocus*, *Supersaurus*, and *Apatosaurus* shown to demonstrate differences in the height of the neural spine relative to the centra. Note also the distally expanded neural spines of both *Supersaurus* and *Apatosaurus*; in lateral view the keel is apparent as well.

The caudal vertebrae of *S. vivianae* are easily distinguishable from the caudal vertebrae of *Diplodocus* or *Barosaurus*. None of the WDC caudal vertebrae demonstrate the classic diplodocine ventral longitudinal hollow. Nor do the anterior caudal vertebrae exhibit tall and narrow neural spines with a deep cleft at the distal end, as in *Diplodocus* and *Seismosaurus*.

We evaluated these characters in referred caudal material in the BYU collections (Table 1). BYU 12854, 12843, 9084 (12 articulated mid caudal vertebrae), and 9077 are incompatible with the vertebrae found at the WDC site, and should be reassigned to Diplodocinae *incertae sedis* based on their well-developed ventral longitudinal hollow.

Based on size and morphological similarity with WDC DMJ-021, BYU caudal vertebrae 12639, 13981, 13016, 12861, 10612, 9085, 17462, and 16679 can be confidently assigned to the type individual of *Supersaurus vivianae*.

Ribs – Marsh (1896) figured pneumatic cavities from a costal element of *A. excelsus*, and Gilmore (1936) published an image and description of a pneumatic cavity in a dorsal rib of *A. louisae* (Fig.9). *Supersaurus* provides unambiguous evidence of pneumatized ribs (Lovelace *et al.*, 2003). If Marsh (1896) and Gilmore (1936) are correct, then this condition may be synapomorphic to apatosaurines. Alternately, amongst diplodocids pneumatic ribs may be an apomorphic condition of *Supersaurus*.

The length of the longest preserved rib is 305cm. Even on an animal as large as *Supersaurus* this is relatively long. This results in a deep thoracic cavity (Fig.7). This is at odds with *Barosaurus* and *Diplodocus*, but similar to *Apatosaurus* (Figs.7-8). The robust, laterally expansive distal portions of the ribs are more similar to *Apatosaurus* (Gilmore, 1936) than to diplodocines, even in large diplodocine taxa like *Seismosaurus*.

Pectoral girdle – The only known pectoral elements for *Supersaurus* are the scapulocoracoids from Dry Mesa (Fig.10). Scapulocoracoid BYU 9025 demonstrates a deltoid ridge that is perpendicular to the acromian ridge and the scapular blade is one-half the entire length of the scapulocoracoid. Both of these features are seen in *Apatosaurus* but not in *Diplodocus* or *Barosaurus,* which have relatively short scapular blades, and an acute angle between the deltoid ridge and the acromian ridge. This angle is much stronger in *Barosaurus* than it is in *Diplodocus*. The apatosaurine nature of the scapulocoracoids further reinforces the referral of BYU elements to the type scapula, as well as our referral of WDC DMJ-021 to *Supersaurus*.

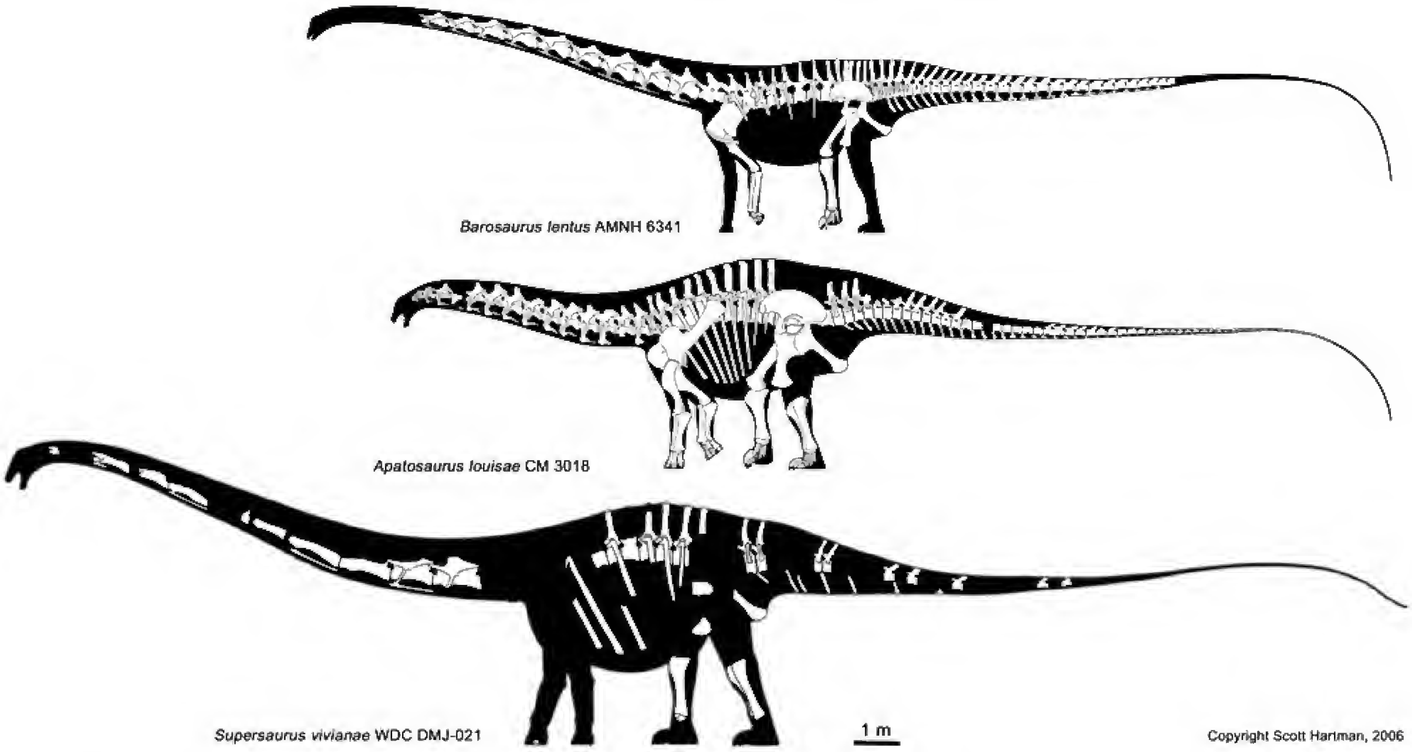

Fig.7- Comparative skeletal reconstructions of *Barosaurus lentus, Apatosaurus louisae,* and *Supersaurus vivianae* to the same scale.

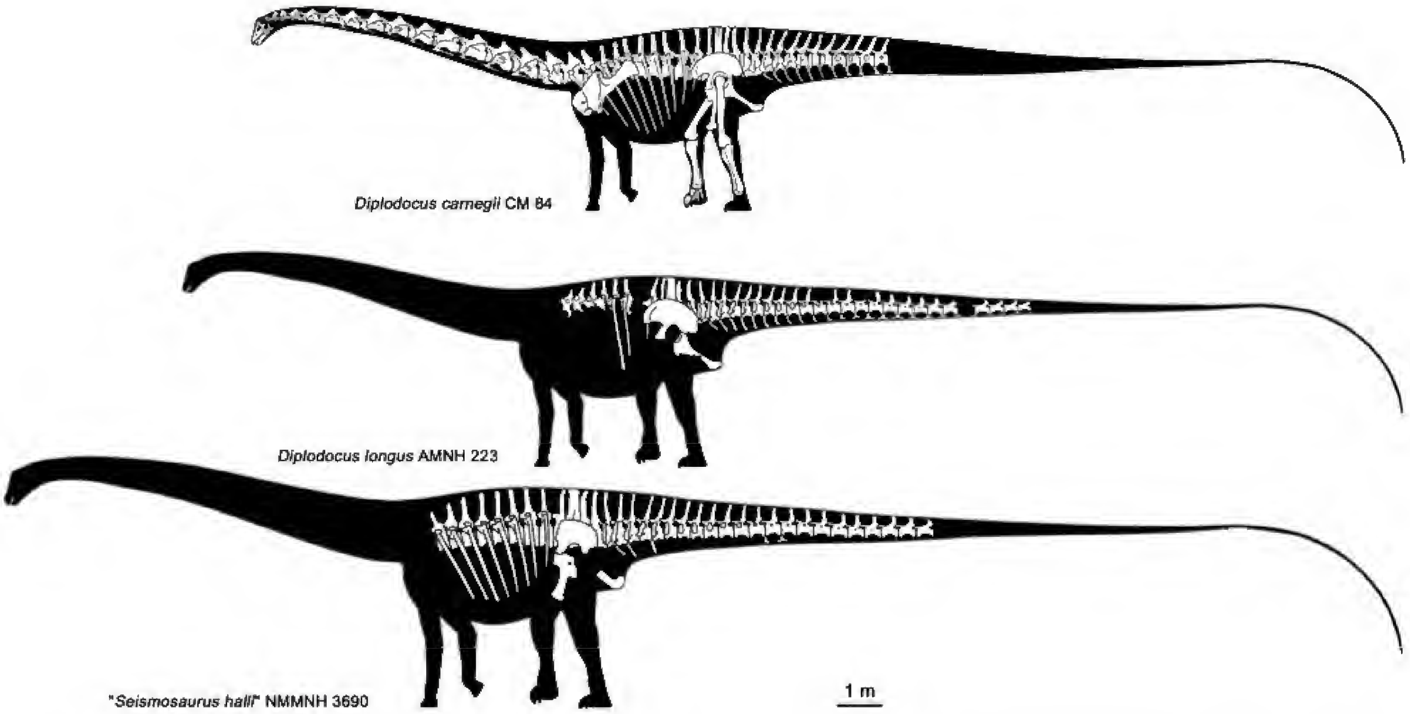

Fig.8- Comparative skeletal reconstruction of *Diplodocus carnegii, D. longus,* and NMMNH 3690, "*Seismosaurus*", to the same scale.

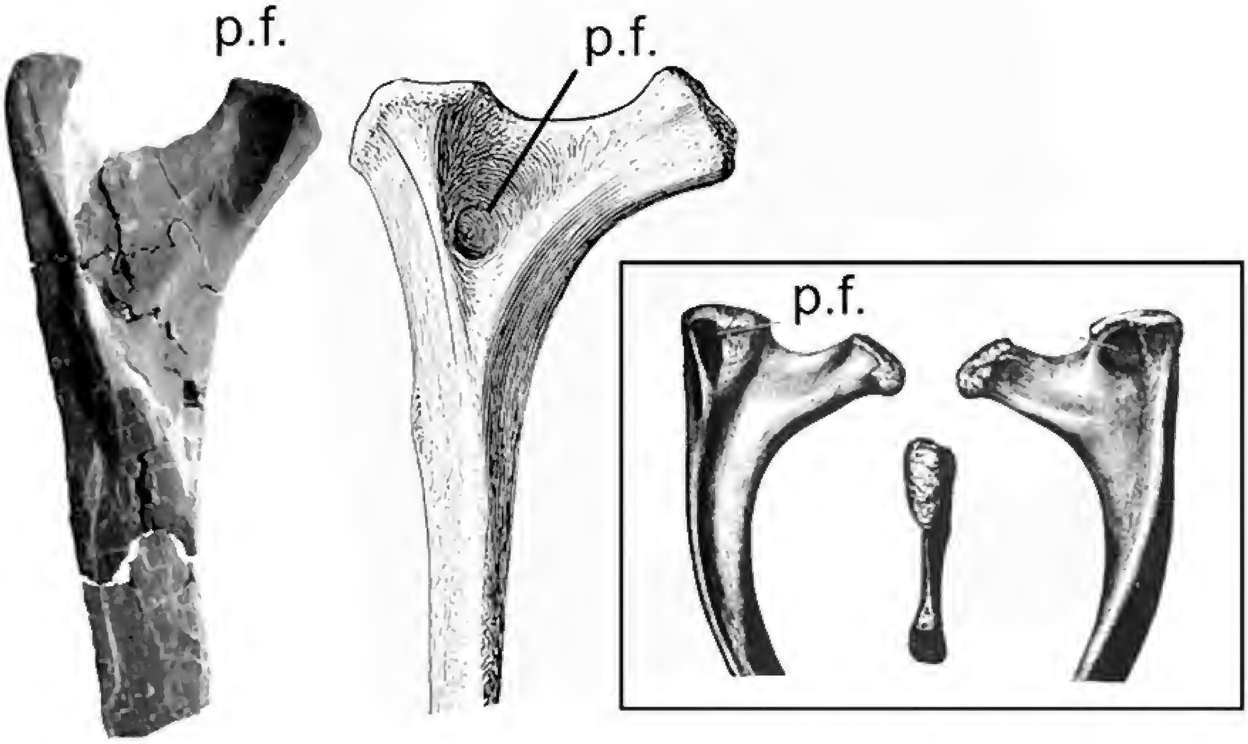

Fig.9- Pneumatic ribs described from the apatosaurines: A, *Supersaurus* (Lovelace *et al.*, 2003); B, *Apatosaurus louisae* (Gilmore, 1936); and C, *Apatosaurus excelsus* (Marsh, 1896). p.f. = pneumatic foramen

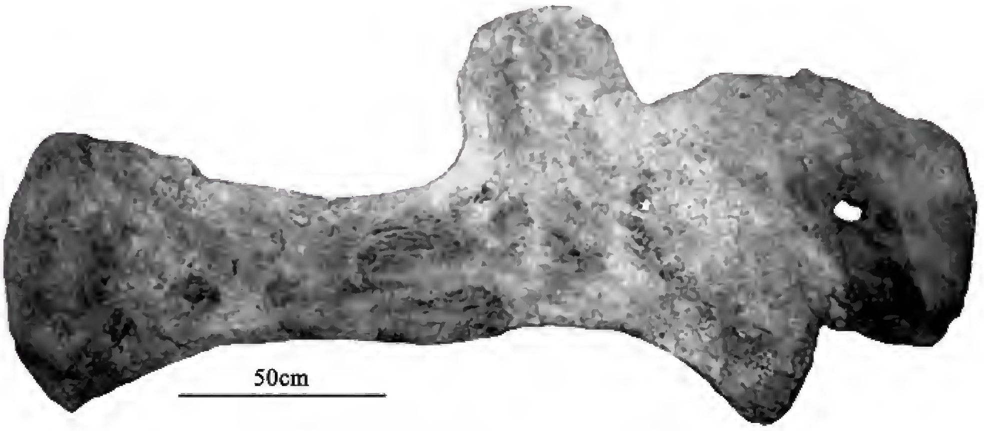

Fig.10- Lateral view of *Supersaurus* right scapulacoracoid (BYU 9025).

Forelimbs – Because *Barosaurus* forelimbs are poorly described, data from *Apatosaurus* and *Diplodocus* (a good proxy for *Barosaurus* limb elements; McIntosh, 2005) are used as a model for diplodocid proportions; expected ratios were used for estimating lengths for missing *Supersaurus* limb elements. Using these predicted ranges, we can safely conclude no additional *Supersaurus* forelimb elements were recovered from the Dry Mesa Quarry. The ulna (BYU 13744) referred to the type specimen of *Supersaurus* (Curtice & Stadtman, 2001) measures 1280mm, while the maximum predicted value (relative to the scapula) for the ulna is 1012mm, a 20% discrepancy. Therefore the referral of BYU 13744 to *Supersaurus* cannot be supported.

No humerus was located in the BYU collection that matched the predicted range of humeral lengths. BYU 17386 has been informally referred to

Supersaurus. Using the same methods as above, a predicted range was generated. The length of BYU 17386 is 1710mm, while the maximum predicted value was 1424mm, a 17% discrepancy.

Pelvic girdle – CURTICE & STADTMAN (2001) referred an articulated sacrum and right illium (BYU 13018), a left ischium (BYU 12555), and a right pubis (BYU 12424) to *Supersaurus*. The pelvis demonstrates dorsoventral shearing that depressed the right illium ventrally and elevated the left sacral ribs dorsally relative to the midline of the sacral centra (Fig.11).

The ischium appears to be the match to the element referred previously by JENSEN (1985), whose referral was supported by CURTICE & STADTMAN (2001). A partial ischium preserved with WDC DMJ-021 is identical to both BYU ischia, supporting referral of these specimens to *Supersaurus*. Likewise, a pubic boot and partial shaft of the left pubis (WDC DMJ-021-233) is represented in the WDC specimen. The boot is very similar to that preserved in the BYU pubis, consistent with previous referrals (Fig.12).

Comparisons of the illium, pubes and ischia with other diplodocids reveal additional apatosaurine affinities, including a short, robust pubic peduncle of the illium, and a large and fully enclosed obturator foramen. In particular, the robust margin surrounding the obturator foramen contrasts with the condition in *Barosaurus*, which is not completely enclosed (MCINTOSH, 2005). *Supersaurus* and *Apatosaurus* also share a large distal expansion of the ischia (MCINTOSH, 1990).

Hind limbs – The tibiae and fibulae of both limbs are present in the WDC specimen. Tibiae are deformed, but exhibit and intermediate level of robusticity, in between that of *Apatosaurus* and *Diplodocus*. The tibia exhibits a large cnemial crest; though less pronounced than in *A. louisae* (GILMORE, 1936) it is at least twice as long (proximodistally) as *Diplodocus carnegii* (HATCHER, 1901). The distal end of the tibia is also expanded mediolaterally, similar to that seen in *A. louisae* (Fig.13).

The fibulae compare well with *Apatosaurus,* including broad anteroposteriorly expanded proximal and distal ends. The *M. biceps femoris* scar is pronounced, as described for *Apatosaurus* (GILMORE, 1936). This contrasts with the weakly expanded proximal and distal ends of the tibia of both *Barosaurus* (MCINTOSH, 2005) and *Diplodocus* (HATCHER, 1901).

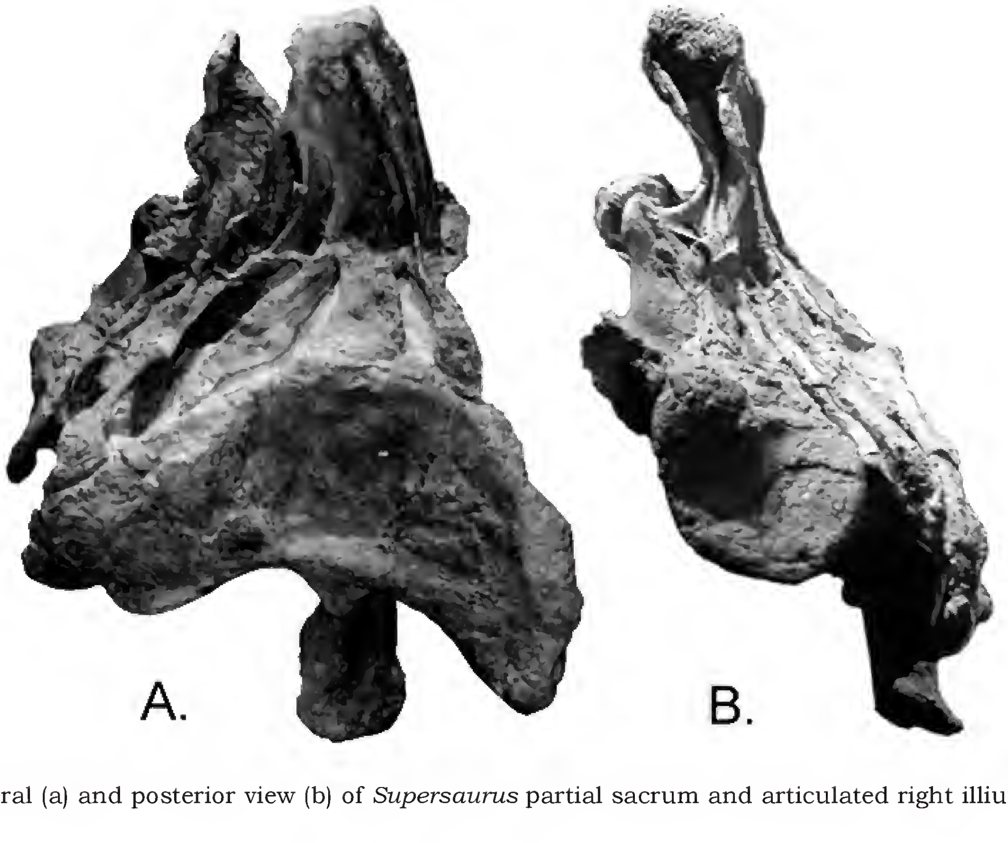

Fig.11- Right lateral (a) and posterior view (b) of *Supersaurus* partial sacrum and articulated right illium (BYU 13018)s.

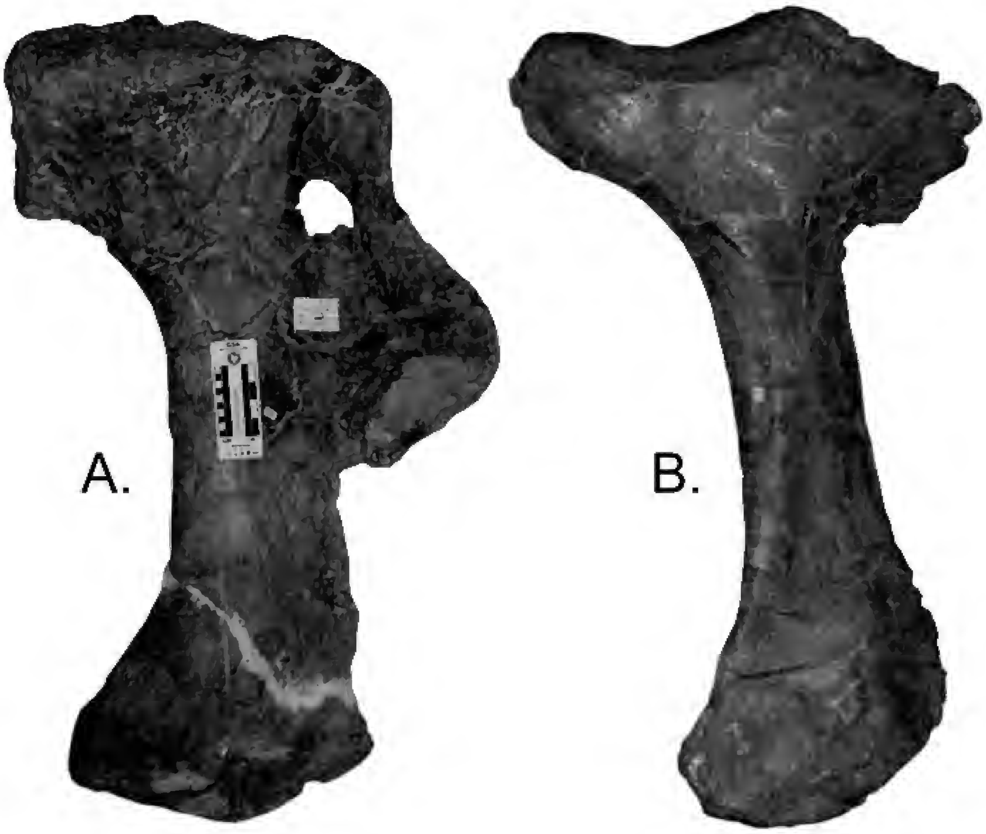

Fig.12- Left lateral view of *Supersaurus* left pubis BYU 12424 (a) and right lateral view of *Supersaurus* right ischium BYU 12946 (b).

PHYLOGENETIC ANALYSIS

The primary phylogenetic analysis (utilizing the modified matrix of HARRIS & DODSON, 2004) resulted in three equally parsimonious trees of 466 steps. The resulting strict consensus tree (Fig.14) has a Confidence Index of 62 and a Retention Index of 78. The analysis recovered a monophyletic Apatosaurinae consisting of *Suuwassea* as the sister taxon to *Apatosaurus* + *Supersaurus*. Inclusion of *Seismosaurus* in the analysis resulted in a sister-group relationship between *Seismosaurus* and *Diplodocus*, with *Barosaurus* as the most basal diplodocine. These results are consistent with the apatosaurine axial morphology of *Suuwassea* (HARRIS, 2006), and corroborates the distinction of *Supersaurus* from *Barosaurus, Seismosaurus,* and *Diplodocus*.

It is possible that some similarities between *Supersaurus* and other apatosaurines result from a size-coupled increase in robustness, but it is worth noting that apatosaurine robustness does not correlate with size, and large diplodocines like *Seismosaurus* do not exhibit markedly more robust pelvic or costal elements, making it unlikely that size is obscuring the phylogenetic signal. Other characters such as proximal centra that are heart-shaped in cross-section, and paired ventral pneumatopores in the cervical vertebrae are certainly decoupled from size. Scoring *Supersaurus* into other published analyses (*e.g.* UPCHURCH *et al.*, 2004) also recovers a monophyletic Apatosaurinae with *Supersaurus* embedded in it (LOVELACE *et al.*, 2005).

Recovery of *Supersaurus* and *Suuwassea* as non-diplodocine diplodocids demonstrates greater apatosaurine diversity than previously suspected. Apatosaurines have not been reported outside of North America, raising the biogeographic possibility that apatosaurines may have been restricted to North America.

DISCUSSION OF *SEISMOSAURUS* VALIDITY

While *Seismosaurus* was recovered as the sister taxa to *Diplodocus*, it was identical to the scoring of *Diplodocus* prior to the addition of our Character 1 (Appendix 1). It has since been discovered that the hook-shaped distal expansion on the ischia of *Seismosaurus* does not exist (LUCAS *et al.*, 2006),

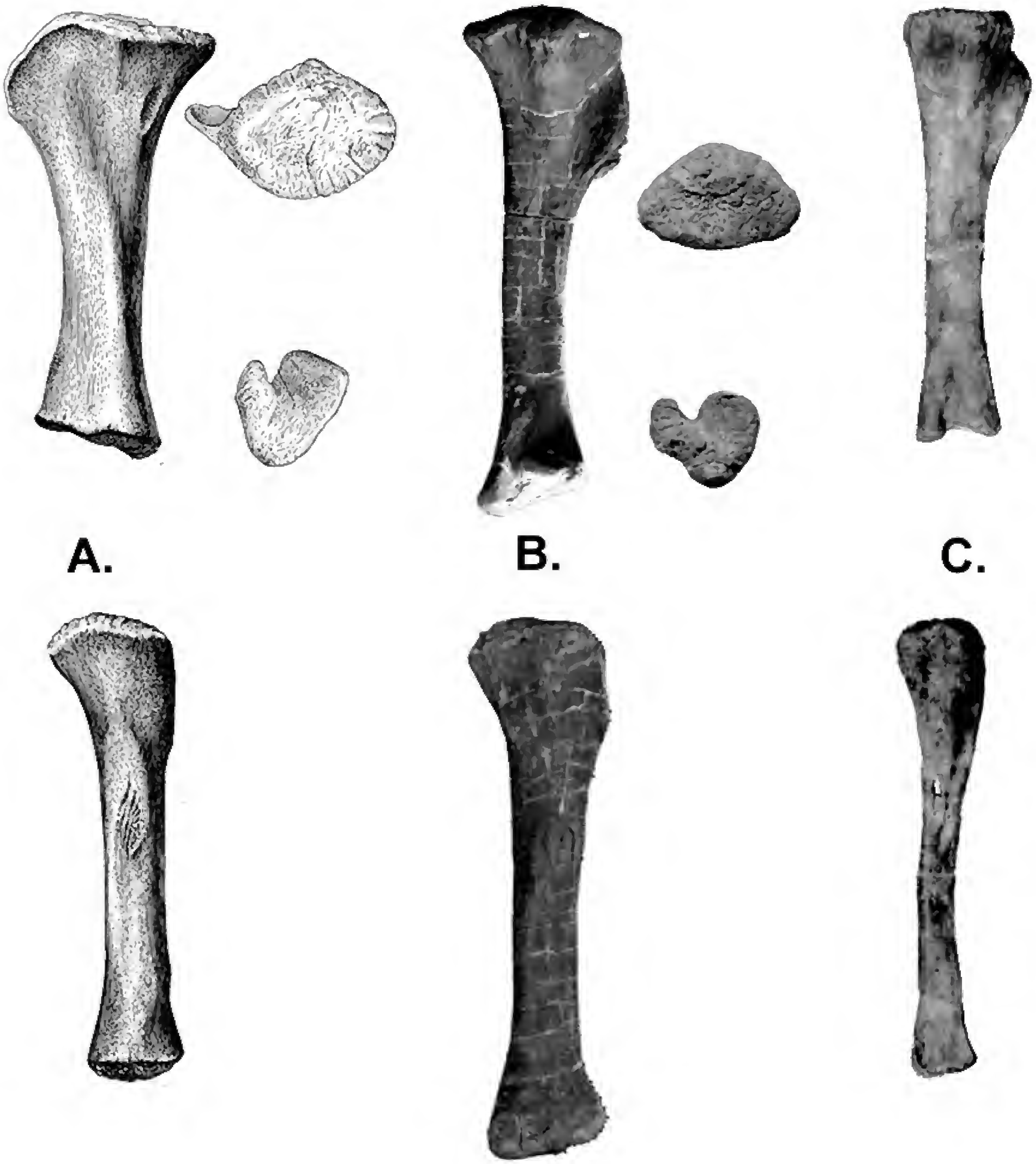

Fig. 13- Comparison of tibiae (upper row) and fibulae (lower row) of: A) *Apatosaurus louisae* (GILMORE, 1936), B) *Supersaurus vivianae* (WDC DMJ-021), and C) *Barosaurus lentus* (MCINTOSH, 2005).

so *Seismosaurus* is once again indistinguishable from *Diplodocus* in our analysis.

Examining descriptive osteology for *Diplodocus* (OSBORN, 1899; HATCHER, 1901; HOLLAND, 1906; GILMORE, 1932; MCINTOSH & CARPENTER, 1998), we concur with CURTICE's (1996) suggestion that the caudal vertebrae of the type of *Seismosaurus* (NMMNH 3690) constitute a nearly continuous series, instead of consisting of major gaps as suggested by GILLETTE (1991). Following GILLETTE's (1991) numbering of the caudals would require morphology not seen in any diplodocid, including extremely elongate mid-caudal vertebrae with hyper-developed mid-caudal neural spines, and a continuation of the transverse processes far past caudal vertebrae 15-18, the termination point in all other diplodocid taxa (MCINTOSH, 2005).

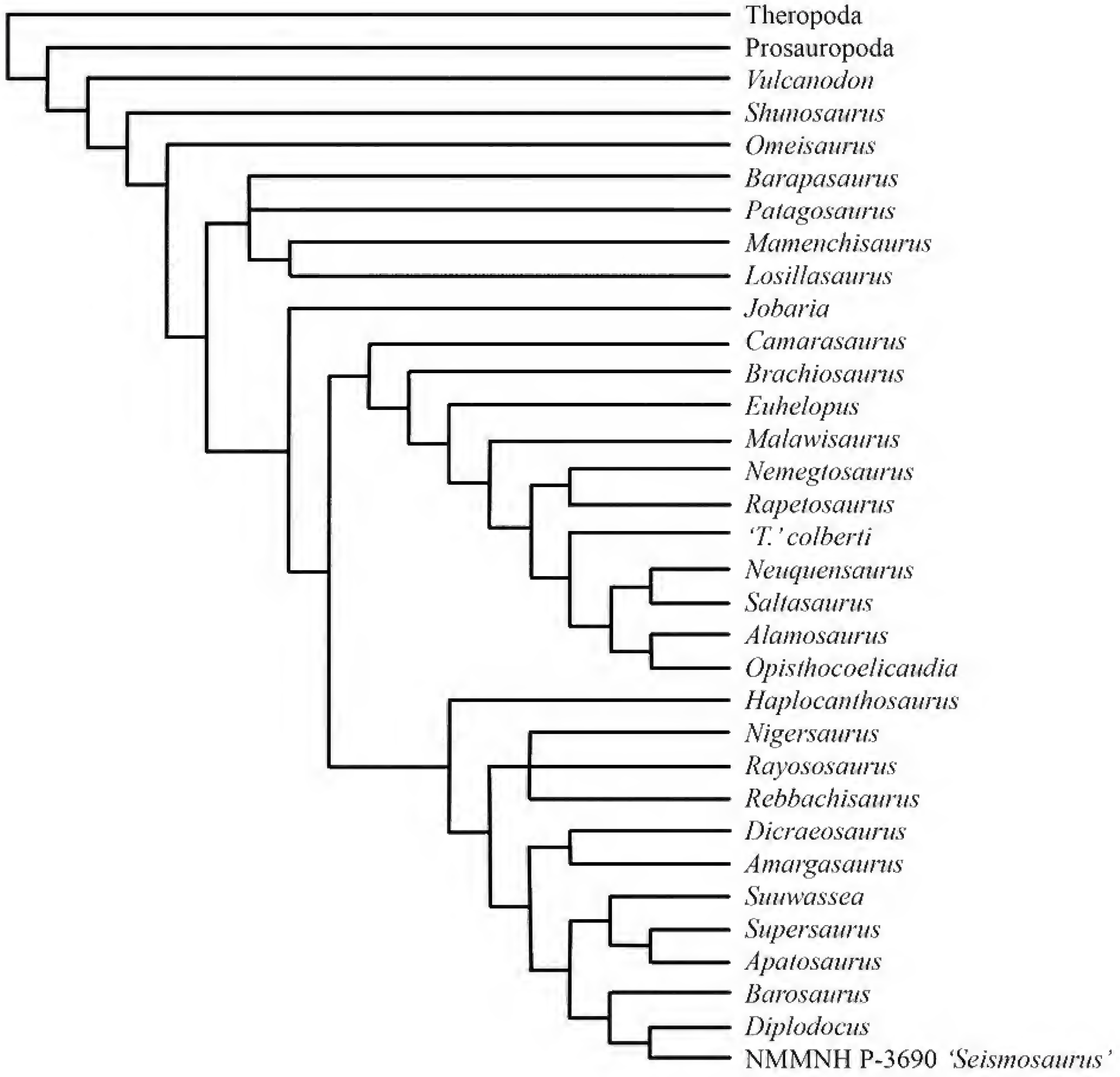

Fig.14- Strict consensus tree resulting from the addition of *Supersaurus* and *"Seismosaurus"* into a modified matrix from Harris & Dodson (2004).

Interpreting the caudal series of *Seismosaurus* as a single series of the 22 anterior-most caudals (with perhaps one missing), the morphology is consistent with other diplodocines, and is nearly identical with that described for *Diplodocus longus* (*e.g.* Osborn, 1899). The maximum centra length reported by Gillette (1991) is 350mm. When compared to the largest caudal vertebrae of *Diplodocus longus* (325mm; Gilmore, 1932) there is only a 2.5cm difference (under 10%). The remaining caudals are within the range of mid-caudal vertebral lengths reported for *Diplodocus longus* by Gilmore (1932).

The phylogenetic placement of *Seismosaurus* reinforces the osteological finding that *Supersaurus* is distinct from *Seismosaurus*. Based on the extremely similar morphology of the *Seismosaurus* axial and pelvic morphology to specimens of *Diplodocus*, we refer NMMNH 3690 to *Diplodocus*, and most likely to *D. longus*.

Size of the Largest Diplodocids

While length and mass estimates of extinct animals have utility for constructing paleo-ecological models, there can be little doubt that public fascination is in part responsible for the numerous size estimates in the scientific literature (Colbert, 1962; Gillette, 1991, 1994; Paul, 1997). Widely varying estimates suggest that more rigor (or perhaps restraint) needs to be applied.

Between the WDC and BYU specimens of *Supersaurus,* most of the presacral axial column is known, and the caudal series is well represented. Using apatosaurine proportions to fill in the missing caudal elements, we reconstruct a length of 33-34m along the axial column for the known specimens of *Supersaurus* (Fig.7), with the BYU specimen being marginally larger.

In comparison, using the proportions of *Diplodocus longus*, we estimate a length of 30m for the NMMNH “seismosaur” specimen (Fig.8). While within the low end of the size estimate provided by D. Gillette (28-36m, 1991), it is far less than the 39-52m length considered “more probable” at the time.

The literature is littered with attempts to estimate the mass of the largest dinosaurs (Colbert, 1962; Anderson, 1989; Gillette, 1994; Paul, 1997). While many studies have used long-bone circumference to estimate mass, we agree with Anderson (1989) and Paul (1997) that variation in the strength index of the femora of extant tetrapods is too great to produce anything more than general ranges. For greater precision we worked with a paleo-life artist to construct a sculpted model based on the proportions of *Supersaurus* for volumetric measurement (Fig.15). Water-displacement measurements where compared against a 3D laser scan of the model to ensure accuracy of measurement. Assuming a specific gravity of 0.8 (Wedel, 2004) provides an estimate 35-40 tons in life.

While the more gracile *Seismosaurus* likely massed significantly less, other sauropods such as *Argentinosaurus* clearly achieved much greater bulk.

CONCLUSIONS

WDC DMJ-021 is the second and most complete specimen of *Supersaurus* to date. Because only a single individual was found in the quarry, it serves as a test against elements referred to the type individual found in the Dry Mesa quarry.

With the additional information provided by WDC DMJ-021, enough morphological differences exist to distinguish *Supersaurus* from other diplodocids. Previously ascribed similarities to *Barosaurus* or “*Seismosaurus*” are based upon material inaccurately referred to *Supersaurus*, or to gross similarities in neck elongation or overall size.

Adding *Supersaurus* to existing phylogenetic analyses recovers a more diverse Apatosaurinae than previously thought. Both *Suuwassea* and *Supersaurus* are found to be more closely related to *Apatosaurus* than to other sauropods. At this point apatosaurines appear to be an indigenous clade of North American diplodocid sauropods.

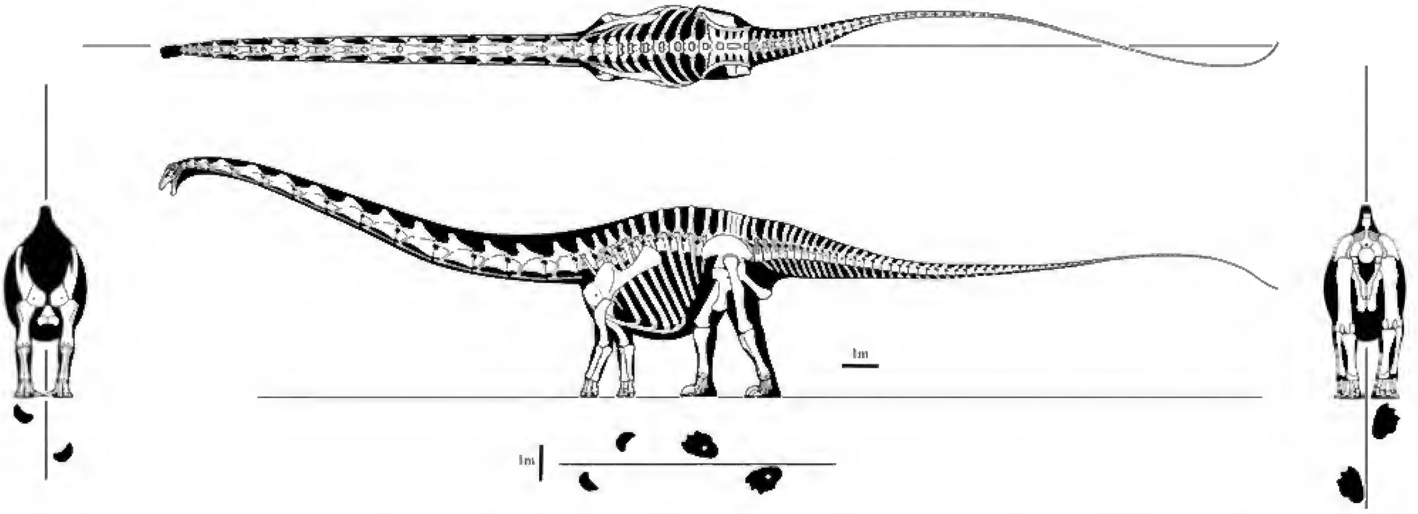

Fig.15- Multiple view skeletal reconstruction used to guide the construction of a physical model for volumetric measurements used in mass estimate.

Greater resolution of diplodocid phylogenetics will likely require a reassessment of individual species of *Apatosaurus* and *Diplodocus*. '*Seismosaurus*' can be referred to the latter, specifically to *D. longus*.

Supersaurus was neither the heaviest nor the longest sauropod, although it is well enough known to place confidence in its estimated length of 33-34 meters, and mass of 35-40 tons.

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APPENDIX 1

SCORING OF *SUPERSAURUS* AND *SEISMOSAURUS*, PLUS ADDITIONAL CHARACTERS (SEE DESCRIPTION IN APPENDIX 2) ADDED INTO THE MATRIX OF HARRIS & DODSON (2004) IN THE PHYLOGENETIC ANALYSIS.

Supersaurus:
??11??0110111111?1
01111111100000021111001100101111011111000001??1110110010110011000???????1011????????
???????111001101000???????0101110????????????????????????00000

Seismosaurus:
??11?10
1111111100000021111001101111111011111111001????0011001????????????????????????????????
?????110????1?00??????????????????????????????????????01111

	235	236	237	238		235	236	237	238
Prosauropoda	?	?	?	?	*Jobaria*	?	?	?	?
Theropoda	?	?	?	?	*Malawisaurus*	?	?	?	?
Vulcanodon	?	?	?	?	*Nigersaurus*	?	?	?	?
Barapasaurus	?	?	?	?	*Rayososaurus*	?	?	?	?
Omeisaurus	?	?	?	?	*Rebbachisaurus*	?	?	?	?
Shunosaurus	?	?	?	?	*Alamosaurus*	?	?	?	?
Patagosaurus	?	?	?	?	*Nemegtosaurus*	?	?	?	?
Mamenchisaurus	?	?	?	?	*Neuquensaurus*	?	?	?	?
Apatosaurus	0	0	0	0	*Opisthocoelicaudia*	?	?	?	?
Barosaurus	0	1	0	1	*Rapetosaurus*	?	?	?	?
Brachiosaurus	?	?	?	?	*Saltasaurus*	?	?	?	?
Camarasaurus	?	?	?	?	*'T.' colberti*	?	?	?	?
Dicraeosaurus	0	1	0	0	*Supersaurus*	0	0	0	0
Diplodocus	0	1	1	1	*Suuwassea*	?	?	?	?
Haplocanthosaurus	?	?	?	?	*Seismosaurus*	1	1	1	1
Amargasaurus	?	?	?	?	*Losillasaurus*	?	?	?	?
Euhelopus	?	?	?	?					

APPENDIX 2

DESCRIPTION OF CHARACTERS ADDED TO HARRIS & DODSON (2004) FOR OUR ANALYSIS.

#235. Posteriodorsal expansion of distal ischium: absent (0); present (1). This character was needed to separate *Seismosaurus* from *Diplodocus*, otherwise they are scored the same. It has been suggested that might in fact be either a new species of *Diplodocus*, or larger specimen of *D. longus* (Fig.12).

#236. Ratio of neural spine height to centrum height (first caudal vertebrae): less than 2 (0); greater than 2 (1). The height of the neural spine is measured from the top of the centrum to the top of the neural spine. The neural spines of both *Apatosaurus* and *Supersaurus* are relatively shorter than those seen in *Dicreaosaurus*, *Barosaurus*, and *Diplodocus* (Fig.6).

#237. Anterior caudal neural spines bifed: absent (0); present (1). Bifed neural spines are present in the apex of the neural spines in *Diplodocus* and *Seismosaurus*. *Supersaurus* exhibits a wide rectangular distal neural spine (Fig.6).

#238. Location of hyposphene on posterior dorsal vertebrae: less than one half total height of vertebra (0); greater or equal to one half total height of vertebra. The neural arches of the diplodocines are taller than in either *Supersaurus* or *Apatosaurus*, making the neural spines relatively shorter in the diplodocines (Fig.5).

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NEW INFORMATION ON *MEGARAPTOR NAMUNHUAIQUII* (THEROPODA: TETANURAE), PATAGONIA: CONSIDERATIONS ON PALEOECOLOGICAL ASPECTS [1]

(With 6 figures)

JUAN D. PORFIRI [2, 3]
DOMENICA DOS SANTOS [2]
JORGE O. CALVO [2]

ABSTRACT: *Megaraptor* is a giant theropod included as a possible Coelurosauria. Its big claw was originally assigned to the digit II of the pes. In the last year, the discovery of complete manus bones of a *Megaraptor* allowed the knowledge of new morphological characters and, therefore, new interpretations on phylogenetic relationships. As a result, *Megaraptor* was proposed to be a basal tetanuran sharing characteristics with charcarodontosaurids and spinosaurids. In general, manus of basal tetanurans are quite unknown as they commonly lack phalanges, carpals or even the complete manus, being the information on them limited. So that, the hand elements of *Megaraptor* here studied represents an important material not only for furnishing new morphological data but also for the understanding of its behavior.

Key words: *Megaraptor*. Theropoda. Portezuelo Formation. Upper Cretaceous. Patagônia.

RESUMO: Nova informação sobre *Megaraptor namunhuaiquii* (Theropoda: Tetanurae), Patagonia: considerações sobre aspectos paleoecológicos.

Megaraptor é um terópoda gigante considerado como um possível Coelurosauria. Sua enorme garra foi originalmente atribuída ao dígito II do pé. No último ano, a descoberta de ossos atribuídos a uma mão completa de *Megaraptor* permitiu o conhecimento de novos caracteres morfológicos e, portanto, novas interpretações sobre as relações filogenéticas. Como resultado, *Megaraptor* foi considerado como um tetanuro basal compartilhando características com os carcarodontossaurídeos e os espinossaurídeos. Em geral, ossos da mão de tetanuros basais são pouco conhecidos, tendo em vista que comumente faltam falanges, carpais ou, até mesmo, a mão completa, limitando a informação. Os elementos de *Megaraptor* aqui estudados representam, portanto, importante material por fornecer novos dados morfológicos e, também, para o entendimento dos hábitos comportamentais.

Palavras-chave: *Megaraptor*. Theropoda. Formação Portezuelo. Cretáceo Superior. Patagônia.

INTRODUCTION

Recently, on the north coast of Barreales Lake in the Neuquén Province, at the Futalognko site, a complete manus (MUCPv-341) of the theropod *Megaraptor namunhuaiquii* Novas, 1998 was discovered (Calvo *et al.*, 2004a). In the present study we improve the description of some manus bones and analyse paleoecological aspects of this enigmatic dinosaur.

Phylogenetic relationships were previously established based on many different skeletal parts of the theropod group taxa although some of the bones are rarely preserved, such as their hands. The anatomical study of the manus bones here developed allowed establishing a more accurate phylogenetic position of this species. Also, it is very profitable for comparative studies with other similar manual elements in other theropods (Calvo *et al.*, 2004a).

Several studies have been made focusing on diets and behaviors of the giant theropods (Farlow & Pianka, 2002). However, many of the results were based on the skull and teeth morphology, stomach contents,

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and coprolites. Anyway, there are several disparities of opinions concerning with these aspects. Although we recognize that it is very hard to interpret dinosaur diets with only postcranial elements, here we analyze the possible behavior of the giant cretaceous predator *Megaraptor namunhuaiquii.*

FOSSILS OF FUTALOGNKO SITE

The preserved forelimbs (MUCPv-341) of *Megaraptor namunhuaiquii* consist of a left scapula and coracoid, a right ulna and a radius, and a complete right manus. These materials were found associated to sauropods remains (Calvo *et al.*, 2001; Calvo, 2006), theropods (Calvo *et al.*, 2004b), ornithopods (Porfiri & Calvo, 2002), fishes (Gallo *et al.,* 2003), plants (Prámparo *et al.*, 2003), turtles, crocodiles, and pterosaurs (Kellner *et al.*, 2006).

MATERIAL AND METHODS

The material consists of a left scapula and coracoid, a right ulna and radius, and a complete right manus and it is housed in the Museo de Geologia y Paleontologia de la Universidad Nacional del Comahue under the number MUCPv-341.

It was examined with a PHILIPS TOMOSCAN MG helicoidal tomography, in sections of 1 to 2mm thickness with an overlapping of 50%. The two-dimensional images were saved in a DICOM (Digital Imaging and Communication in Medicine) standard format on the Philips system that provides mechanism for supporting the use of JPEG (Joint Photographic Expert Group) Image. The data was converted into three-dimensional images and saved as JPEG archives for visualization. The application of a computed tomography to the manus bones of *Megaraptor namunhuaiquii* demonstrates morphological data for a forelimb muscular insertion study (Porfiri *et al.*, 2005). As a result, it was possible to obtain data on the surface of the bones, allowing the proposed study.

RESULTS

Description of the Material

The large theropod *Megaraptor* presents well developed forelimbs. Digit I has a deep and wide sulcus on the ventral surface of phalanx I (Fig.1). This sulcus suggests the existence of a strong ligament uniting phalanx I (18.4cm long) with flexor tuberculum of ungual phalanx I (42cm long). Moreover, the enlarged laminar olecranon process of the ulna in *M. namunhuaiquii* indicates the insertion of a massive triceps (Fig.2). This muscle would give a higher force to *Megaraptor* hand during extensional movements. The triceps and flexor ligament would be efficient in seizing prey (Fig.3). Unfortunately, the humerus of *Megaraptor* was not preserved; however, the scapula and the coracoid preserved are morphologically similar to those of *Baryonyx* Charig & Milner, 1986. So, it is probably that the humerus had a similar robustness.

The acromial process of the scapula is oriented 90° with respect to the scapular blade and it is united one to another by a thin lamina. The distal end of the scapular lamina is compressed laterally. It is possible to observe a thin lamina on the posteroventral region. Approximately 1/3 of the distal end of the scapula is not preserved. So, it is not possible to know if there is a distal expansion similar to other theropods as *Allosaurus* Marsh, 1877 (Madsen, 1976). The glenoid cavity is convex and formed by the articular facet for humerus. In anterior view, the scapula articulation with the coracoid has a semicircular shape in the ventral part. It expands dorsally in a thin lamina. The articulation is oriented perpendicular to the scapular lamina presenting an expansion on the ventral zone with respect to the dorsal one.

Metacarpals are articulated on the proximal region. Metacarpal I has asymmetrical distal condyles separated by a shallow sulcus. This asymmetry allowed a lateromedial rotation of digit I during the flexion movement (Calvo *et al.,* 2004a). Metacarpal II occupies almost 50 % of the dorsal surface of the carpals. Metacarpal III and their phalanges are flattened and deformed by postdepositional compression. This digit is more gracile than digits I or II. Concerning *Megaraptor* hand, one of the most important features is the presence of a metacarpal IV, which represents more than 1/3 of the total length of metacarpal III. This metacarpal is present in many primitive theropods. It is possible that metacarpal IV did not have mobility since it is fused to Metacarpal III and that it was almost imperceptible on the *M. namunhuaiquii* manus.

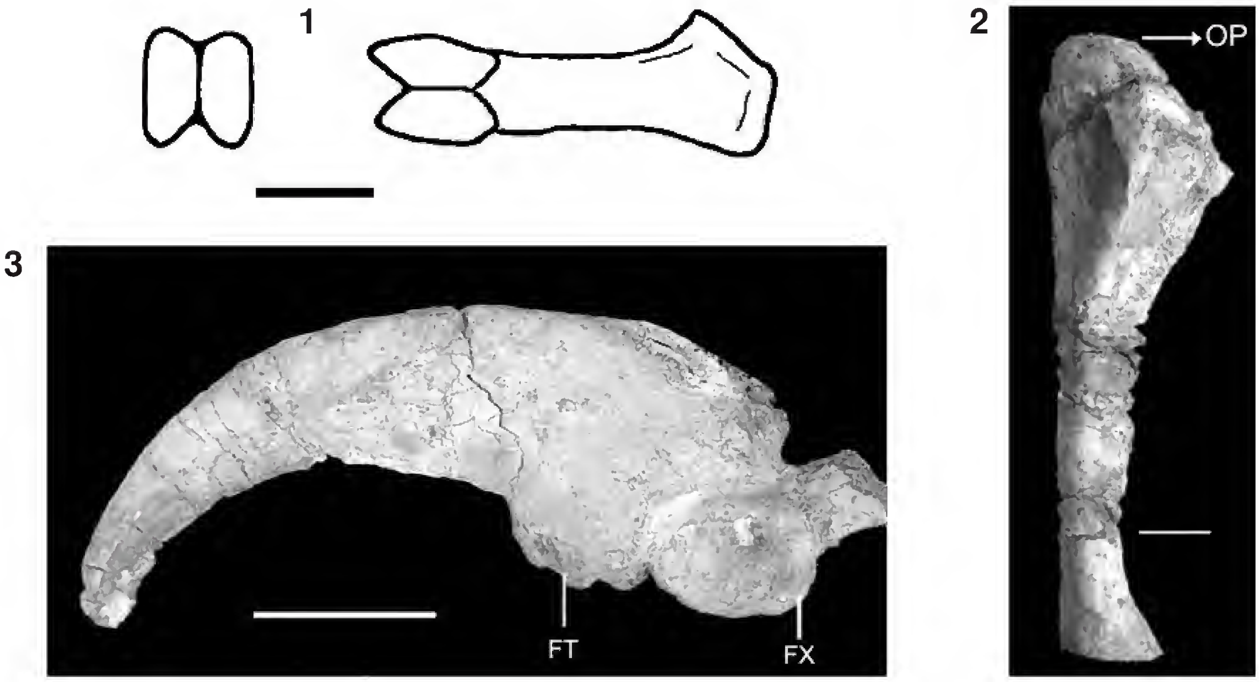


Fig.1- Phalanx I of the digit I in distal and ventral views. Scale bar = 5cm; fig.2 - ulna in lateral view. Abbreviation: (OP) olecranon process. Scale bar = 3cm; fig.3 - claw I of the digit I of *Megaraptor* in medial view. Abbreviations: (FT) flexor tubercle, (FX) phalanx I. Scale bar = 6cm.

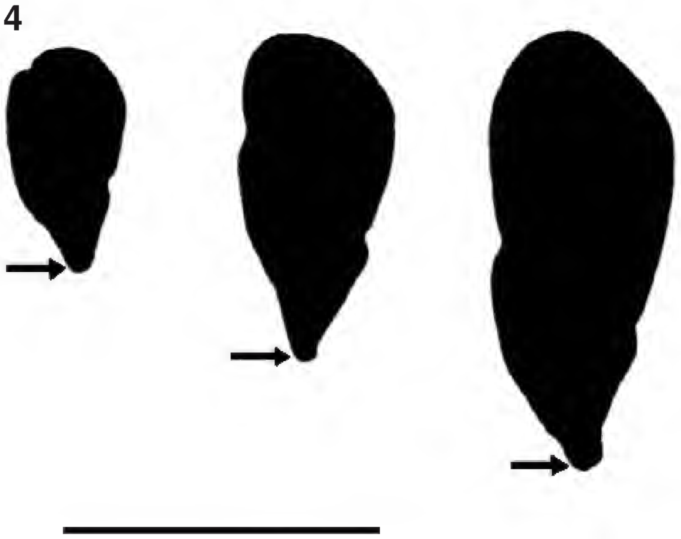
DISCUSSION AND CONCLUSION

One important feature of *Megaraptor* is the presence of a sharp ventral border on its ungual phalanx of the digit I, finger I, indicating efficient raptorial abilities (Fig.4). This character is absent in other theropods in which the ventral border is rounded (Fig.5). The phalanx of digit I has a wide dorsal surface, strong enough to support a massive extensor muscle. The phalanges of digit II have smaller dorsal surfaces than those of the digits I and III. It suggests that the movement during hyperextension of the ungual phalanx was very strong, a condition needed to animals with raptorial habits. A claw with a sharp ventral surface is also present in dromaeosaurids (Ostrom, 1969; Novas & Pol, 2005) as *Deinonychus* Ostrom, 1969 and *Neuquenraptor* Novas & Pol, 2005. This characteristic is only observable in the claw II of the pes of these animals since the other claws have flat ventral surfaces. *Deinonychus* hand has claws with rounded ventral surfaces as in *Allosaurus* (Madsen, 1976). Therefore, the main tool for attack in *Deinonychus* was the claw II on the foot and the manus were used just for sustainability. The other claws of the foot would have only a support utility. Due to the shape observed in the ventral border of *Megaraptor* manus, we deduce that the claw of phalanx I had the same function to that observed in *Deinonychus* and the claws II and III could also be related with the body support. Also, based on the fact that *Deinonychus* and *Neuquenraptor* were hunters and that it was possible to associate similarities between the ventral border of the foot claw II of these dromaeosaurids and the hand claw I of *Megaraptor*, it is here supposed that this giant predator of Patagonia had a hunter habit (Fig.6).

The radio rescued for the carcharodontosaurid *Mapusaurus roseae* (Coria & Currie, 2006) showed that its hands are larger, different from those observed in other large theropods as tyrannosaurids and abelisaurids (Coria & Currie, 2006). The interpretation given by those authors to the metacarpals considering them as metacarpals II and III in *Mapusaurus* (MCF-PVPH-108.48) may be similar to that given to the metacarpals I and II of *Megaraptor* due to their similarity. As manual elements rescued in *Megaraptor* have close similarities to the carcharodontosaurid *Mapusaurus* it is possible to consider both having similar cranial morphology, which may indicate that *Megaraptor* used the skull as main weapon and the forelimbs only for opening carcasses. Also, considering hands' morphology, both *Megaraptor* and *Baryonyx* (Charig & Milner, 1997) are basal tetanurans that have similar ones. Kitchener (1987) proposed that the spinosaurid *Baryonyx* could have been a carnivorous animal considering that their claws could have been utilized for opening dead bodies. Otherwise, *Baryonyx* was also interpreted as a piscivorous dinosaur (Rayfield & Milner, 2005) based not only on the enormous claws, but also on the skull morphology, the tooth shape, and the stomach contents (*sensu* Farlow & Holtz, 2002). However, evidence about *Megaraptor* dietary habits can only be related to its hand morphology since there are no cranial materials to be studied. The teeth described by Calvo *et al.* (2004a) are not associated with cranial materials and, for this reason, were not considered in the present study. So that there are no enough data to support that *Megaraptor* had scavenger piscivorous habits.

Furthermore, based on related materials of more than one individual of *Megaraptor* from Barreales Lake, it is possible to indicate a social behavior for the genus (Porfiri *et al.*, 2007) which is observed in other basal tetanurans, such as in *Mapusaurus* (Coria & Currie, 2006). For this reason, it is possible that *Megaraptor* was an animal with group hunting habits, behavior observed in some living animal as lions and hyenas (Farlow, 1976).

4



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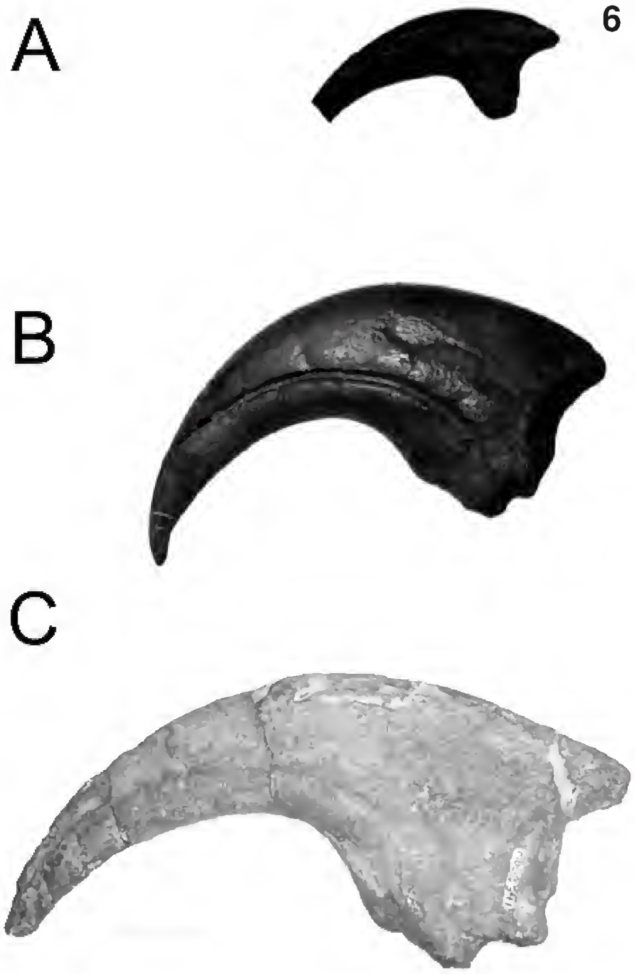

Fig.4 - Cut of the *Megaraptor*'s claw I of the digit I. The arrows show the cutting surface. Scale bar = 3cm; fig.5 - Claw II of the digit II. Scale bar = 2.5cm; fig. 6 - (A) pedal claw II of digit II in the dromaeosaurid *Neuquenraptor*; (B) ungual attributed to left manual digit I in the spinosaurid *Baryonyx*; (C) manual ungual in the Tetanurae *Megaraptor*. Only comparative, without scale.

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FOSSIL BIRDS OF CHILE AND ANTARCTIC PENINSULA[1]

(With 7 figures)

MARTIN CHAVEZ [2]

ABSTRACT: All fossil bird orders recorded from the Mesozoic and Cenozoic periods in deposits of Chile and the Antarctic Peninsula have been summarized. Chilean insular territory and quaternary records have been excluded. The Bahía Inglesa Formation located in Copiapó province in northern Chile and the La Meseta Formation of Seymour Island have been identified as the richest fossiliferous fossil bird-bearing localities for Chile and the Antarctic Peninsula respectively. The importance of these records as indicators of paleoenvironmental conditions is discussed.

Key words: Fossil birds. Chile. Antarctic Península.

RESUMO: Aves fósseis do Chile e da Península Antártica.

Um resumo de todas as ordens de aves registradas para o Mesozóico e o Cenozóico em depósitos do Chile e da Península Antártica é aqui apresentado. Registros relacionados ao território insular chileno e ao Quaternário foram excluídos. A Formação Bahía Inglesa, localizada na província de Copiapó, e a Formação La Meseta, localizada em Seymor Island, foram identificadas como as mais ricas localidades fossilíferas com registros de ocorrência de aves, respectivamente para o Chile e para a Península Antártica. A importância desses registros como indicadores de condições paleoambientais é discutida.

Palavras-chave: Aves fósseis. Chile. Península Antártica.

INTRODUCTION

Studies of Chilean fossil avifauna have been undertaken since the XVI century, but modern studies were only established in XIX century. More than 460 species in 55 families have been documented in Chile since then, representing 4.76% of the current worldwide avian diversity (Araya & Millie, 1998). Fossil birds and the origin of the current avian diversity in Chile have been poorly studied, despite the relative abundance of fossils in coastal formations. In contrast, the Antarctic avian remains have a long history of study (*e.g.*, Wiman, 1905; Marples, 1953; Myrcha *et al.*, 2002).

The few revisions concerning the ornithological works in Chile before the year 2000 have been conducted exclusively by foreigners (*e.g.*, Mones, 1986; Tambussi & Noriega, 1996). In 1895, R. Phillipi mentioned Chilean fossil birds for the first time, describing subfossil remains from Mejillones and Tarapaca in guano sites. Later, only two species were described: *Neogaeornis wetzelli* Lambrecht, 1929 and *Meganhinga chilensis* Alvarenga, 1995. These constitute the main works during the XX century. At present, an increasing number of studies have been conducted in this area by national researchers (*e.g.*, Fritis, 2001) as well as foreign scientist (*e.g.*, Walsh & Hume, 2001; Acosta-Hospitaleche & Tambusi, 2004). The author of this work has also been contributing to the study of the Chilean ornithofauna (*e.g.*, Chavez, 2001, 2005a, b).

In the current work, the fossil records of the Republic of Chile are summarized including material described for the Antarctic territory from W 53° to 90°. All the orders recorded from Mesozoic and Cenozoic deposits are included. Insular Chilean territory and Quaternary records are excluded.

The formations in which fossil bird remains can be found in Chile (Fig.1) are restricted to sequences directly associated with aquatic environments, mainly marine ones, except the Curamallin Formation. Thus, orders of seabirds or birds associated with lacustrine systems are the only type of known fossil bird communities. It is necessary to study continental formations to obtain better information about terrestrial birds because our present knowledge is barely sufficient and restricted to the Late Cretaceous and Neogene. The Bahía Inglesa locality is the most important in abundance and diversity of fossil birds in Chile (Fig.3B). Information about the Paleogene is lacking (Fig.3A). There are few fossiliferous formations of the Paleogene and prospections from these are limited.

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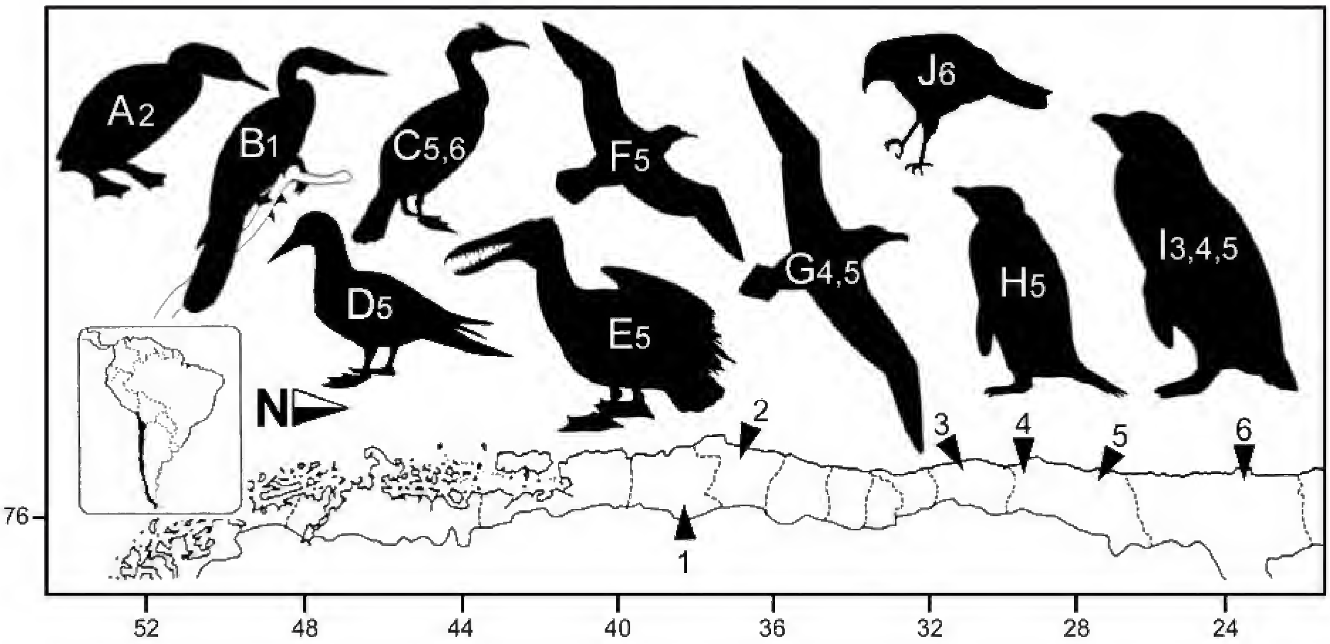

Fig.1- Localities bearing fossil birds in Chile. Localities: (1) Rucañanco hill, (2) Tumbes Peninsula, (3) Coquimbo, (4) Chañaral de Aceituna, (5) Bahia Inglesa, (6) Mejillones Peninsula. Taxa: (A) Gaviidae, (B) Anhingidae, (C) Phalacrocoracidae, (D) Sulidae, (E) Pelagornithidae, (F) Procellaridae, (G) Diomedeidae, (H) *Pygoscelis*, (I) Spheniscidae, (J) Falconidae.

Antarctic Peninsula fossiliferous locations (Fig.2), corresponding mainly to formations associated with marine or deltaic edges like the Lopez de Bertodano Formation or La Meseta Formation, have provided Chilean ornithofauna workers with the opportunity of having a record of continental elements (Fig.3C). Due to the scarcity of Neogene fossiliferous formations in that region and the glacial conditions that began in the Middle Miocene, the records are chronologically restricted to the Late Cretaceous and Paleogene (FORDYCE & JONES, 1990). The Seymour Island locality is the most important as far as Antarctic fossil avian abundance and diversity are concerned. Since, there are no Paleogene records in Chile, the Antarctic record has become a useful tool for understanding the conditions in the austral extreme during the early Tertiary (Fig.3A).

A total of 56 records are considered in 10 orders, 24 of them coming from Chilean territory (see Appendix): 20 taxa correspond to species described on the basis of material found within the studied area, 15 of them collected on the Antarctic Peninsula (Tab.1).

Institutional abbreviations: CPDG: Coleccion Paleontologica Departamento de Geologia, Universidad de Chile (Santiago-Chile); GPMK: Geologisch-Palaontologisches Institut und Museum (Kiel-Germany); MPC: Museo Paleontologico de Caldera (Caldera-Chile); MUSM: Museo de Historia Natural de la Universidad de San Marcos (Lima-Peru); SGO–PV: Museo Nacional de Historia Natural (Santiago-Chile); SNGM: Servicio Nacional de Geologia y Mineria (Santiago-Chile); USNM: United States National Museum, Smithsonian Institution (Washington D.C.-USA); UOP: University of Portsmouth (Portsmouth -United Kingdom).

SYSTEMATICS AND GENERAL SIGNIFICANCE

ORNITHURINES

The record of Mesozoic birds is virtually restricted to Neornithes in the studied area. However, other Ornithurine information in the Antarctic continent are known. ZINSMEISTER (1985) mentions the existence of Ichthyornithes in the Late Cretaceous of Seymour Island, Antarctica. That publication does not include figures of the material collected and it is barely descriptive. For this reason it has been broadly ignored and not been able to be revised (CLARKE, 2004). FEDUCCIA (1999) mentions another possible record without indicating a specific location: "Hou Lian-Hai is currently describing a Hesperornithiform from the Lower Cretaceous of Antarctica" (:161). No description or images of these materials have been published (A.Feduccia, pers. comm., 2005). Due to the limited available information these records are not included in the figure 2.

RATITES

Ratites are flightless cursorial paleognathes generally of great size. Though the phylogeny of this group is still being discussed, recent revisions confirm that they are a monophyletic group (DYKE & VAN TUINEN, 2004). Extant representatives are restricted to the austral continents.

There is only one known record consisting of a tarsometatarsus from the La Meseta Formation (Late Eocene) of Seymour Island, Antarctica (TAMBUSSI *et al.*, 1994). It is not possible to make a more specific taxonomic classification based on the known materials. The presence of these birds in Antarctica is congruent with an early Gondwanan dispersion suggested for ratites (VAN TUINEN *et al.*, 1998).

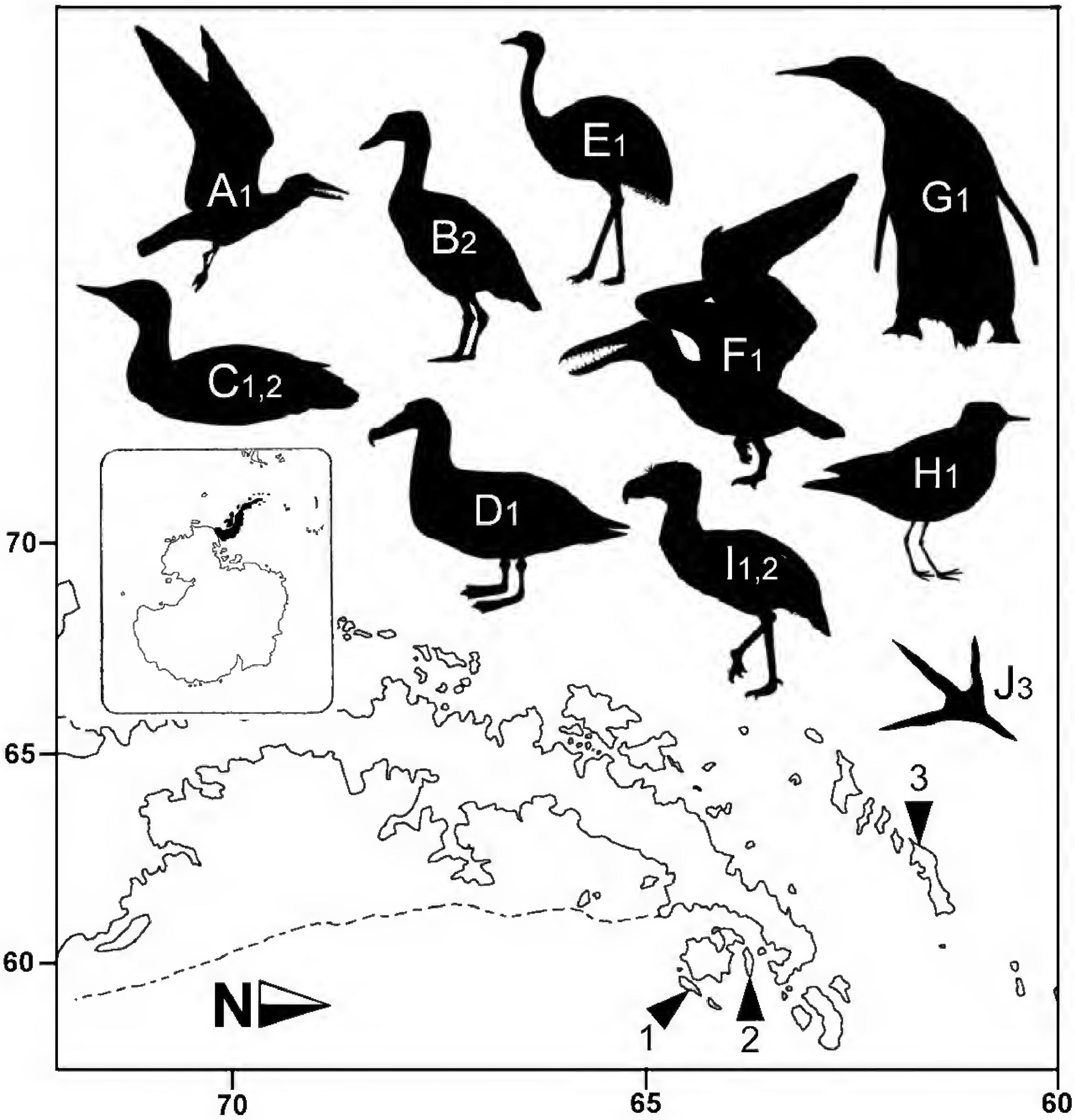

Fig.2- Localities bearing fossil birds in Antarctic Peninsula. Localities: (1) Seymour Island, (2) Vega Island, (3) Rey Jorge Island. Taxa: (A) *Ichthyornis*?, (B) Anseriformes, (C) Gaviidae, (D) Diomedeidae, (E) Ratites, (F) Pelagornithidae, (G) Spheniscidae, (H) Charadriiformes, (I) Cariamae, (J) Tracks.

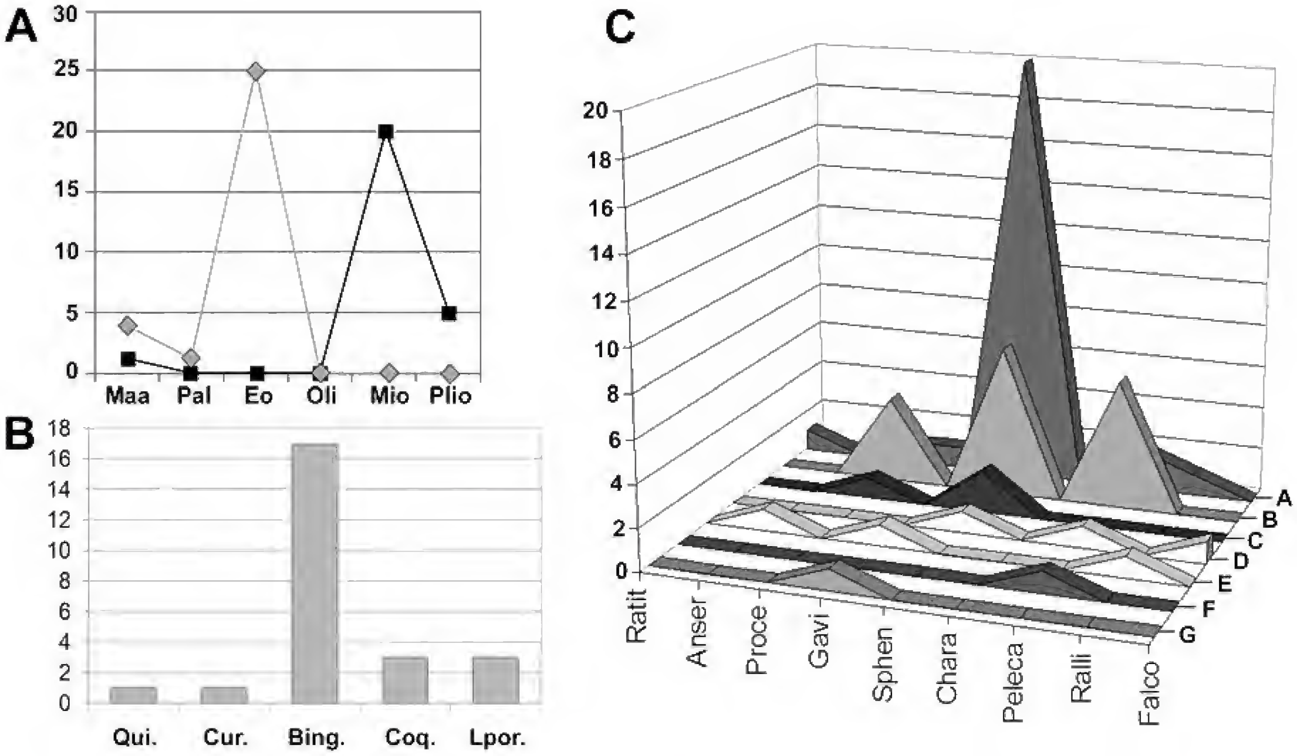

Fig.3- (A) Comparison of fossil bird record of Chile and Antarctic Peninsula considering geological periods. Both areas possess Cretacic records. The Antarctic record (gray rhombus), during Cenozoic, is restricted to Paleogene, whilst Chilean records (black squares) are restricted to Neogene. (Maa) Maastrichtian, (Pal) Paleocene, (Eo) Eocene, (Mio) Miocene, (Plio) Pliocene; (B) total numbers of records in the main Chilean formations. Bahía Inglesa Formation is the place where the greatest number of records has been obtained. (Qui) Quiriquinas, (Cur) Curamallin, (Bing) Bahía Inglesa, (Coq) Coquimbo, (Lpor) La Portada; (C) species recorded by order in the fossiliferous localities of Chile and Antarctic Peninsula. Seymour Island and Bahía Inglesa possess the greatest diversity of fossil birds. (Ratit) Ratites, (Anser) Anseriformes, (Proce) Procellariiformes, (Gavi) Gaviiformes, (Sphen) Sphenisciformes, (Chara) Charadriiformes, (Peleca) Pelecaniformes, (Ralli) Ralliformes, (Falco) Falconiformes. (A) Seymour Island, (B) Bahía Inglesa, (C) Coquimbo, (D) La Portada, (E) Vega Island, (F) Curamallin, (G) Quiriquina.

TABLE 1. Species of birds typified in Chile and Antarctic Peninsula in chronological order.

Delphinornis larsenii Wiman, 1905
Anthropornis nordenskjoeldii Wiman, 1905
Anthropornis grandis (Wiman, 1905)
Palaeeudyptes gunnari (Wiman, 1905)
Neogaeornis wetzelli Lambrecht, 1929
Archaeospheniscus wimani (Marples, 1953)
Palaeeudyptes klekowskii Myrcha, Tatur & del Valle,1990
Meganhinga chilensis Alvarenga, 1995
Delphinornis gracilis Myrcha, Jadwiszczak, Tambussi, Noriega, Gaździcki, Tatur & del Valle, 2002
Delphinornis arctowskii Myrcha, Jadwiszczak, Tambussi, Noriega, Gaździcki, Tatur & del Valle, 2002
Mesetaornis polaris Myrcha, Jadwiszczak, Tambussi, Noriega, Gaździcki, Tatur & del Valle, 2002
Marambiornis exilis Myrcha, Jadwiszczak, Tambussi, Noriega, Gaździcki, Tatur & del Valle, 2002
Polarornis gregorii Chatherjee, 2002
Spheniscus chilensis Emslie & Guerra, 2003
Vegavis iaai Clarke, Tambussi, Noriega, Erickson & Ketcham, 2005
Crossvallia unienwillia Tambussi, Reguero, Marenssi & Santillana, 2005
Pygoscelis calderensis Acosta-Hospitaleche, Chavez & Fritis, 2006
Pygoscelis grandis Walsh & Suarez, 2006
Tonniornis mesetaensis Tambussi, Acosta Hospitaleche, Reguero & Marenssi, 2006
Tonniornis minimum Tambussi, Acosta Hospitaleche, Reguero & Marenssi, 2006

ANSERIFORMES

Anseriforms are cosmopolitan aquatic (mostly freshwater) birds. The greatest variety of species has been found in the Southern Hemisphere.

Fossil records are restricted to the Antarctic Peninsula. *Vegavis iaai* (CLARKE *et al.*, 2005) of Vega Island, Maastrichtian in age, was described on the basis of materials mentioned originally as a possible Presbyornithidae (NORIEGA & TAMBUSSI, 1995). The holotype of *V. iaai* consists of a partially disarticulated skeleton enclosed in a concretion, which made the initial observation of diagnostic characters for the specimen difficult. Later studies demonstrated that the skeletal proportions of *V. iaai* are different from those observed in the Presbyornithidae. There are no characters suggesting a stronger affinity with Presbyornithidae than with the Anatidae, resulting in an unresolved tricotomic position with both families (CLARKE *et al.*, 2005). This record is consistent with the hyphotesis of a Gondwanic origin of the clade and suggests an early radiation of the order (OLSON, 1989; CLARKE *et al.*, 2005).

PROCELLARIIFORMES

This order comprises four families of variable size sea birds that live in all the oceans. Many of them are associated with cold currents. The actual greatest diversity is found in the Southern Hemisphere.

The Diomedeidae includes the largest living seabirds. They are concentrated in the southern seas between S 45° and 70°, reaching the Northern Hemisphere in the Pacific Ocean. The earliest record of the family on the hemisphere was found in the Late Eocene of the La Meseta Formation on Seymour Island (TAMBUSSI & TONNI, 1988). The worldwide family record is more abundant in the Neogene and the fossil records in South America are concentrated along the Pacific coast. The work undertaken in the Bahía Inglesa Formation (Late Miocene) in the Atacama Region includes the first mention of procellariiforms for Chile. This material was referred to post cranial elements of *Diomedea* sp. (WALSH & HUME, 2001). Just recently new elements have been identified from the bonebed of the same formation. They include a partial skull assigned to *Diomedea* (MPC1011) (Fig.4A) and two indeterminate ones, possibly close to *Thalassarche* (MPC1012, MPC1015) (Fig.4B) (CHAVEZ, 2005a). The size of the known elements is congruent with the size range of *Thalassarche* although this does not necessarily indicate a taxonomic affinity. Consequently, it is not possible to determine a generic identification by now. Additionally, fragmentary material has been identified from the Coquimbo Formation in Chañaral de Aceituna, Atacama Region, although its affinity is yet undetermined (MPC1018) (Fig.4C) (CHAVEZ, 2005b).

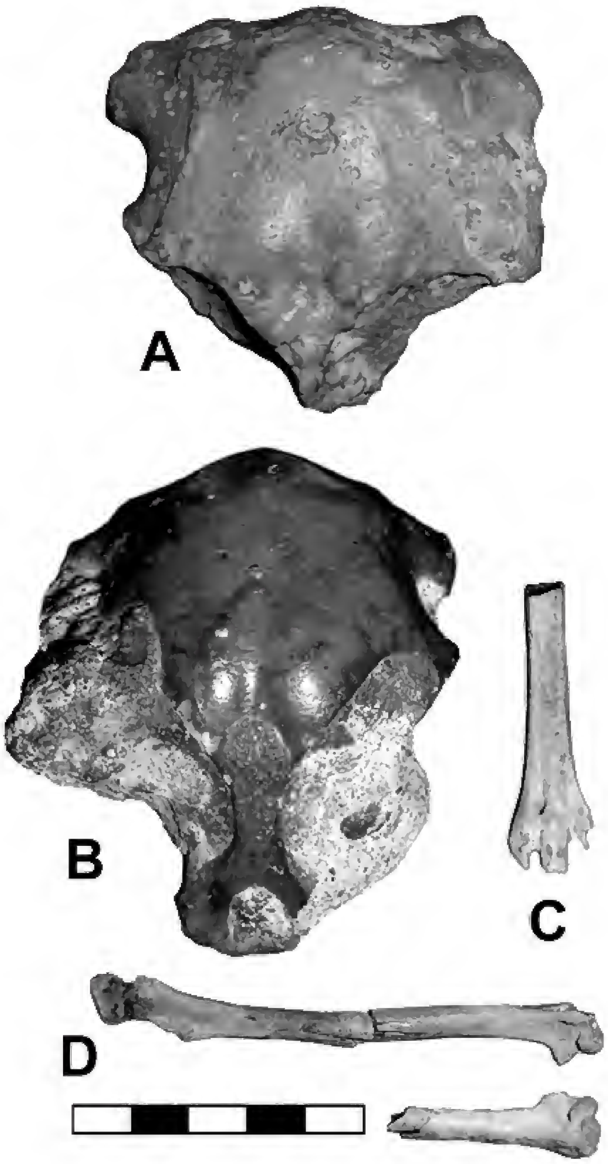

Fig.4- Procellariiformes. Diomedeidae: (A) cf. *Diomedea*; partial skull (MPC1011) and (B) aff. *Thalassarche*?; partial skull (MPC1012); both from Bahía Inglesa Formation (Late Miocene). (C) Diomedeidae indet.; distal portion of right tarsometatarsus (MPC1018) from Coquimbo Formation (Late Miocene). Procellariidae: (D) Right humerus (MPC1013) and left distal extreme of humerus (MPC1014) from Bahía Inglesa Formation (Late Miocene). Scale bar = 5cm.

The family Procellariidae is distributed from the Artic Ocean to the Antarctic Ocean and it has a wide trophic niche and a wide diverse body size range. In Chile, records of the Procellariidae are limited to the Bahía Inglesa Formation where two species have been reported. It represents an indeterminate member of the tribe Puffini and is based on two partial humeri (MPC1013, MPC1014) (Fig.4D) from the nearby sands of the Miocene bonebed levels of the formation (Chavez, 2005a). This extensively distributed tribe comprises the genera *Puffinus*, *Calonectris*, *Lugensa*, and *Ardenna*. The dorsoventral compression of the diaphysis and the supracondylar ventral area of these specimens are similar to those of *Puffinus* and *Ardenna*. The close morphological similarity of these genera hinders differentiation based on osteology, thus the referring evidence to a particular genera for these fragmentary fossils is avoided. The latter taxon is represented by cranial elements assigned to the genus *Pachyptila* (Sallaberry *et al.*, 2007). At present, this genus is restricted to cold currents in the Southern Hemisphere and considered as an indicator of such conditions (Olson, 1983; Chavez, 2005a). The limited record of Procellariids in Chilean formations is probably a result of taphonomic factors or collection biases. It is hoped that future prospecting will provide new and better handled materials to be studied.

Gaviiformes

This order comprises a unique Holartic bird family which is marine but visiting freshwater.

Neogaeornis wetzelli Lambrecht, 1929 from the Tumbes Peninsula, Bio-Bio Region, was originally considered a Baptornithidae. This idea has been retained by some authors (*e.g.*, Cracraft, 1982; Feduccia, 1999). Later studies reassigned it to the modern family Gaviidae (Olson, 1992). The holotype (GPMK 123) comprises an incomplete tarsometatarsus. A second specimen from San Vicente Bay, Bio-Bio Region (Oliver-Schneider, 1940), has not been correctly described. Both specimens from the Quiriquina Formation (Maastrichtian) represent the only cretaceous records from Chile. *Polarornis gregorii* Chatterjee, 2002 was described from the Lopez de Bertodano Formation (Maastrichtian) on the Seymour Island. The holotype consists of a partial skeleton which includes a "well-preserved skull" (Chatterjee, 1997, 2002), although the illustrations are not sufficiently descriptive and some authors (*e.g.*, Martin, 1998; Feduccia, 1999) regard the state of preservation and interpretation of that material as doubtful. Substantial parts of the skull were reconstructed and are not preserved in the specimen (Mayr, 2004). In spite of being originally poorly described, the affinity of the material with the Gaviidae seems to be supported. The specimens exhibit similarities with *Colymboides* of the Paleogene of Europe and North America (S.Olson, pers. comm., 2005). Recently, a new species of *Polarornis* has been suggested (Chatterjee *et al.*, 2006). The synonymy of *Polarornis* with *Neogaeornis* is not discarded (Mayr, 2004) although new revisions are required to confirm such proposal. A close relationship between this Holartic order and other ones better represented in the Southern Hemisphere, such as the Sphenisciformes and Procellariiformes, has been suggested (*e.g.*, Olson, 1985, 1992). Therefore, the early incidence of the family in this hemisphere can be related to the meridional origin of this order and its early radiation during the Cretaceous.

Sphenisciformes

The Sphenisciformes consist of only one highly derived seabird family. These birds are adapted for wing-propelled diving. They are restricted to the Southern Hemisphere and associated with cold currents.

They are the most abundant birds in the Cenozoic marine deposits of the Southern Hemisphere. The earliest record comes from the Late Paleocene of the Cross Valley Formation in Seymour Island and is based on an isolated humerus recently accepted as a new species of penguin (Tambussi *et al.*, 2005a). The La Meseta Formation (Late Eocene) of Seymour Island is one of the richest deposits of fossil penguins in the world (Fig.5). It has been studied by several authors (*e.g.*, Wiman, 1905; Marples, 1953; Simpson, 1971). Nevertheless, the fragmentary state of the specimens and the criteria used for their classification have hindered the correct interpretation of these materials (Fordyce & Jones, 1990; Fordyce, 1991). Only recently revisions of the collections have been undertaken, allowing a better understanding of penguin diversity during the Antarctic Paleogene. For the present summary, the species proposed by Myrcha *et al.* (2002) have been validated. These authors reviewed the species based on tarsometatarsus, indicating a minimum of nine species and a total of 15 records. Other related studies indicate a minimum of nine species and a total of 10 records

(Jadwiszczak, 2006a; Tambussi *et al.*, 2006). Two taxa have been excluded in the present work: *Wimanornis seymourensis* Simpson, 1971 for not being considered as a distinct species, and *Ichtyopteryx garcilis* Wiman, 1905 which was excluded because it was considered a *nomen dubium* (Jadwiszczak, 2006a).

This abundance of sympatric species in Antarctica has led some authors to have little confidence in the diagnostic criteria used since diagnoses have mostly been based on isolated bones, particularly the tarsometatarsus and humerus (*e.g.*, Olson, 1985; Fordyce & Jones, 1990; Jadwiszczak, 2006b). Recent analyses of the morphological variability of such elements suggest that they can partially contribute to the generic differentiation but that their effectiveness is limited for specific differentiation. The tarsometatarsus seems to be a better source of taxonomic information (Walsh *et al.*, 2004; Jadwiszczak, 2006b). Nevertheless, it is clear that the penguins of the La Meseta Formation differ strongly from the forms observed in the Neogene, showing a marked tendency to reach a greater size than those of the living forms, with few exceptions as for example *Delphinornis* and *Tonniornis*.

The similarities between the Eocene penguins found in Antarctica and New Zealand have been mentioned several times (*e.g.*, Marples, 1953; Simpson, 1971; Fordyce, 1991) and there exist shared genera between both localities (*Palaeeudyptes* and *Archaeospheniscus*) as well as with Australian Oligocene localites (*Anthropornis*) and recently new related genera are found in Peruvian localities (Clarke *et al.*, 2007). This suggests an early and strong interaction among the spheniscid populations in the austral seas (Tambussi *et al.*, 2006).

Just recently, advances in the study of Chilean fossil penguins have revealed a wide record in the Neogene deposits. The greatest diversity comes from the bonebed of the Bahía Inglesa Formation, for which seven records are known (Chavez, 2007) including partial skulls. A first study of the avifauna from that formation postulated the existence of the genera *Palaeospheniscus* and *Paraptenodytes* described originally from the Early Miocene of Argentina (Fritis, 2001).

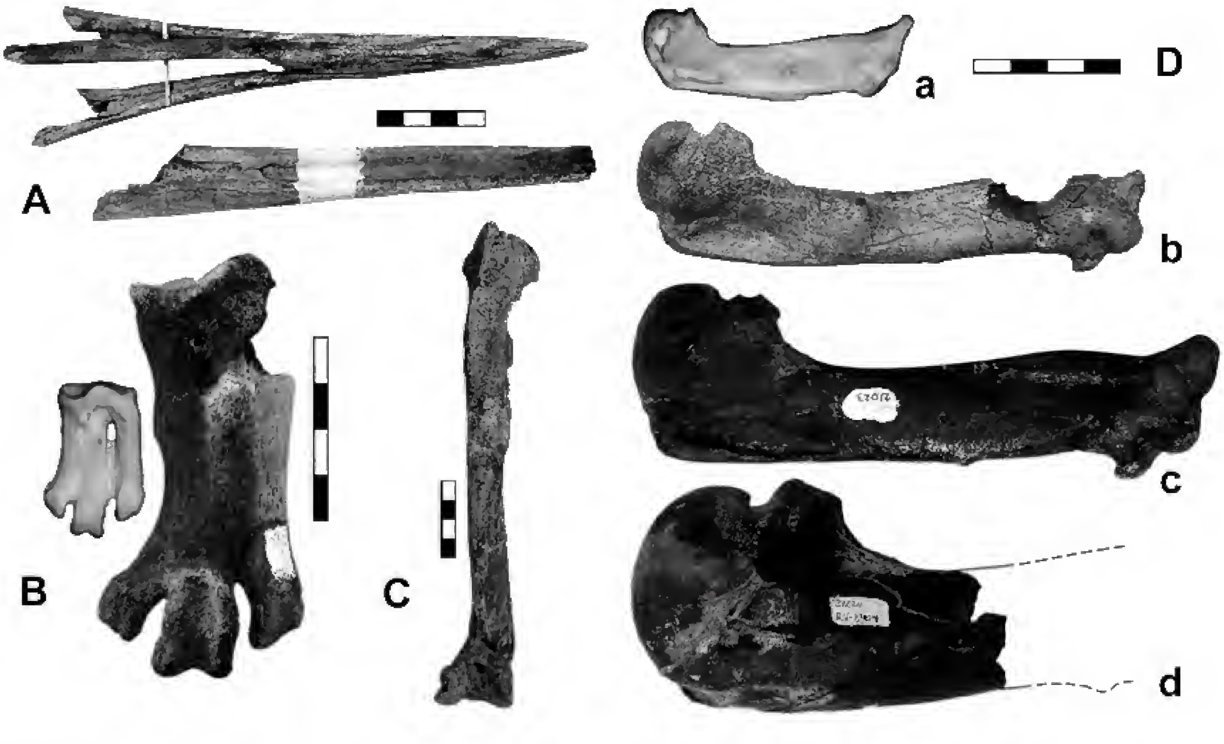

Fig.5- Spheniscids from Eocene of Seymour Island, Antartica. (A) ?*Palaeeudyptes* sp.; anterior portion of rostrum in dorsal view (USNM 244152) and left mandibular fragment in medial view (USNM 244151). (B) Spheniscidae indet. cf. *Anthropornis*; left tarsometatarsus (USNM 21032) compared with *Spheniscus humboldti*. (C) Spheniscidae indet. cf. *Anthropornis*; left tibiotarsus (USNM 402212). (D) Comparison of right humeri: (a) *Spheniscus humboldti*; (b) *Palaeeudyptes gunnari* (USNM 21027); (c) *Palaeeudyptes antarticus* (USNM 21023); and (d) Spheniscidae indet. (USNM 21124). Scale bar = 4cm. Photographs by Marcelo Stucchi.

Later on, these conclusions were accepted (Acosta-Hospitaleche *et al.*, 2002; Acosta-Hospitaleche & Tambussi, 2004; Tambussi *et al.*, 2005b). Nevertheless, neither a formal description of materials nor a detailed diagnostic verification have been carried out. The work of O. Fritis is the most extensive about this, although his work does not present characters that validate the specific identifications. Similarly, the association of skull material to *Palaeospheniscus* has been undertaken using criteria which cannot be widely accepted. Fritis (2001) recognizes a close similarity of the skulls with the genus *Spheniscus*. He assigned them to *Palaeospheniscus* because he considered that *Spheniscus* had appeared during the Late Pliocene. More recently, Acosta-Hospitaleche & Canto (2005) assigned isolated skulls (*e.g.*, SGO–PV 1063) to the genus, considering as improbable their correspondence with other Spheniscidae of the formation. However, they did not present characters that differentiate the specimens from the genus *Spheniscus*. Recently, the species proposed by Acosta-Hospitaleche *et al.* (2002) have been revised by Chavez (2007). Additionally, the first assignable remains to *Spheniscus urbinai* Stucchi, 2002 (MPC1007) and *S. megaramphus* Stucchi, Urbina & Giraldo, 2003 (UOP/01/89; MPC1008; MPC1009) (Walsh, 2004; Chavez, 2005a), originally described for the Miocene of Peru (Stucchi *et al.*, 2003) have been presented. One of the characteristics of both species is that they are between 25% and 30% larger in size than the living species of the genus, being differentiated only by cranial elements. Due to this fact, the author has only referred isolated rostrums for these species (Chavez, 2005a), though they are coincident with the size range of the majority of the postcranial elements known from the formation. It is probable that the materials previously reported as cf. *Spheniscus* (UOP/01/93) (Walsh & Hume, 2001), belong to one of these two species (Walsh, 2004). Additionally, congeneric materials are known in the Pliocene levels of the Bahía Inglesa Formation (MPC1020), which are in the size range of the current species of the genus (Walsh, 2004; Chavez, 2005a). Similarly, a spheniscid with affinities to the modern genus *Pygoscelis* (Fritis, 2001; Acosta-Hospitaleche *et al.*, 2002) has been mentioned and recognized as a new species, *Pygoscelis calderensis* Acosta-Hospitaleche, Chavez & Fritis, 2006, that was described on the basis of partial skulls (*e.g.*, SGO–PV 790). The existence of a second species, *Pygoscelis grandis* Walsh & Suarez, 2006, has been mentioned from the Late Miocene and Pliocene of the formation. Its size is similar to the current genus *Aptenodytes*. At present, the genus is restricted to Antarctic and sub Antarctic regions. This close association with cold environments suggests the existence of these conditions for the coast of Chile during the Miocene.

The abundance of fossils and the existence of young individuals suggest the presence of reproductive colonies in the area.

Other specimens are known from the Coquimbo and Chañaral de Aceituna localities (Coquimbo Formation) with the presence of Spheniscidae indet. cf. *Palaeospheniscus* and *Spheniscus* sp. (MPC1016; MPC1017) (Acosta-Hospitaleche *et al.*, 2006a; Chavez, 2005b) and La Portada Formation (Late Pliocene) in Antofagasta Region with the presence of *Spheniscus chilensis* Emslie & Guerra, 2003.

Charadriiformes

This is the most diverse and numerous order of mostly migratory coastal birds. The greatest variety is found in the Northern Hemisphere. There are currently 13 living families visiting or resident in South America.

The Charadriidae is one of the most widely distributed family of the order living on all continents except frozen zones. Fossil records of the family are limited to the La Meseta Formation (Late Eocene) of Seymour Island (Tambussi & Noriega, 1996). The material has not been published yet, and there are no available descriptions.

Pelecaniformes

These fish-eating birds need sources of water to subsist, and are found mainly on coastal and occasionally lacustrine areas. The five extant families are present in South America.

The Sulidae are well represented along the Pacific coast of South America, unlike the Atlantic coast, where the family is restricted to the northeast border with records in the Argentinian coast. The family is associated with high productive marine areas, particularly of a warm or mild influence. Some species also live in polar areas of the North Atlantic. In Chile, the fossil record is limited to Bahía Inglesa, where the presence of the genus *Sula* has been reported on the basis of postcranial and mandibular materials (Walsh & Hume, 2001). Review of unpublished material in the Museo Paleontologico de Caldera shows a great quantity of skulls, mostly assignable to *Sula*. One of them (MPC1019) (Fig.6A) was previously classified incorrectly as Phalacrocoracidae indet aff. *Hypoleucos* (Fritis, 2001). This sulid corresponds to a big booby, in the size range of *S. dactylatra*. Although the general size and proportions are very similar to those of some specimens collected in the Pisco Formation of Peru (Miocene) (MUSM229) (Stucchi, 2003), the cranial morphology does not permit the assessment for a specific designation. From the illustrations published by Walsh & Hume (2001) it can be observed that the materials are within the expected size range for the mentioned skulls, although the author thinks that only one species in the genus can be identify in the bonebed. Recently a new skull had been identified, representing a bigger species than the previously known and with some characteristics in common with the Peruvian genus *Ramphastosula* Stucchi & Urbina, 2004 (Chavez & Stucchi, 2006). Additionally, the presence of *Morus* in Bahía Inglesa Formation has been suggested (S.Walsh, pers. comm.). More materials are known from the Mejillones Peninsula, referred to *S. variegata* (Murphy, 1936), but originally described as *S. antiqua* (Phillipi, 1895). There are neither images of these materials nor certainty of their exact stratigraphic source, and they have even been mentioned as subfossil remains by many authors (*e.g.*, Nelson, 1978; Mones, 1986). For this reason they have not been included in the present summary.

The Phalacrocoracidae includes the main guano birds of the Pacific coast of South America. They are almost cosmopolitan except for extreme polar zones, dry zones, and oceanic islands. It is the most widely distributed family within the order. Although the fossil record of the family in the area is very poor, living representatives are abundant. The only known records are related to isolated fragments from the Bahía Inglesa Formation (Walsh & Hume, 2001) and La Portada (Emslie & Guerra, 2003). Only a generic identification can be approached, *Phalacrocorax* sp., in both cases. The specimens found in Bahía Inglesa correspond to a large cormorant with similar dimensions presented by *P. bougainvilli*. With regard to the specimen of La Portada, it belongs to a small bird, similar in size to *P. brasilianus* although particular morphological affinities are difficult to establish (Emslie & Guerra, 2003). Size differences are significant; hence, it is possible to consider them as different species. A report of remains from guano sites of Tarapaca, described as *P. sulcatus* (Phillipi, 1895) lacks images of the material and does not provide a confident stratigraphic provenance. The specimens are considered as Quaternary and not included in the appendix.

The current deposit of these material is unknown and *P. sulcatus* must be considered a *nomen dubium*.

Fig.6- Pelecaniformes. Sulidae: (A) *Sula* sp.; partial skull (MPC1019) from Bahía Inglesa Formation (Late Miocene). Anhingidae: (B) *Meganhinga chilensis*; right tarsometatarsus (holotype SGO-PV4001) from Curamallin Formation (Early Miocene). Pelagornithidae: (C) *Pelagornis* sp.; proximal extreme of left humerus in palmar view (MPC1000), from Bahía Inglesa Formation (Late Miocene). Scale bar = 5cm.

The Anhingidae comprises at present a single genus of aquatic fish-eating birds, with two allopatric species (*Anhinga anhinga* and *A. melanogaster*). These birds are the only Pelecaniforms living exclusively in freshwater. They are associated with fluvial systems and shallow bays; hence, they are considered continental birds. Their records in Chile are restricted to the Early Miocene (Santacrusian) Malla Malla Member of the Curamallin Formation in Cerro Rucañanco locality, Malleco Province, Araucania Region. The environment is interpreted as fluvial, surrounded by forests in a cold and rainy climate (WALL *et al.*, 1991). The taxon was described as *Meganhinga chilensis* on the basis of postcranial associated elements (Fig.6B) (ALVARENGA, 1995). It is plausible that the material belongs to two individuals of larger size than any known living form. The relative size of the wings with regard to the body proportion suggests that these birds were flightless, so that they were possibly specialized on diving. The incidence of the family is congruent with the proposed fluvial environment. At present, these birds are restricted to template-warm zones or tropical zones what contrasts with the conditions suggested for the formation. The presence of the family in Chile shows a wider distribution during the Tertiary than during the present.

The family Pelagornithidae (Paleocene-Pliocene) constitutes one of the most spectacular and mysterious bird clade within Aves. These worldwide birds reached a large wingspan, being characterized by extreme pneumatic bones and the existence of numerous bone projections like teeth along the tomial margins. Remains found in undetermined strata of La Meseta Formation, Seymour Island are known. They probably belong to two species dated as Eocene in age (TONNI, 1980; TONNI & TAMBUSSI, 1985). Specimens correspond to the earliest record of the family in the southern hemisphere. In Chile, most of the records come from the bonebed of Bahia Inglesa Formation from which diverse specimens have been recovered (WALSH, 2000; WALSH & HUME, 2001; CHAVEZ, 2001; CHAVEZ & STUCCHI, 2002). Some of the previously reported cranial elements have been associated to the genus *Pseudodontornis* (MPC1001; MPC1002; MPC1003) (CHAVEZ & STUCCHI, 2002). Nevertheless, the use of cf. *Pelagornis* is recommended for the specimens due to the complex taxonomy of the group and the insufficiently established diagnosis (CHAVEZ *et al.*, 2007). The only elements which can be generically identified correspond to a partial humerus (MPC1000) (Fig.6C) recently assigned to *Pelagornis* (CHAVEZ *et al.*, 2007).

RALLIFORMES

These birds belong to a heterogeneous continental order, occupying most of the families present in South America lacustrine habitat.

The family Phorusrhacidae was one of the main groups of predators during the isolation of South America during the Tertiary. They were cursorial and flightless birds. They have different sizes and play different roles as predators. The record of these birds corresponds to a pre-maxillar fragment coming from La Meseta Formation (CASE *et al.*, 1987). It has been suggested recently that the material would correspond to the mandibular symphysis of a Brontornithinae, close to *Brontornis* (ALVARENGA & HOFLING, 2003). More recently, a new possible record of these birds has been reported from the Late Cretaceous of the Lopez de Bertodano Formation on Vega Island, Antarctica (CASE *et al.*, 2006). The presence of this family in the Antarctic continent demonstrates the permanent faunistical interchange during the Paleogene facilitated by its geographical connection between South America and West Antarctica.

FALCONIFORMES

Falconiforms belong to the order of diurnal birds of prey. They are small and medium sized birds. They tend to be cosmopolitan and play very different roles such as aerial predators, scavengers or opportunistic birds. South America concentrates the highest variety of these taxa.

There is only one record of this family in Chile, *Milvago* sp., coming from Mejillones Peninsula in Antofagasta Region (EMSLIE & GUERRA, 2003). The material, found within the strata of the La Portada Formation (Late Pliocene) corresponds to a distal fragment of tarsometatarsus. It corresponds to the unique record of a non strictly aquatic birds in Chile and the oldest one for this genus.

ICHNITES

The fossil ichnites constitute indirect evidence of the presence of birds. They can be associated to families or taxa from which taxonomical, ethological, and physiological inferences can be obtained.

The main records of this type in the studied area come from Fossil Hill Formation on Fildes Peninsula, Rey Jorge Island, Antarctica. The formation outcrops at the Southwestern part of the island and it was initially dated as Late Paleogene to Early Neogene (Covacevich & Lamperein, 1970). At present it is considered to be Late Paleogene in age (Paleocene–Eocene) (Torres, 2003). The lithology and fossil flora suggest lacustrine environments, where angiosperms forests of warm and humid climates predominated (Torres, 2003). Four morphotypes have been reported, including the ichnospecies *Antarctichnus fuenzalidae* Covacevich & Lamperein, 1970, originally associated to the family Rallidae (Fig.7D). General similarities of the tracks exist with those of the expected ones for the rails. It is not possible to discard that they could have been made by birds belonging to other families; hence, the initial association can not be supported (Covacevich & Rich, 1982).

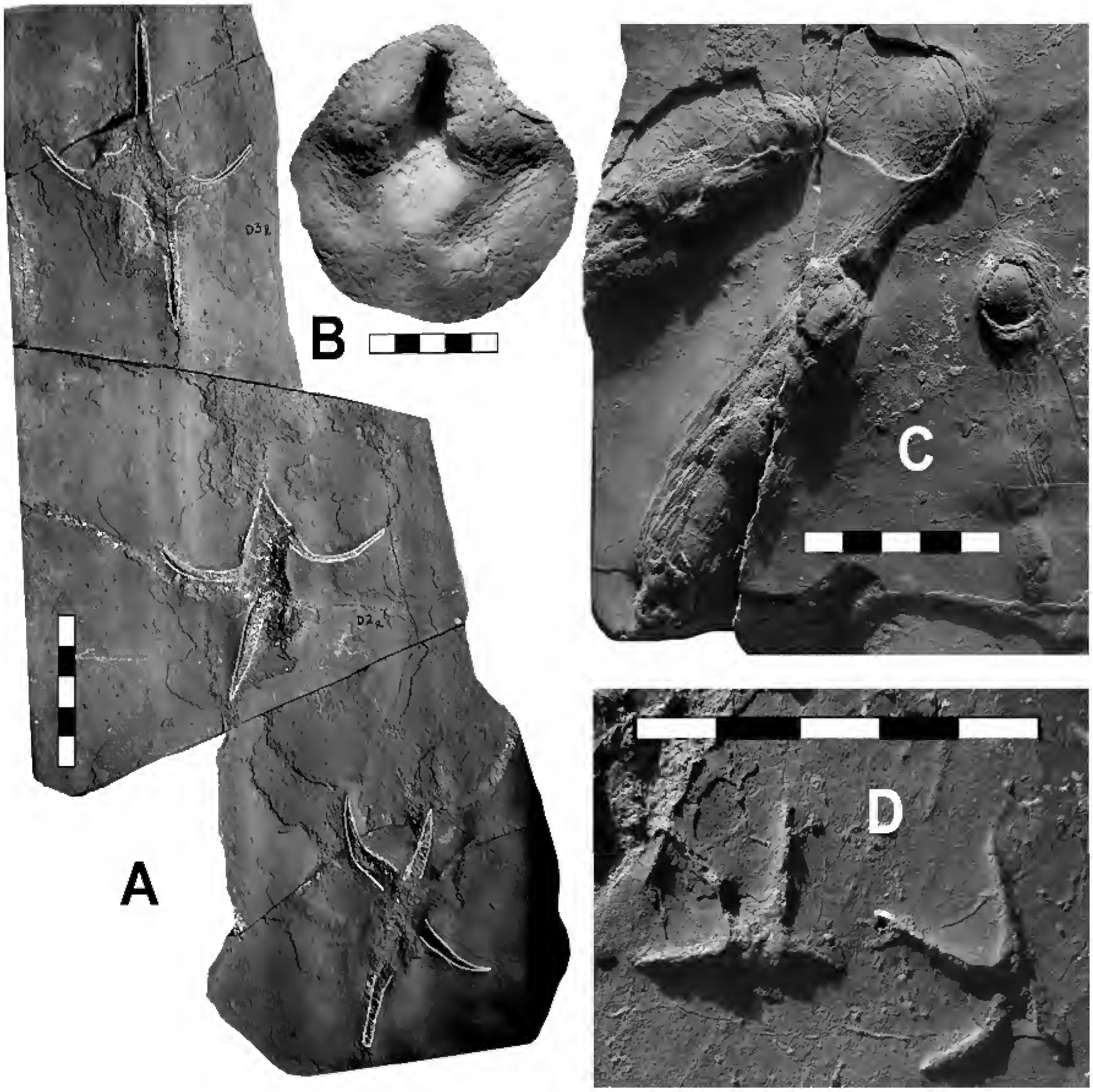

Fig.7- Ichnites from Paleocene-Eocene of Rey Jorge Island, Antartica. (A) Morphotype III (CPDG,T-351) assesses to Aves indet. (B) Morphotype II (plastotype SNGM7695) assesses to Anseriformes indet. (C) Morphotype I (CPDG,T-350) assess to Ratites or Phorusrhacidae indet. D. *Antarctichnus fuenzalidae* Covacevich & Lamperein, 1970 (holotype CPDG,T-353). Morphotypes *sensu* Covacevich & Rich, 1982. Scale bar = 5cm.

The rest of the morphotypes offered by COVACEVICH & RICH (1982) correspond to ichnites which were related to a medium sized anseriform (Fig.7B), to a big cursorial bird (Ratites or Phorusrhacidae) (Fig.7C) and to a medium sized bird of undeterminated classification (Fig.7A). It is not possible for the moment to discard or confirm the taxonomical associations suggested for the tracks. Nevertheless, the paleoichnological evidence of big cursorial birds in the Paleogene on the Antarctic is congruent with the fragmentary fossil records of Ralliformes and Ratites on that continent.

The only mention of bird ichnites in Chile correspond to COVACEVICH (1989) from the El Cóndor Formation (Early Miocene) in Tierra del Fuego. The report is poorly descriptive and there is no formal publication about it.

DISCUSSION AND CONCLUSIONS

THE MESOZOIC RECORDS AND THE ANTARCTIC PALEOGENE

There are three known sites with records of Mesozoic birds within the studied area. The only Chilean records correspond to Quiriquina Formation in Tumbes Peninsula, Concepcion Province, Bio-Bio Region. Although there is a relative abundance of vertebrates described for the formation (*e.g.*, SUAREZ *et al.*, 2003), there are only two mentions related to birds (LAMBRECHT, 1929; OLIVER-SCHNEIDER, 1940). The formation is Maastrichtian in age (STINNESBECK, 1986) and corresponds to marine depositional environments. The fragmentary state of the materials have hindered their interpretation, nevertheless, they confirm the presence of birds in the Occidental border of South America during the Cretaceous period. The other two known sites are located in the Antarctic Peninsula. The marine Lopez de Bertodano Formation, in the southern of Seymour Island, ranges from Maastrichtian to Paleocene and corresponds to the unit containing *Polarornis* whose associated fauna confirms its association with the Cretaceous strata of the formation (CHATTERJEE, 2002). Additionally, Seymour Island is the known location of *Ichthyornis* (ZINSMEISTER, 1985). Otherwise, Vega Island records includes *Vegavis* described for the unit K3 in the locality VEG 9303 (CLARKE *et al.*, 2005), a new species of *Polarornis* (CHATTERJEE *et al.*, 2006) and a possible Cariamae, all from the Lopez de Bertodano Formation (CASE *et al.*, 2006).

The world record of Neornithes for the Mesozoic is very poor and highly fragmentary. This hinders the precise moment determination of the origin of the modern birds (DYKE & VAN TUINEN, 2004; FOUNTAINE *et al.*, 2005). In this context, the Antarctic records are considered as exceptional since they consist on partial specimens (*e.g.*, CHATTERJEE, 2002; CLARKE *et al.*, 2005). The probable presence of Anseriformes in the Antarctica is consistent with the hypothesis of an austral origin of the order (OLSON, 1989), whereas the presence of loons in the Southern Hemisphere not only has phylogenetic implications but also suggests a strong change in the distributional area of that order nowadays, restricted to the Northern Hemisphere. The environmental conditions suggested for the formation containing Gaviidae in the Antarctica are congruent with the habitats occupied by these birds at present: marine areas under the influence of cold periods (TORRES, 2003). However, the true phylogenetic meaning of these specimens have been discussed, specially in the case of *Polarornis* (FEDUCCIA, 1999; MARTIN, 1998; DYKE & VAN TUINEN, 2004), which renders important repercussions, since the placement of this taxon on the Gaviidae-crown to calibrate molecular clocks, throw doubts about the results (VAN TUINEN & HEDGES, 2004). In this sense, with *Vegavis* more plausible results could be obtained (CLARKE *et al.*, 2005; SLACK *et al.*, 2006).

The lack of information about Paleogene Chilean ornithofauna does not allow knowing properly the early development of these ecosystems and the exact origin of the current diversity, which was probably established for the Late Neogene. Only recently the first records of Spheniscidae for the Eocene of the South American Pacific in Peru have been presented (ACOSTA-HOSPITALECHE & STUCCHI, 2005; CLARKE *et al.*, 2007). In this context, the Antarctic record is quite interesting since it represents the richest area in Paleogene formations of the Austral–Antarctica region. The only Paleocene record comes from Cross Valley Formation, in the Southern border of Seymour Island (TAMBUSSI *et al.*, 2005a). Although, La Meseta Formation on the northern part of the Seymour Island represents the richest formation in fossil birds of the Antarctic continent it is dated as Eocene (DINGLE & LAVELLE, 1998; MYRCHA *et al.*, 2002; TORRES, 2003).

The incidence of penguins has been recorded from the Paleocene to the Late Eocene. It is probable that the penguins have been continually present from the Paleocene to the present time, but the absence of Neogene records does not permit confirmation of that. The earliest records come from the Paleocene of Antarctica and New Zealand (Slack *et al.*, 2006; Tambussi *et al.*, 2005a) represented by early forms adapted to wing-propelled diving. The possible existence of other basal forms in the Eocene of Tierra del Fuego (Clarke *et al.*, 2003) suggests a very early dispersion of the group around the meridional continents and a probable Antarctic origin of the order. This has been recently suggested on the basis of molecular studies (*e.g.*, Baker *et al.*, 2006). The high amount of recorded species raises unresolved issues about the early systematics and ecology of these fossil birds. At present, penguins tend to live in sympatry forming mixed colonies in South America, Antarctica, New Zealand (and several subantarctic islands) being this last area the one that concentrates the greatest diversity with a maximum of eight species (Acosta-Hospitaleche, 2004). The fossil records also suggest abundance of sympatryc species in other localities, such as Argentina, Chile, and New Zealand (Acosta-Hospitaleche, 2004). The existence of so many sympatric fossil species can be explained by the descriptive criteria used (Fordyce & Jones, 1990). Nevertheless, it is clear that during the Paleogene there were a wide variety of penguins in the austral seas and in the areas where these birds could live in sympatry.

Among the orders registered in Paleogene formations, the Pelecaniforms, Charadriiforms, Sphenisciforms, and Procellariiforms are still present in the area nowadays. Only Sphenisciforms and Procellariiforms have temporal continuity within the current families (Spheniscidae and Diomedeidae). The record of continental birds from La Meseta Formation permits verification of the presence of typical forms of the South American fauna in the Antarctic continent (Phorusrhacidae and Ratite), which is an evidence of the faunistical continuity within both areas during the Paleogene.

The decline of the diversity of birds in the Antarctic continent is associated with the successive glaciations which affected the continent. However, the absence of Neogene records does not permit a better understanding of this process.

The avifauna of the Neogene in the Southeastern Pacific

The ornithofauna of the Neogene formations along the South American Pacific coast has been only recently investigated. The greatest vertebrate diversity has been found in two formations: Pisco Formation, in the Southern of Peru, and Bahía Inglesa Formation, in northern Chile. The Peruvian formation is the most extensively studied formation, being notable for the studies about fossils of marine mammals (*e.g.*, Muizon, 1984, 1988), and fossil birds (*e.g.*, Stucchi, 2002, 2003). More recently, the Bahía Inglesa Formation has yielded a rich record, which has demonstrated the similarity of the taxa present in both areas.

The first mentions of fossil birds from the Bahía Inglesa Formation were done during different scientific conferences (*e.g.*, Walsh, 2000; Chavez, 2001). Fritis (2001) studied fossil birds of Bahía Inglesa for the first time, in particular Sphenisciformes. However, he did not provide reliable results. Walsh & Hume (2001) undertook the most extensive revision of the ornithofauna of that formation, reporting five taxa. Later on, new species have been reported (*e.g.*, Acosta-Hospitaleche *et al.*, 2002; Chavez & Stucchi, 2002; Chavez, 2005a). This formation, that outcrops in the coast of the Atacama region, is represented by coquinas, sandstone, and phosphorites. The phosphatic sediments have yielded marine vertebrate fossils called the bonebed. Micropaleontological studies assessed it on an age that ranges from Middle Miocene to Pliocene, suggesting marine environments from sublitoral to neritic, strong climatic fluctuations, and influenced by subantartic to warm waters (Marchant *et al.*, 2000). Recently, the minimal age of the formation has been extended to the Late Pliocene (Achurra, 2004; Walsh & Suarez, 2005).

The reports from other formations of similar age on the coast of Chile and Peru complement the observations made in Pisco and Bahía Inglesa. Two sites in the Coquimbo Formation have records of fossil birds: Chañaral de Aceituna in Huasco Province, Atacama Region (Chavez, 2005b), and Coquimbo in Elqui Province, Coquimbo Region (Acosta-Hospitaleche & Tambussi, 2004; Acosta-Hospitaleche *et al.*, 2006a). The outcrop units on the coast of Atacama and Coquimbo regions include coquinas, sandstone, and conglomerates types of strata (Moscoso *et al.*, 1982). Martinez (1979) proposed a shallow and warm water environment, assessing most part of the column to the Middle Miocene. Recently, the review of chondrichthyes findings has corroborated this time-date and suggests a correlation with Bahía Inglesa Formation (Suarez & Marquardt, 2003). The reported ornithofauna complement these observations because the taxa of both formations are similar, in particular, the sphenisciform specimens. The geographical and faunistical continuity of Coquimbo and Bahía Inglesa formations and their lithological similarities and possible synchronization, suggest a close relationship within both units. It is not possible to discard the synonymy between Coquimbo and Bahía Inglesa formations. New geological studies to confirm these observations are needed.

Mejillones Peninsula in Tarapaca Province, Antofagasta Region, has been mentioned in several occasions as a location bearing fossil birds, being Phillipi (1895) the first one in doing prospections. Only recently, more extensive works have been done and three new records have been formally reported (Emslie & Guerra, 2003). These last reports are the only ones which have been assigned to a specific geological unit: "Caleta Herradura of Mejillones Formation". The Late Cenozoic formations in this location are: Caleta Herradura (Miocene), La Portada (Pliocene), and Mejillones (Quaternary). The geological description and the associated fauna presented by Emslie & Guerra (2003) indicate a Pliocene age, more similar with La Portada Formation. Presently, the author considers that the original assessment of Caleta Herradura Formation is a nomenclatural mistake. Nowadays, it is considered that La Portada Formation includes Miocene sediments of Caleta Herradura (Ferraris & Di Biase, 1978; Marquardt *et al.*, 2003). The fossil record of the Mejillones Peninsula permits to corroborate the presence of manuring birds in the area from the Late Pliocene and a very similar fauna to the one that is now living at the site.

The spheniscids are the most abundant birds in the marine Neogene formations of the southeast Pacific. The known species for the Pisco Formation correspond to *Spheniscus urbinai, S. megaramphus*, and *S.* aff. *humboldti*, all of them found at the Miocene strata of the formation (Stucchi & Urbina, 2005). *Spheniscus urbinai* and *S. megaramphus* have been presented at Bahía Inglesa Formation (Walsh, 2004; Chavez, 2005a). Abundant postcranial materials of similar size in this and other formations are known (Chavez, 2005b; Chavez, 2007) suggesting a wide distribution of these species in the southern Pacific coast of South America. It is thought that the distribution of the genus *Palaeospheniscus* might be wider, living not only in the Atlantic but also in the Pacific coasts of the South American continent. It was recorded to the Early Miocene in the Gaiman Formation (Argentina), Chilcatay (Peru) (Acosta-Hospitaleche, 2004; Acosta-Hospitaleche & Stucchi, 2005), and possibly in the Miocene of Coquimbo Formation (Acosta-Hospitaleche *et al.*, 2006a). Similarly, the genus *Paraptenodytes* has been reported for both coasts in the Early and Late Miocene of the following argentinean formations: Monte Leon, Gaiman and Puerto Madryn (Acosta-Hospitaleche, 2003, 2004) and possibly in the Miocene of Bahía Inglesa (Acosta-Hospitaleche *et al.*, 2002). The presence of these two genera is tentative, by now (Chavez, 2007). At present, South American Spheniscidae is better represented in the Pacific coast, occupying only the austral extreme of the Atlantic coast. The diversity of fossil penguins, exclusive of the Chilean coast corresponds to *Pygoscelis calderensis*, *Pygoscelis grandis*, and *Spheniscus chilensis* (Acosta-Hospitaleche *et al.*, 2006b; Walsh & Suarez, 2006; Emslie & Guerra, 2003). This high diversity of penguins in the south eastern Pacific coincided with a strong glacial advance in the Antarctic region and the second great radiation of living species, suggested on basis of recent molecular studies (Baker *et al.*, 2006).

The Procellariiformes and Pelecaniformes known for Bahía Inglesa Formation are similar to those from Pisco Formation. Though the Procellariiformes record in Pisco is rather poor, it is congruent with those of Chilean families. Puffini remains and Diomedeidae remains of similar size are recognized in both localities (Stucchi & Urbina, 2005). There exist exclusive records from both formations: *Fulmarus* sp. from Pisco (Stucchi & Urbina, 2005) and *Pachyptila* sp. from Bahía Inglesa (Sallaberry *et al.*, 2007). In the case of Pelecaniformes, the size range of Phalacrocoraracidae and some Pelagornithidae and Sulidae coincides in both formations. Sulidae is well represented in Pisco where five species in three genera are known (Stucchi, 2003). Only three species of the genera *Sula* and *Morus* are known from Bahía Inglesa (Chavez & Stucchi, 2006). There is no record of the present existence of *Morus* in South America, being *M. peruvianus* (Stucchi, 2003) from Pisco Formation the only record in this continent. The genus *Pelagornis* is represented in both formations and there exists a smaller Pelagornithidae on the base of Pisco Formation from which there are no records in Chile (Chavez *et al.*, 2007). The Pelecanidae family only appears in Pisco Formation (Stucchi & Urbina, 2005).

The incidence of shore and continental birds is concentrated in Pisco Formation, being *Milvago* sp. from Pliocene of La Portada Formation the only record of non-aquatic birds in Chile (Emslie & Guerra, 2003).

The records exclusive of the Peruvian coast correspond to Scolopacidae, Laridae, Ciconiidae, and Vulturidae (STUCCHI & URBINA, 2005). The absence of these families in Chilean records can have a taphonomic origin, vinculated to the deposition conditions of Pisco Formation, which may have turned it into a more appropriate place to preserve the fossil material (MAROCCO & MUIZON, 1988). Nevertheless it is probable that such birds can be found in future prospections of Bahía Inglesa or other Chilean localities.

Excepting the extinct pelagornithids, all the recorded families are present nowadays on the same territory. Most of extant marine bird families have been living in Chile from the Late Miocene, excepting the order Charadriiformes. Consequently, the marine ornithofauna of the Pacific coast has a strong familiar continuity from the Neogene (Tab.2). This fact and the record of forms close to the current ones in the Pliocene (*e.g.*, La Portada Formation) suggest the definitive settling down of the current marine ornithofauna of the North of Chile towards the end of Neogene. From all the taxa known in the area, only *Ramphastosula* (STUCCHI & URBINA, 2004) and pelagornithids are completely extinct at present. It is known that *Ramphastosula* is a specialized form of bobby whose habits have not been well defined and some authors suggest that the pelagornithids could play a similar role to that of current pelicans and albatrosses (*e.g.*, CHENEVAL, 1993; OLSON, 1985). The extinction of both groups towards the end of the Pliocene was probably the result of climatic changes and the ecological replacement on the part of modern families.

The diversity of Sulidae is greater in Pisco Formation than in the Chilean formations. This family is associated to warm-template conditions in the Southern Hemisphere and high marine productivity zones. Spheniscids and procellariiforms are better represented in the Chilean formation of Bahía Inglesa. Both groups are associated to cold currents, suggesting the same conditions for the Neogene, idea that is congruent with micropaleontological studies (MARCHANT *et al.*, 2000; TSUCHI *et al.*, 1988) and supported by the incidence of *Pygoscelis* and *Pachyptila*. It is probable that these differences in the diversity of both areas are related to a latitudinal temperature falling off, originated by the early antartic influence. If it is so, a major record of cold forms will be expected in the Chilean localities with regard to Peruvian ones, aspects that can be observed at present. Specific studies to confirm this hypothesis are needed.

TABLE 2. Record of representative sea and shore birds, fossil and extant species of Chile and Peru. The number of extant Argentinean species is also offered. Only the Neogene fossil forms are considered. The accidental species from Chile are excluded. The extant species, according to MARTÍNEZ & GONZÁLEZ (2005) and CANEVARI *et al.* (1991) are offered.

	CHILE		PERÚ		ARGENTINA
FAMILY	FOSSIL	EXTANT	FOSSIL	EXTANT	EXTANT
Phaetontidae	0	3	0	2	0
Fregatidae	0	1	0	2	0
Sulidae	3	3	9	6	0
Phalacrocoracidae	2	6	2	3	6
Anhingidae	1	0	1	1	1
Pelecanidae	0	1	1	1	0
Pelagornithidae	1	--	2	--	--
Diomedeidae	3	12	1	8	8
Procellaridae	2	26	2	26	22
Spheniscidae	10	9	5	2	5
Vulturidae	0	3	1	6	6
Laridae	0	22	1	27	21
Scolopacidae	0	20	2	36	24

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APPENDIX

List of fossil birds from Chile and Antarctic Peninsula know from the Cretaceous to late Pliocene.

	Taxon	Locality	Stratigraphy	Reference
ICHTHYORNITHES				
1	*Ichthyornis*? sp.	Seymour Island, Antarctic Peninsula, Antartica	Late Cretaceous	Zinsmeister, 1985
RATITES				
2	Ratites *incertae sedis*	Seymour Island, Antarctic Peninsula, Antartica	La Meseta Formation, Late Eocene	Tambussi *et al.*, 1994
PROCELLARIIFORMES				
3	*Diomedea* sp.	Bahía Inglesa, Copiapo, Atacama	Bahía Inglesa Formation, Late Miocene	Walsh & Hume, 2001
4	aff. *Thalassarche?* sp.	Bahía Inglesa, Copiapo, Atacama	Bahía Inglesa Formation, Late Miocene	Chavez, 2005a
5	Diomedeidae indet. 1	Seymour Island, Antarctic Peninsula, Antartica	La Meseta Formation, Late Eocene	Tambussi & Tonni, 1988
6	Diomedeidae indet. 2	Chañaral de Aceituno, Huasco, Atacama	Coquimbo Formation, Middle Miocene	Chavez, 2005b
7	*Pachyptila* sp.	Bahía Inglesa, Copiapo, Atacama	Bahía Inglesa Formation, Late Miocene	Sallaberry *et al.*, 2007
8	Puffinini indet.	Bahía Inglesa, Copiapo, Atacama	Bahía Inglesa Formation, Late Miocene	Chavez, 2005a
GAVIIFORMES				
9	*Neogaeornis wetzelli*	Tumbes Peninsula, Concepcion, Bio-Bio	Quiriquina Formation, Late Cretaceous (Maastrichtian)	Lambrecht, 1929
10	*Polarornis gregorii*	Seymour Island, Antarctic Peninsula, Antartica	Lopez de Bertodano Formation, Late Cretaceous	Chatherjee, 2002
11	*Polarornis* nov. sp.	Vega Island, Antarctic Peninsula, Antartica	Late Cretaceous	Chatherjee *et al.*, 2006
SPHENISCIFORMES				
12	*Crossvallia unienwillia*	Seymour Island, Antarctic Peninsula, Antartica	Cross Valley Formation, Late Paleocene	Tambussi *et al.*, 2005a
13	*Anthropornis nordenskjoeldii*	Seymour Island, Antarctic Peninsula, Antartica	La Meseta Formation, Late Eocene	Wiman, 1905
14	*Anthropornis grandis*	Seymour Island, Antarctic Peninsula, Antartica	La Meseta Formation, Late Eocene	Wiman, 1905
15	*Antropornis* sp.	Seymour Island, Antarctic Peninsula, Antartica	La Meseta Formation, Late Eocene	Myrcha *et al.*, 2002
16	*Palaeeudyptes gunnari*	Seymour Island, Antarctic Peninsula, Antartica	La Meseta Formation, Late Eocene	Wiman, 1905
17	*Palaeeudyptes klekowskii*	Seymour Island, Antarctic Peninsula, Antartica	La Meseta Formation, Late Eocene	Myrcha *et al.*, 1990
18	*Palaeeudyptes* sp.	Seymour Island, Antarctic Peninsula, Antartica	La Meseta Formation, Late Eocene	Myrcha *et al.*, 2002
19	*Delphinornis larsenii*	Seymour Island, Antarctic Peninsula, Antartica	La Meseta Formation, Late Eocene	Wiman, 1905
20	*Delphinornis gracilis*	Seymour Island, Antarctic Peninsula, Antartica	La Meseta Formation, Late Eocene	Myrcha *et al.*, 2002
21	*Delphinornis arctowskii*	Seymour Island, Antarctic Peninsula, Antartica	La Meseta Formation, Late Eocene	Myrcha *et al.*, 2002
22	*Delphinornis* sp.	Seymour Island, Antarctic Peninsula, Antartica	La Meseta Formation, Late Eocene	Myrcha *et al.*, 2002
23	*Archaeospheniscus wimani*	Seymour Island, Antarctic Peninsula, Antartica	La Meseta Formation, Late Eocene	Marples, 1953
24	*Archaeospheniscus lopdelli*	Seymour Island, Antarctic Peninsula, Antartica	La Meseta Formation, Late Eocene	Tambussi *et al.*, 2006
25	*Mesetaornis polaris*	Seymour Island, Antarctic Peninsula, Antartica	La Meseta Formation, Late Eocene	Myrcha *et al.*, 2002
26	*Mesetaornis* sp.	Seymour Island, Antarctic Peninsula, Antartica	La Meseta Formation, Late Eocene	Myrcha *et al.*, 2002
27	*?Mesetaornis* sp.	Seymour Island, Antarctic Peninsula, Antartica	La Meseta Formation, Late Eocene	Myrcha *et al.*, 2002
28	*Marambiornis exilis*	Seymour Island, Antarctic Peninsula, Antartica	La Meseta Formation, Late Eocene	Myrcha *et al.*, 2002
29	*Tonniornis mesetaensis*	Seymour Island, Antarctic Peninsula, Antartica	La Meseta Formation, Late Eocene	Tambussi *et al.*, 2006
30	*Tonniornis minimum*	Seymour Island, Antarctic Peninsula, Antartica	La Meseta Formation, Late Eocene	Tambussi *et al.*, 2006
31	aff. *Paraptenodytes*	Bahía Inglesa, Copiapo, Atacama	Bahía Inglesa Formation, Late Miocene	Chavez, 2007
32	*Pygoscelis calderensis*	Bahía Inglesa, Copiapo, Atacama	Bahía Inglesa Formation, Late Miocene	Acosta-Hospitaleche *et al.*, 2006b
33	*Pygoscelis grandis*	Bahía Inglesa, Copiapo, Atacama	Bahía Inglesa Formation, Middle Miocene-Pliocene	Walsh & Suarez, 2006
34	*Spheniscus urbinai*	Bahía Inglesa, Copiapo, Atacama	Bahía Inglesa Formation, Late Miocene	Chavez, 2005a
35	*Spheniscus megaramphus*	Bahía Inglesa, Copiapo, Atacama	Bahía Inglesa Formation, Late Miocene	Chavez, 2005a

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Taxon		Locality	Stratigraphy	Reference
SPHENISCIFORMES				
36	*Spheniscus chilensis*	Mejillones Peninsula, Tarapaca, Antofagasta	La Portada Formation, Late Pliocene	Emslie & Guerra, 2003
37	*Spheniscus* sp.1	Bahía Inglesa, Copiapo, Atacama	Bahía Inglesa Formation, Middle-Late Miocene	Walsh, 2004
38	*Spheniscus* sp.2	Chañaral de Aceituno, Huasco, Atacama	Coquimbo Formation, Late Miocene	Chavez, 2005b
39	*Spheniscus* spp.	Bahía Inglesa, Copiapo, Atacama	Bahía Inglesa Formation, Pliocene	Chavez, 2007
40	Cf. *Palaeospheniscus*	Coquimbo, Elqui, Coquimbo	Coquimbo Formation, Middle Miocene	Acosta-Hospitaleche *et al.*, 2006a
41	Sphenisciformes indet.	Seymour Island, Antarctic Peninsula, Antartica	La Meseta Formation, Early Eocene	Jadwiszczack, 2006a
PELECANIFORMES				
42	*Sula* sp.1	Bahía Inglesa, Copiapo, Atacama	Bahía Inglesa Formation, Late Miocene	Walsh & Hume, 2001
43	*Sula* sp.2	Bahía Inglesa, Copiapo, Atacama	Bahía Inglesa Formation, Late Miocene	Chavez & Stucchi, 2006
44	*Morus* sp.	Bahía Inglesa, Copiapo, Atacama	Bahía Inglesa Formation, Late Miocene	Unpublished
45	*Phalacrocorax* sp.1	Bahía Inglesa, Copiapo, Atacama	Bahía Inglesa Formation, Late Miocene	Walsh & Hume, 2001
46	*Phalacrocorax* sp.2	Mejillones Peninsula, Tarapaca, Antofagasta	La Portada Formation, Late Pliocene	Emslie & Guerra, 2003
47	*Meganhiga chilensis*	Cerro Rucañanco, Malleco, Temuco	Curamallin Formation, Early Miocene	Alvarenga, 1995
48	*Pelagornis* sp.	Bahía Inglesa, Copiapo, Atacama	Bahía Inglesa Formation, Middle Miocene	Chavez *et al.*, 2007
49	cf. *Pelagornis*	Bahía Inglesa, Copiapo, Atacama	Bahía Inglesa Formation, Middle Miocene	Chavez *et al.*, 2007
50	Pelagornithidae indet. 1	Seymour Island, Antarctic Peninsula, Antartica	La Meseta Formation, Late Eocene	Tonni, 1980
51	Pelagornithidae indet. 2	Seymour Island, Antarctic Peninsula, Antartica	La Meseta Formation, Late Eocene	Tonni & Tambussi, 1985
ANSERIFORMES				
52	*Vegavis iaai*	Vega Island, Antarctic Peninsula, Antartica	Unit K3, Late Cretaceous (Maastrichtian)	Clarke *et al.*, 2005
CHARADRIIFORMES				
53	Charadriidae indet.	Seymour Island, Antarctic Peninsula, Antartica	La Meseta Formation, Late Eocene	Tambussi & Noriega, 1996
RALLIFORMES				
54	Brontornithinae indet.	Seymour Island, Antarctic Peninsula, Antartica	La Meseta Formation, Late Eocene	Case *et al.*, 1987
55	cf. Cariamae indet. ?	Vega Island, Antarctic Peninsula, Antartica	Lopez de Bertodano Formation, Late Cretaceous	Case *et al.*, 2006
FALCONIFORMES				
56	*Milvago* sp.	Mejillones Peninsula, Tarapaca, Antofagasta	La Portada Formation, Late Pliocene	Emslie & Guerra, 2003

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NEOGENE VERTEBRATE PALAEOICHNOLOGY OF THE NORTH ATLANTIC COAST OF THE RIO NEGRO PROVINCE, ARGENTINA [1]

(With 10 figures)

SILVIA A. ARAMAYO [2]

ABSTRACT: Tetrapod footprints assigned to mammals and birds were discovered at continental deposits from the Atlantic coast of Rio Negro Province, Argentina. The study took place along 30km of a marine beach area between Balneario El Condor and La Lobería (41°S, 62°30'-64°30'W); in the region, abrasion platforms crop out as remnants of eroded high cliffs. The stratigraphic sequence begins with continental deposits at the base of the profile, followed by marine sediments and continental beds cropping out on the cliff wall; thus the stratigraphic range of the continental ichnofauna extends from late Miocene (imprints on abrasion platforms) to early Pliocene (footprints on fallen rocks, lying at the base of the cliffs). The footprints are assigned to tardigrad xenarthrans (*Megatherichnum oportoi* and cf. *Mylodontidichnum* isp.); ungulates *indet*. A trackway assigned to a carnivorous marsupial and isolated footprints of a hydrochoerid rodent also occur, as well as trace fossils assigned to phorusrhacids birds and flamingos, among others. The ichnofauna is registered in interdune pool and ephemerous lagoon sediments, such as it is indicated by lacustrine deposits with desiccation mud-cracks.

Key words: Palaeoichnology. Mammals. Birds. Late Miocene. Early Pliocene.

RESUMO: Paleoicnologia de vertebrados do Neógeno da costa do Atlântico Norte da Província do Rio Negro, Argentina.

Pegadas de tetrápodes atribuídas a mamíferos e aves foram descobertas em depósitos continentais da costa atlântica da Província de Rio Negro, Argentina. O estudo foi realizado ao longo de 30km da praia entre os Balneários El Condor e La Lobería (41°S, 62°30'-64°30'W); na região, plataformas de abrasão afloram como remanescentes de grandes falésias erodidas. A seqüência estratigráfica se inicia com os depósitos continentais na base do perfil, seguido por camadas de sedimentos marinhos e continentais. A variação estratigráfica da icnofauna continental se estende do Mioceno Superior (impressões em plataformas de abrasão) ao Plioceno Inferior (pegadas em seixos rolados, situados na base da falésia). As pegadas são atribuídas a xenartras tardígrados (*Megatherichnum oportoi* e cf. *Mylodontidichnum* isp.); ungulates *indet*. São também observados uma pista, atribuída a um marsupial carnívoro, e pegadas isoladas de um roedor hidroquerídeo, assim como traços fósseis atribuídos a aves da família Phorusrhacidae e a flamingos, entre outras. A icnofauna é registrada em sedimentos de reservatório interdunar e de lagoas efêmeras e temporárias, assim como é indicado por depósitos lacustres com gretas de contração.

Palavras-chave: Paleoicnologia. Mamíferos. Aves. Mioceno Superior. Plioceno Inferior.

INTRODUCTION

Tetrapod footprints assigned to mammals and birds were discovered at continental deposits from the Atlantic coast of Río Negro Province, Argentina, in addition to earlier findings (Casamiquela, 1974; Angulo & Casamiquela, 1982; Aramayo, 1999; Aramayo *et al.*, 2004). Footprints are impressed on abrasion platforms cropping out along 30km marine beach between Balneario El Cóndor and La Lobería (41°S, 62°30'- 64°30'W) (Fig.1).

GEOLOGICAL SETTING

The abrasion platforms are remnants of eroded high cliffs, with an average height of 50m, extending from East to West; footprints are impressed either on silty clay platforms or on the plane surfaces of fallen blocks lying at the base of the cliffs. The stratigraphic succession begins with continental aeolian deposits at the base of the section, followed by a marine level providing a rich invertebrate fauna. At the top of the sequence, lacustrine deposits crop out bearing

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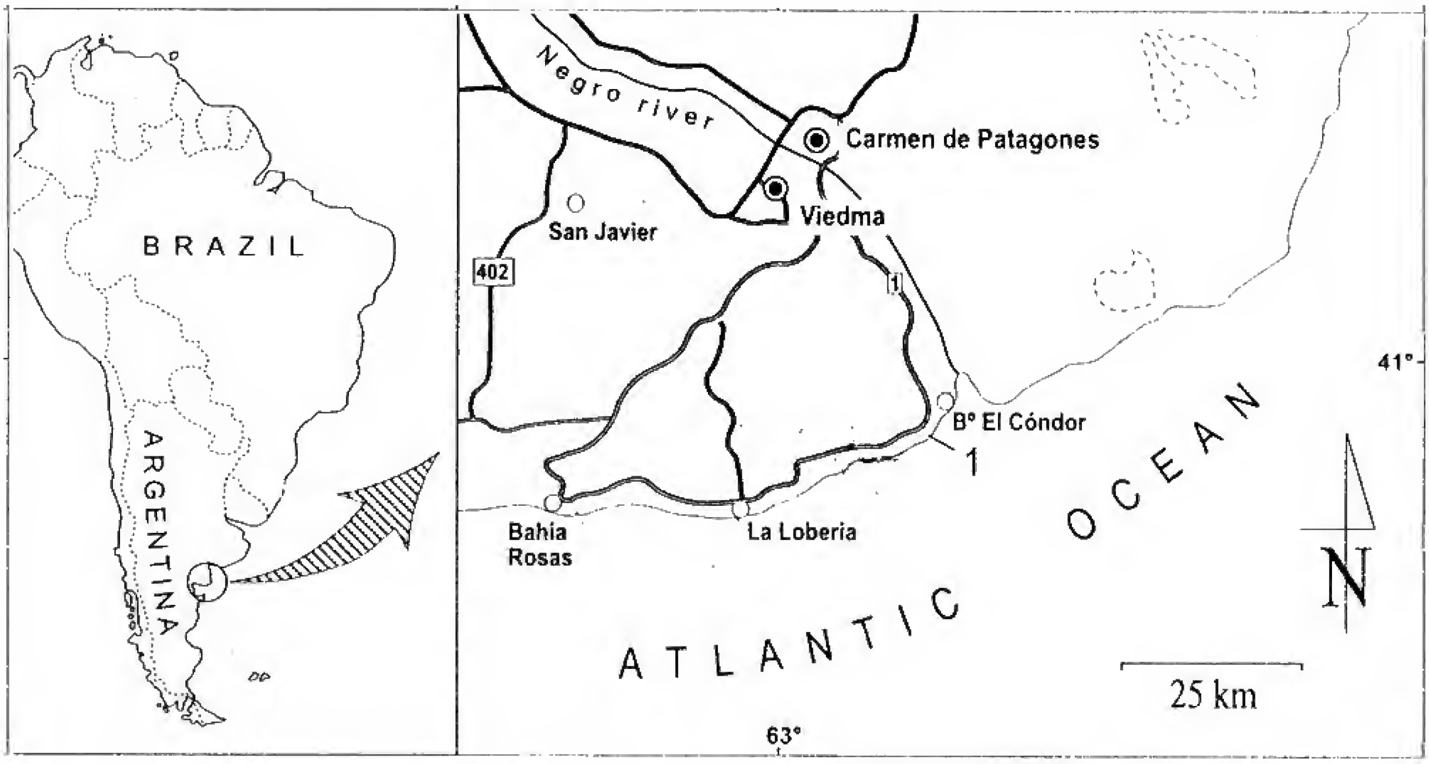

Fig.1- Location map. 1: Lighthouse beach.

trace fossils preserved such as those from the basal deposits. The whole sequence is referred to Río Negro Formation, from Late Miocene to Early Pliocene age; each unit are lower, middle and upper Members (Zavala & Freije, 2001) (Fig.2).

Trace fossils are impressed on platforms and on the plane surfaces of the fallen blocks. Trackways found at La Lobería belong to the Lower Member and some details are not clearly preserved. In contrast, those occurring in slabs of The Upper Member cropping out towards the East of the cliff exposures, near the Lighthouse access to the beach, show a high quality of preservation.

Abbreviations: Institutional. P.ICHN.U.N.S., Paleoichnology repository, Universidad Nacional del Sur.

ICHNOTAXONOMY

Ichnogenus: *Megatherichnum* Casamiquela, 1974

Ichnospecies: *Megatherichnum oportoi*
Casamiquela, 1974

Occurrence – 7km to the west of Lighthouse beach, Atlantic coast, Río Negro Province, Argentina.

Description – A trackway of eight footprints impressed by the hind feet of ground sloths (Xenarthra, Tardigrada) in a plantigrade stance and preserved as a concave epirelief. Each footprint has an elliptical shape, rather wider in the anterior part, and disposed in a parallel way as regards the middle line of the trackway. A rim is observed on the anterior and lateral side due to the rotated position of the feet stepping on the lateral side of the foot. Also a deep subtriangular scar is observed at the inner anterior rim assigned to the scar of the 3rd toe claw. A bipedal locomotion is inferred from the trackways (Figs.3A-B).

Dimensions – Trackway: length: 4.50m; width: 0.80m; step angle: 97°; stride: 0.70m. Footprint (average): length: 0.50m; width: 0.30m; depth: 0.10m

Discussion – The ichnotaxonomic assignation is adopted from Casamiquela (1974), who described some footprints observed on fallen blocks; however, sizes are rather smaller assuming that there is a kind of variation in size among specimens of the same species.

Casamiquela (1974) and Angulo & Casamiquela (1982)

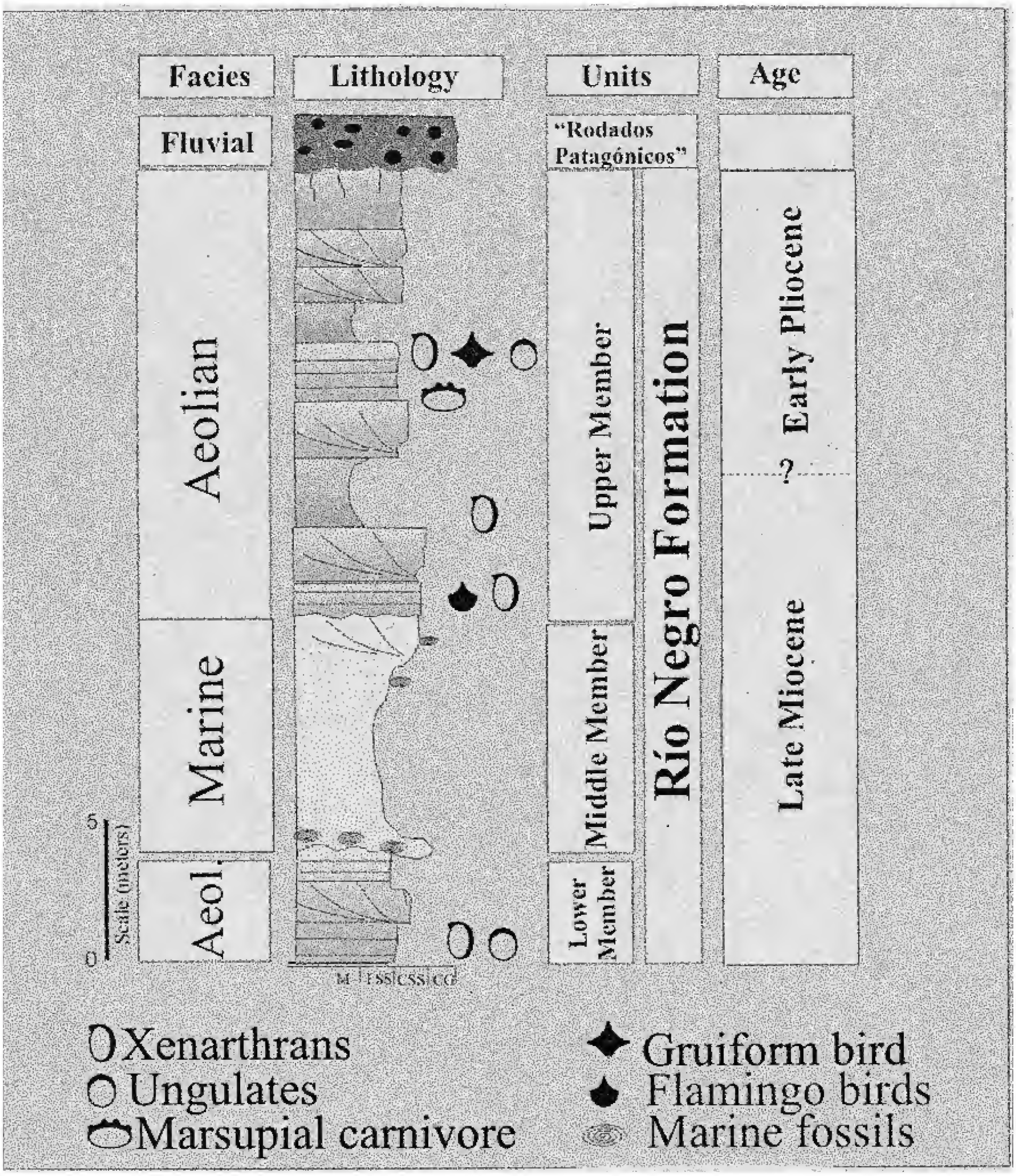

Fig.2- Stratigraphic sequence (modified from Zavala & Freije, 2001).

described the posterior part (or heel) of the footprint as bearing a scar, when the scar was indeed printed by the third finger toe. The latter is confirmed by the great number of ground sloth trackways registered at Pehuen-Co palaeoichnological site (Aramayo & Manera de Bianco, 1987, 1996).

The measured step angle is of very low value considering a bipedal locomotion. The latter one is due to the unusual anatomy of ground sloth tarsus, unable to flex the foot up and down (Aramayo, 2001); the astragalus tibial trochlear joint is formed by a flat external facet and a prominent upwards projection on the inner side (odontoid process), thus only inward rotation movements are produced. The displacement rim on the lateral side supports that ankle morphology.

cf. *Mylodontidichnum* isp.

Occurrence – A trackway registered on a fallen block found at 1.5km to the west of Ligthhouse beach.

Description – The footprints are impressed on a red clay platform at the base of the cliff; they are assigned to a plantigrad mammal of median to small size, forming a trackway of ten footprints in concave epirelief. The footprints are subelliptical, with same width in the anterior and medial part, narrower in the posterior part. The scar of the third toe claw is observed (Fig.3C).

Dimensions – Trackway: total length: 3m; width: 0.80m; stride: 0.60m; step angle: 75°. Footprint (average): length: 0.30m; width: 0.15m; depth: 0.11m.

Plaster cast – P.ICHN.U.N.S. 100

Discussion – This trackway is assigned to cf. *Mylodontidichnum* isp. Aramayo & Manera de Bianco, 1987, ichnotaxon from the Late Pleistocene site at Pehuen-Co with similar features but bigger in size. This is consistent with the existence of ground sloths of smaller size like *Proscelidodon* sp. registered at Late Miocene/Early Pliocene mammal ages.

Ungulates indet.

Occurrence 1 – Lighthouse beach.

Description – A trackway of 19 footprints preserved as negative epirelief (subtrace) with a rounded shape. They are impressed on the top surface of a dark grey sandstone fallen block at 200m to the west of Lighthouse beach (Fig.4). In order to infer the actual size, a 50% of reduction was calculated from the measurements of the subtraces. In some parts of the trackway the couples of hand and feet may be distinguished. They are assigned to an ungulate of median to small size.

Dimensions – Trackway: total length: 3.20m; maximum width: 0.40m; stride: 1.40m (based on the reduction of the subtrace); step angle: 152°. Subtrace – average diameter: 0.22m; average height: 0.04m; inferred depth: 0.02m Footprint: average diameter: 0.11m.

Discussion – The high step angle and the reduced diameters of the footprints allow assigning this trackway to litoptern ungulates (Proterotheridae family). They were ungulates of very long limbs, and the lineal path trail observed in the trackway is proper of a long-limb ungulate locomotion. Proterotherids were very cursorial mammals thus considered like ecological akin or morphologically convergent with the Equidae of the northern hemisphere (Scott, 1937).

The morphology is similar to *Caballichnus impersonalis* (Angulo & Casamiquela, 1982), however that nomination is not adopted here since the authors used that name for the description of Equidae footprints (Order Perissodactyla). According to the land mammal records, horses did not inhabited South America during Pliocene times. They migrated from North America and reached Argentina by Late Pleistocene.

Occurrence 2 – La Lobería beach. A proterotherid trackway of six footprints and two isolated footprints impressed on the abrasion platform at the intertidal zone of the beach.

Description – Footprints assigned to ungulate mammals of median size. Each footprint (hand or feet undistinguishable) is subcircular in shape and some of them show a narrow rim around it. Toes and pad details are not observed.

Dimensions – Trackway: total length: 1.65m; maximum width: 0.60m; stride: 0,55m; step angle: 130°. Ichnite: average length: 0.135m; average width: 0.11m; depth: 0.04m.

Carnivora Marsupials

cf. *Thylacosmilidae*

Occurrence – About 200m to the West of Lighthouse beach. The footprints are impressed in a red brown clay fallen block.

Description – Trackway formed by six footprints impressed by a digitigrad mammal of median to big size. Each footprint shows five toes clearly marked, particularly the 3rd, the 4th, and the 5th. The scar of short claws is also inferred into the basin of the footprint because the feet sank in the mud at every step. A wide and thick sole pad is inferred resulting in a footprint wider than longer (Fig.5). Thick pads are inferred from the comparison with *Thylacinus*.

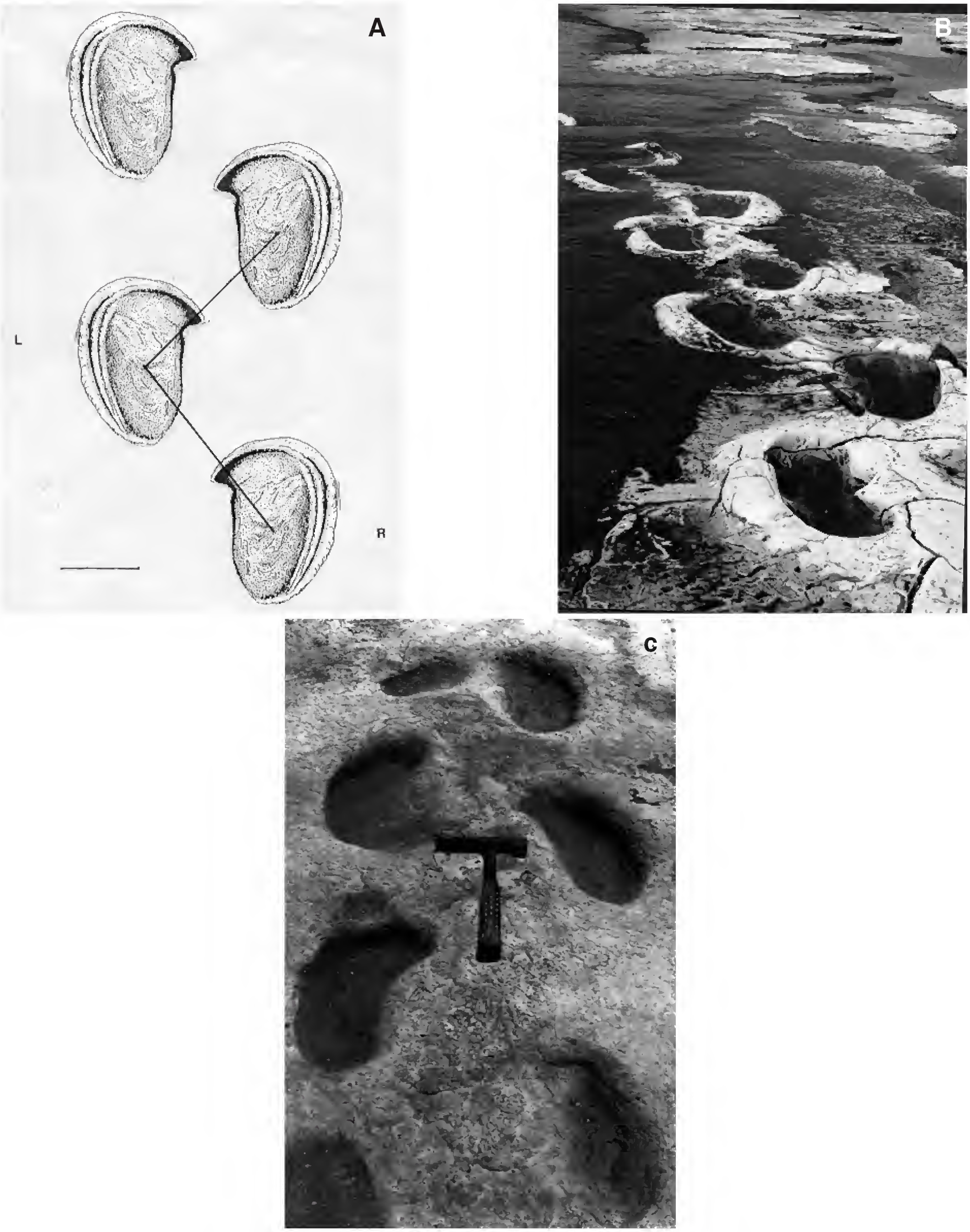

Fig.3- Ground sloths footprints. (A) Pattern of a bipedal locomotion. L: left; R: right. Lines indicate step angle. Scale bar = 0.25m; (B) cf. *Megatherichnum oportoi*. Trackway of bipedal locomotion; observed *in situ* at 7km to the west of Lighthouse beach. Hammer = 0.30m; (C) cf *Mylodontidichnum* isp. trackway of bipedal locomotion, observed *in situ* at 1.5km to the west of Lighthouse beach.

Fig.4- Ungulate *indet*. Circular subtraces on the top of a fallen block; 200m to the west of Lighthouse beach.

Dimensions – Trackway: total length: 1.61m; maximum width: 0.55m; central width: 0.65m; step angle: 163°45'; stride: 1.095m. Footprint: width: 0.096m; length: 0.075m; average depth: 0.0525m.

Plaster cast – P.ICHN.U.N.S. 101

Discussion – Hands and feet are undistinguishable; however, features like footprints wider than longer, toes with acute claws, depth of footprints, and digitigrade stance allow to assign the trackway to a conspicuous carnivorous mammal. Considering the fact that there were not true Carnivora at early Pliocene, and that some marsupials exerted the carnassial role, it is possible to assign those footprints to a carnivorous marsupial, similar in size at least with *Thylacosmilus* sp.

Caviomorph Rodents

cf. *Porcellusignum* isp. Angulo & Casamiquela, 1982

Occurrence – Lighthouse beach.

Fig.5- Cf. Thylacosmilidae Ichnite *in situ* and plaster cast P.ICHN.U.N.S.101

Description – Imprints in trampling, showing three and four digits footprints, on platforms and isolated blocks. They are printed in concave epirelief and show a deep rounded palm/plant impression (Fig.6).

Dimensions – Footprints: four toes: width: 0.10m; length: 0.95m; depth: 0.04m; average divarication angle: 55° (Fig.7). Three toes: width: 0.09m; length: 0.85m; depth: 0.025m; average divarication angle: 58°.

Discussion – The footprints are assigned to hand (four toes) and feet (three toes) of a hydrochoerid rodent, which is consistent with the finding of teeth and jaws of *Protohydrochoerus,* an unusual discovery made in a fallen block (ANGULO & CASAMIQUELA, 1982; PASCUAL & BONDESIO, 1985). The footprints are assigned to *Porcellusignum* isp., according to the diagnosis proposed by ANGULO & CASAMIQUELA (1982) although the provided illustration is not eloquent.

AVES

Order: G*ruiformes (Ralliformes)*
cf. *Cariamidae*

Occurrence – Lighthouse beach, 200m to the west of Lighthouse beach. A bird trackway on the top surface of a fallen block together with trackways of an ungulate (Figs.8-9).

Description – Tridactyl footprints impressed by birds of big size. The footprints are preserved in a negative epirelief. They are rather assimetric being the 3rd toe of bigger size as regards the lateral toes and of wider base; 2nd and 4th lateral fingers diverging from the middle toe in a different angle. Lateral toes are half the size of the middle one. The impression of the convergence point of the three fingers (node) is deeply marked indicating the step of a heavy bird.

Dimensions – Trackway: stride: 1.61m; step angle: 157°; average height of the subtrace: 0.07m. Subtrace: length: 0.38m; width: 0.353m. Footprints: length: 0.25m; width: 0.176m; divarication angle 82° (2nd toe); 72° (4th toe).

Plaster cast – P.ICHN.U.N.S. 102

Assigned material – An isolated imprint from the platforms at La Lobería; only central and one lateral toe is preserved.

Discussion – The trackway is assigned to a phorusrhacid bird due to the big size and stride. It is remarkable that the 2nd or inner toe has a higher divergence angle than the 4th toe. No impression of the 1st toe is observed, probably because it was very short and did not reach the substrate.

Other bird footprints

Occurrence 1 – Two trackways located at 400m to the West of Lighthouse beach, printed on a fallen block of dark gray sandstone.

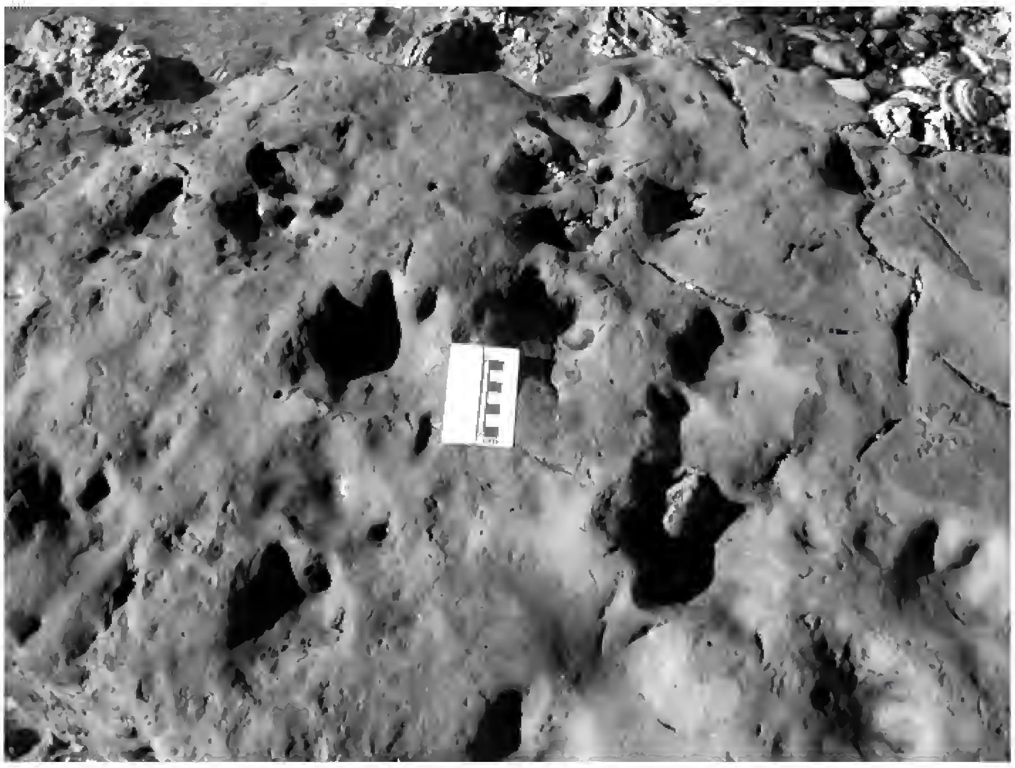

Fig.6- Cf. *Porcellusignum* isp. Block with footprints. Scale in cm

Fig.7- Cf. *Porcellusignum* isp. Isolated hand imprint.

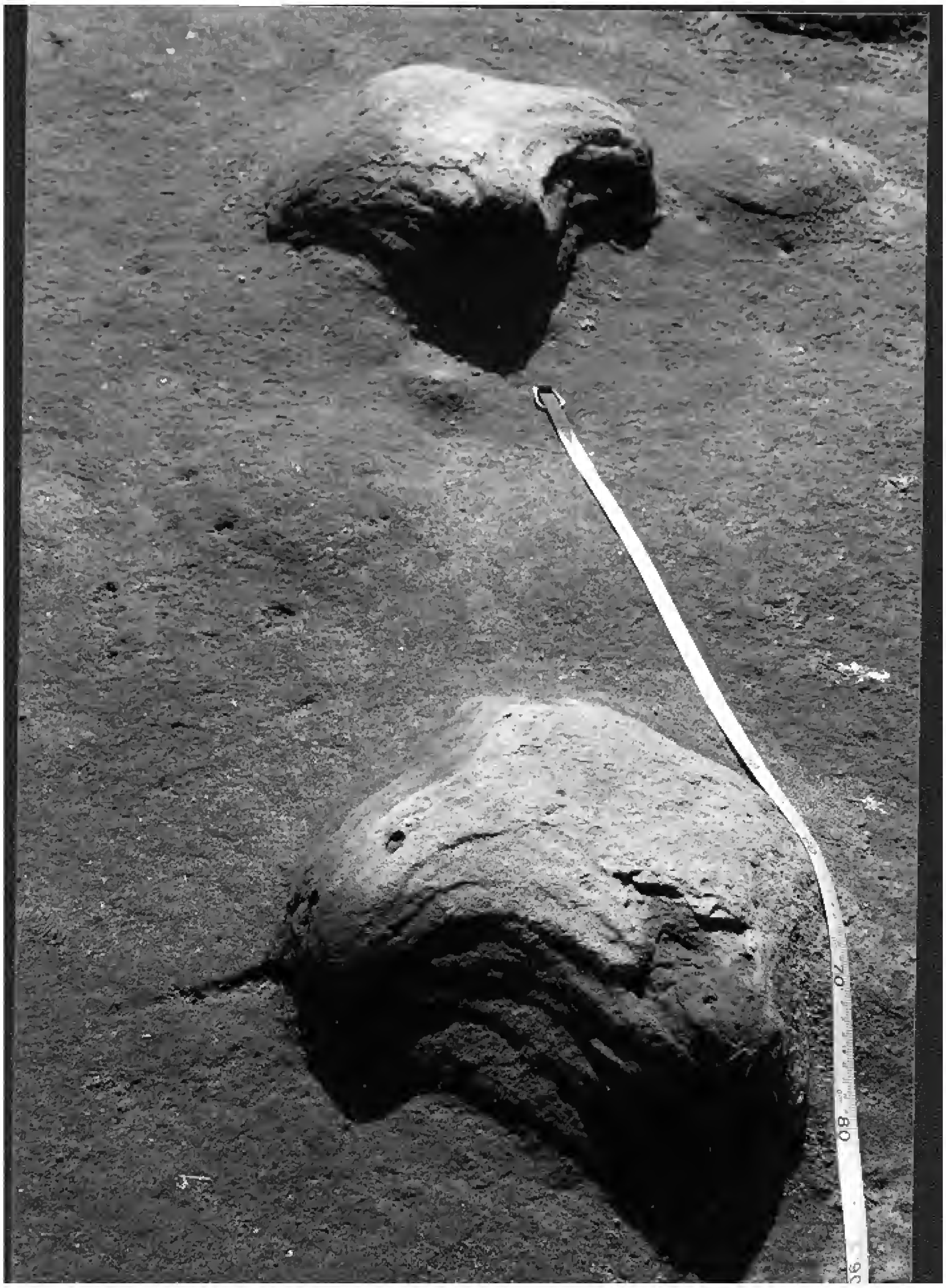

Fig.8- Cf. Cariamidae. Two subtraces. The extended metric ribbon is 0.90m long.

Description – Undetermined tridactyl footprints with straight toes, 3rd toe slightly longer than 2nd and 4th. The node is separated from the toes and is indicated by a shallow depression.

Dimensions – Trackway: length: 0.43m; Footprint: length: 0.063m; width: 0.063m; 3rd toe: 0.049m; average divarication angle of 2nd and 4th toes: 40°.

Occurrence 2 – Lighthouse beach, platforms at the low tide line coast, formed by brown and yellow clays.

Description – A trackway of tridactyl imprints with an interdigital web, reminding the living flamingoes footprints (Fig.10).

Dimensions – Trackway: length: 1.90m; Average pace length: 0.35m. Footprint: length: 0.08m; width: 0.12m.

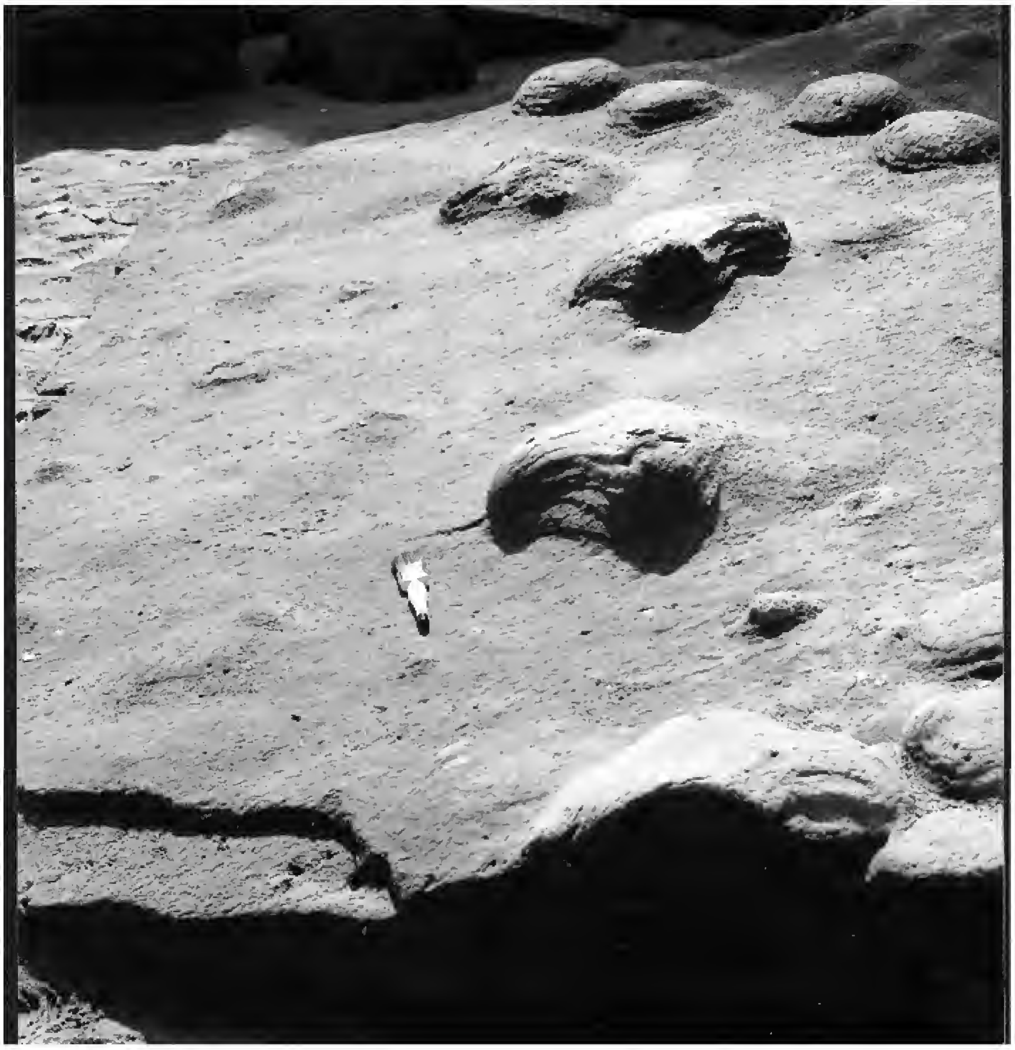

Fig.9- Cf Cariamidae and ungulate subtraces.

AGE AND PALAEOENVIRONMENTAL FEATURES

The age of the outcrops are estimated between 7 and 4 My (Late Miocene/Early Pliocene), considering the fossil bones obtained from the continental bed cliffs. Some of the material were studied by Casamiquela (1974), Pascual & Bondesio (1985) and Aramayo (1987), and agree with the estimated age. Fossil bones of that age are also found in Buenos Aires Province and in other parts of Argentina, but only one finding of a few footprints were registered at La Rioja Province (Bonaparte, 1965).

Zavala & Freije (2001) stated that the ichnites were printed on the borders of shallow pools found between dunes, where animals joined looking for food and freshwater. Ground sloths and ungulates are herbivorous mammals while carnivorous marsupials and the big birds had carnivore or scavenger habits. They represent also a faunistic autochtonous association before the entrance of North America immigrants, the "true carnivorous mammals", which will drive to extinction the mentioned marsupials and phorusrhacid birds.

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Fig.10- Flamingo footprints. Hammer = 0.30m.

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THE TRACE FOSSIL RECORD FROM THE GUARÁ FORMATION (UPPER JURASSIC?), SOUTHERN BRAZIL [1]

(With 15 figures)

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ABSTRACT: In the southwest region of Rio Grande do Sul State, the eolian facies of the Guará Formation (Late Jurassic?) reveals footprints and trackways of vertebrates, as well as burrows made by invertebrates and vertebrates. The footprints are not well preserved and can be distinguished only by the deformation of the sandstone laminations. Some eolian sand sheet layers are totally disturbed by superimposed trackways. Rounded footprints, with diameters about 50cm, can be seen in these sand sheets facies, isolated or forming trackways, and can be observed both on surfaces and in section. The size and shape of the footprints lead us to attribute them to middle-sized sauropods. Inside some of these tracks, little vertical burrows that terminate in basal horizontal chambers are attributed to insects. Three-fingered footprints – isolated or forming trackways –, can also be seen both in section and on surfaces, in sand sheet layers or cutting the foresets of paleodunes. Footprints occur in different sizes (the longest reaching about 45cm in length) and shapes. Although their outlines are often not well-defined, it is possible identify some characteristic patterns pointing to bipedal ornithopods and theropods. In a paleodune, associated with footprints, elongate horizontal partially filled burrows about 20cm wide are tentatively attributed to burrowing mammals. Association of sauropods, ornithopods, and theropods is common from Triassic to Cretaceous periods, and does not support a precise age establishment for the Guará Formation. Nevertheless, it is compatible with the Late Jurassic age attributed to the basal member of the Tacuarembó Formation from Uruguay (lithostratigraphically coeval to the Guará Formation).

Key words: Ichnofossils. Jurassic/Cretaceous. Paraná Basin. Stratigraphy.

RESUMO: Registro de traços fósseis da Formação Guará (Jurássico Superior?), sul do Brasil.

Na região sudoeste do estado do Rio Grande do Sul, nas fácies eólicas da Formação Guará (Jurássico Superior?), foram encontradas pegadas e trilhas de vertebrados, bem como escavações feitas por invertebrados e vertebrados. As pegadas não estão bem preservadas e podem ser distingüidas somente pela deformação do sedimento. Algumas camadas de lençóis de areia eólicos estão completamente bioturbadas por pegadas superpostas. Pegadas arredondadas com cerca de 50cm de diâmetros podem ser encontradas nesses lençóis de areia eólicos, isoladas ou em trilhas, e podem ser observadas tanto em planta quanto em perfil. O tamanho e a forma das pegadas permitem classificá-las como saurópodes de médio porte. Dentro de algumas pegadas foram encontradas pequenas escavações terminadas em câmaras atribuídas a insetos. Pegadas tridátilas – isoladas ou formando trilhas –, podem também ser vistas em planta e em perfil, nos lençóis de areia eólicos ou cortando o *foreset* de uma paleoduna. Nestes foram encontradas pegadas de diferentes tamanhos (a maior com 45cm de comprimento) e formas. Os contornos, em alguns casos, não são bem definidos dificultando a identificação mais precisa. Entretanto, foi possível reconhecer alguns padrões que apontam para ornitópodes e terópodes bípedes. Associado a pegadas em uma paleoduna, tocas preenchidas e horizontais com diâmetros ao redor de 20cm são tentativamente atribuídas a mamíferos. A associação de saurópodes, ornitópodes e terópodes não possibilita uma datação precisa, mas é compatível com a idade Jurássico Superior atribuída à Formação Tacuarembó, unidade correlata do Uruguai, embora nenhum táxon comum tenha sido encontrado, até o momento, para as duas unidades.

Palavras-chave: Icnofósseis. Jurássico/Cretáceo. Bacia do Paraná. Estratigrafia.

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INTRODUCTION

The Guará Formation has a wide geographical distribution (Fig.1), cropping out in the southwestern portion of the Rio Grande do Sul State. Its northwestern limit is controlled by a NW-trending fault system. Lithologically, it is composed of fine to coarse-grained sandstone, and rare mudstones, deposited by fluvial and eolian depositional systems (Scherer *et al.*, 2000). Although highly variable, it has a medium thickness of 200m and rests unconformably over the fluvial deposits of the Lower Triassic Sanga do Cabral Formation. Above, the Guará formation is unconformably overlaid by the eolian deposits of the Lower Cretaceous Botucatu Formation (Scherer *et al.*, 2000).

The Guará Formation is characterized by marked facies variation along the outcropping sequence. The SW portion is characterized by the alternation of eolian and fluvial sediments while the NW one is dominated by fluvial layers. These last show an erosive basal surface and are composed of sandstones with granules, moderately-sorted, with trough cross-bedding and low-angle cross lamination. The eolian sediments are characterized by the presence of fine to medium sandstones, well-sorted, presenting large cross-bedding composed of grain flow, grain fall, and wind-ripple laminations, interpreted as eolian dune deposits, or horizontal wind-ripple strata, interpreted to represent eolian sand sheet deposits.

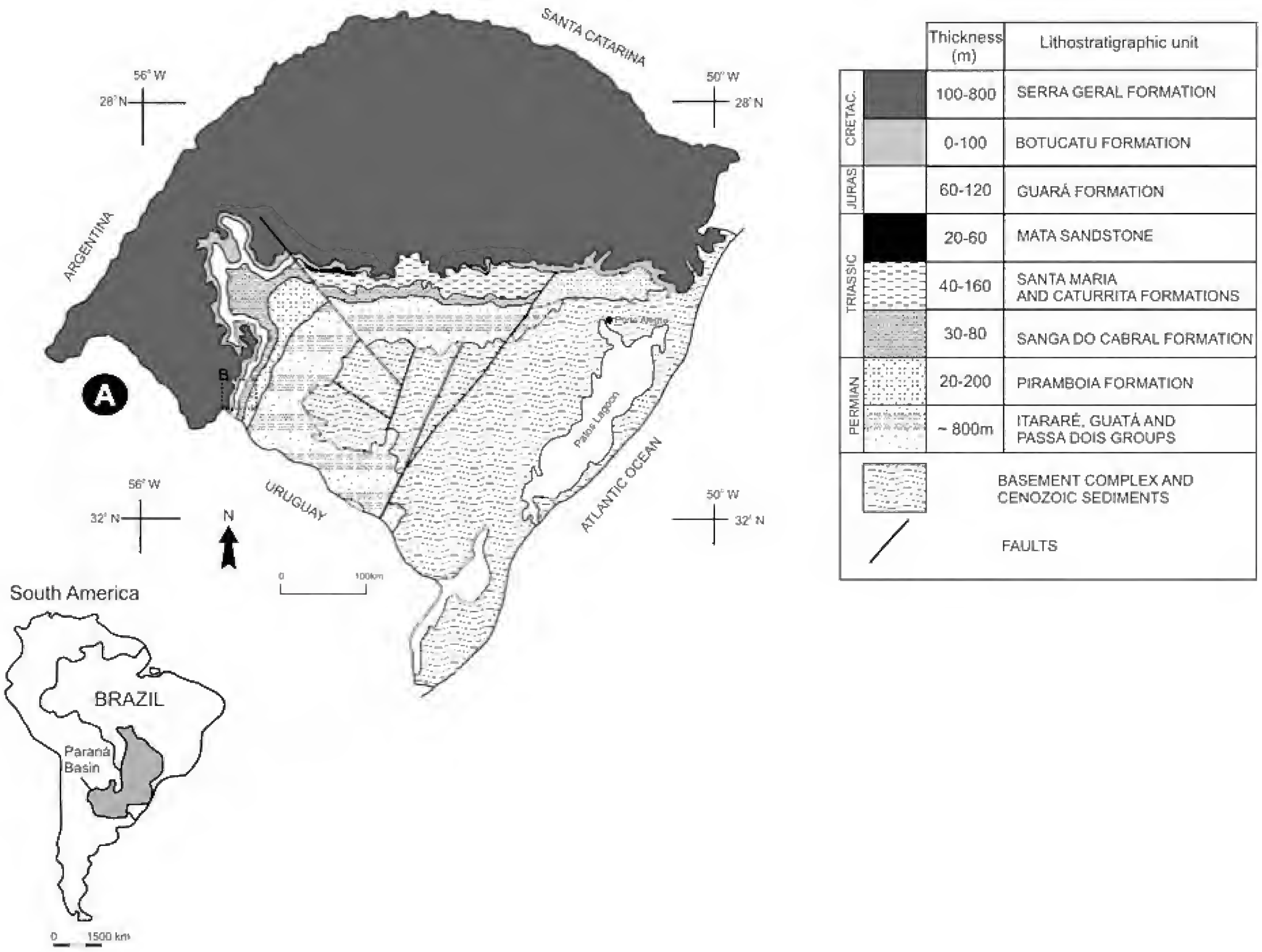

Fig.1- Geological map of the Permian and Mesozoic lithostratigraphic units of the Paraná Basin in the Rio Grande do Sul State, Brazil (After Scherer & Lavina, 2005).

The Guará Formation extends from the Southwest of Rio Grande do Sul State to the Uruguay territory, where it corresponds, lithostratigraphically, to the basal member of the Tacuarembó Formation (LAVINA *et al.,* 1985), which yields a rich and diversified fossil record, including a crocodile, semionotiform fish, gastropods and conchostracans (MONES & FIGUEIRA, 1980; FERRANDO *et al.*, 1987). Nevertheless, no common taxon was found until now for both the Tacuarembó and Guará formations.

In the Guará Formation, near Santana do Livramento and Rosário do Sul cities, where the eolian facies outcrop, footprints and trackways, attributed to sauropod, theropod, and ornithopod dinosaurs, occur. In all the cases, the sediments that cover the footprints are the same as those in which the footprints were produced (*i.e.*, sand), so that no lithological discontinuities occur between the footprints and the infilling sediment. Due to this fact, the footprints can be identified only by the deformation of the sandstone laminations. They often have no relief, and only their outlines can be distinguished, both in surface view and in section. So, anatomical details, such as marks of digits or claws, are very difficult to distinguish. In addition to the footprints, different kinds of burrows, some attributed to little vertebrates and others to invertebrates, were also found at the eolian facies (SCHULTZ *et al.*, 2002; DIAS *et al.*, 2002; DIAS & SCHULTZ, 2003; DENTZIEN-DIAS & BERTONI-MACHADO, 2005).

Some of these ichnofossils (including footprints, trackways, and burrows), originating from five different outcrops, are described in this paper.

The Guará Formation also contains, subordinate to the eolian facies, various fluvial layers, that outcrop between Rosário do Sul and Santana do Livramento cities.

If a Late Jurassic age is confirmed for the Guará Formation, the occurrence of these footprints and burrows in the SW of Rio Grande do Sul State would represent a unique record of tetrapod fossils from that age to Brazil.

MATERIAL AND METHODS

A stratigraphic section was made at each fossiliferous outcrop, in which the layers with ichnofossils were marked. The sedimentary facies were described following the model of READING (1986). The small thicknesses of the stratigraphic sections results from the fact that the outcrops are sparse and not continuous.

The footprints were catalogued following the methodology of LEONARDI *et al.* (1987): all the footprints are represented by four letters; the first two refer to the municipal district and the last two to the locality, obtained from topographic maps (scale 1:50000). The codes and the numbers follow the order in which the footprints were discovered.

Following these rules we have:

SLCP = Santana do Livramento – Cerro Palomas (*Chart of Palomas* - 2992/3)
RSSJ = Rosário do Sul – Sanga do Jacaré (*Chart of Saicã* - 2979/2)
RSCT = Rosário do Sul – Cerro Torneado (*Chart of Saicã* - 2979/2)
RSGV = Rosário do Sul – Granja Santa Vitória (*Chart of Saicã* - 2979/2)
RSTP = Rosário do Sul – Touro Passo Stream (*Chart of Saicã* - 2979/2)

All the ichnological material was photographed and measured. The parameters of the footprints, such as length, width and variation of digits, as well data regarding the trackways (width of pace, step angle, length of stride and oblique pace), also follow the model of LEONARDI *et al.* (1987).

In outcrop RSCT it was possible to collect two separate footprints. In the RSSJ outcrop one pair was collected. They were registered in the Laboratory of Palaeovertebrates of the Universidade Federal do Rio Grande do Sul (UFRGS PV 0003 J/K , UFRGS PV 0004 J/K and UFRGS PV 0005 J/K).

RESULTS

DESCRIPTION OF FOSSILIFEROUS OUTCROPS

The first outcrop bearing dinosaur trackways is located in the KM 549 of BR-158 road (SLCP). It is represented by the section shown in figure 2. From the base to the top there is a succession of eolian dunes, eolian sand sheets, lacustrine layers and a new succession of dunes at the top. The footprints occur only in the eolian layers, whose palaeocurrents are always directed to E. The SLCP footprints occur at three different levels inside the eolian sand sheet layer.

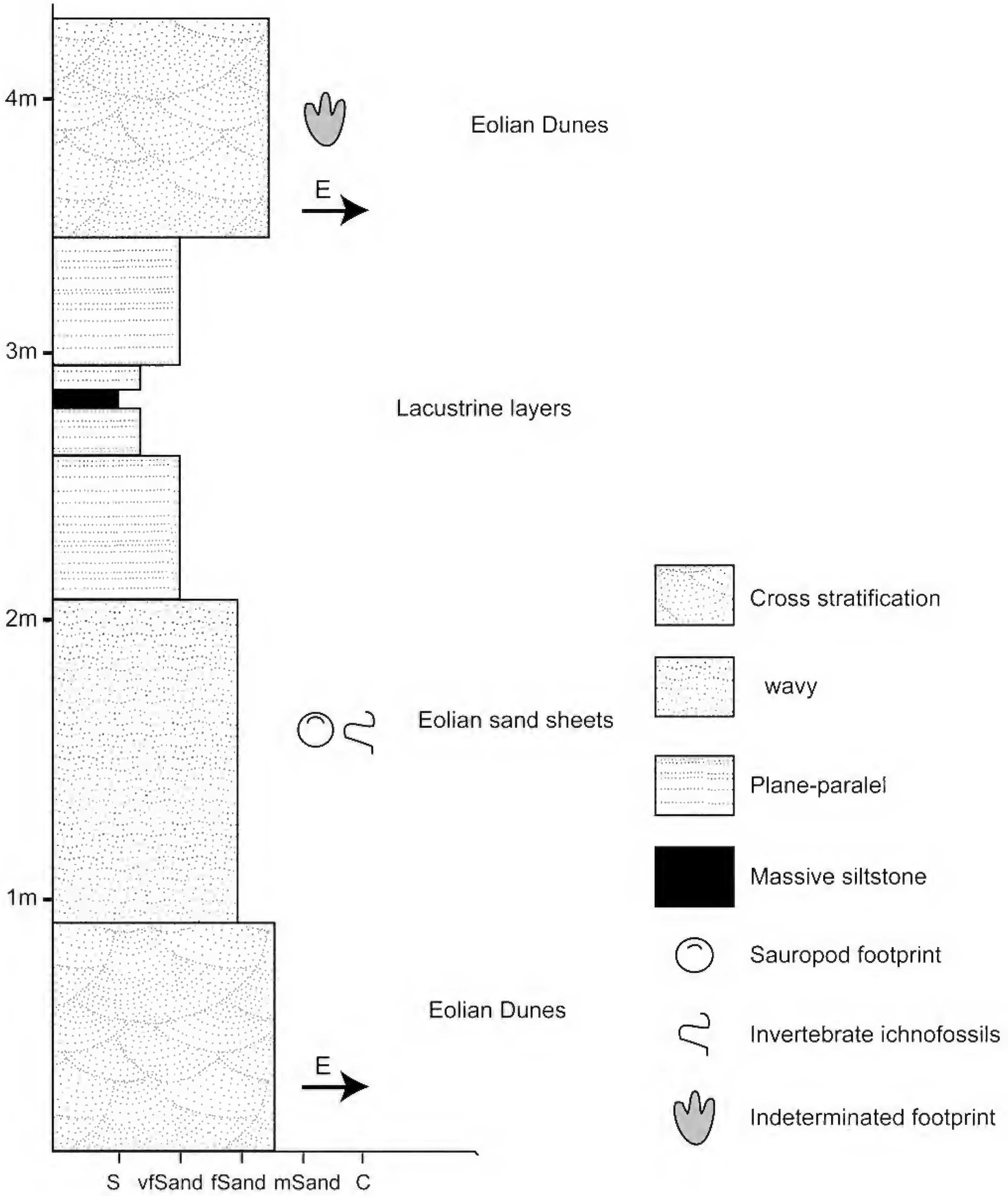

Fig.2- Stratigraphic section of the SLCP outcrop.

On the surface of the outcrop it is revealed trackways and isolated footprints on the surface and in section. The footprints are all rounded (Fig.3), without traces of digits, and two almost parallel trackways can be observed, as well as some isolated footprints. The medium diameter of the footprints is about 50cm. One of the isolated footprints shows deformational features that suggest that the animal was moving from NW to SE.

The trackways were made by a quadruped in spite of there is no manus track. This conclusion is based on the "trackway configuration" (step, stride, and pace angulation). Probably this pattern is due to the poor preservation of the footprints and/or to the overlap of the *pes* overstepping the *manus* footprints, a common phenomenon in sauropod trackways (Moreno & Benton, 2005). We believe, from the evidence of pace angulation patterns and footprint shape (Faria dos Santos *et al.*, 1992), that it is better to attribute them to the pes of a sauropod. The morphology and the size of the footprints suggest the presence of a sauropod with a body size similar to an extant elephant. Nevertheless, these proportions could be also compatible with those of a big prosauropod (like *Riojasaurus* from Argentina, for example). This observation is important because the age of the Guará Formation is not yet surely established. Its basal layers overlay the Early Triassic Sanga do Cabral Formation, so that the presence of rounded footprints in the Guará Formation, by itself, should not exclude an age older than Jurassic for that unit given that such footprints are known from the Triassic.

Inside most footprints, several little vertical burrows can be observed. One of them was excavated to allow its observation in section. These small burrows begin as vertical tubes which become horizontally enlarged at their bases, forming little chambers (Fig.4). These morphological features lead us to attribute these burrows to insects (Renata Guimarães Netto, pers.com).

Other two layers with trackways can be seen in the SLCP outcrop, but only in section, at the wall of the roadcut. The upper one shows only some shallow and not well-defined deformations in the stratification, which do not furnish reliable information. Near the base of the roadcut wall a bigger and very clear trackway is present (Fig.5).

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Fig.3- Sauropod footprints on the surface from the outcrop SLCP. The trackways were highlighted by white (south trackway) and black (north trackway) circles, while the grey ones represent isolated footprints; fig.4- Sauropod footprint in surface view and in section (outcrop SLCP). In detail, an ichnofossil made by an insect.

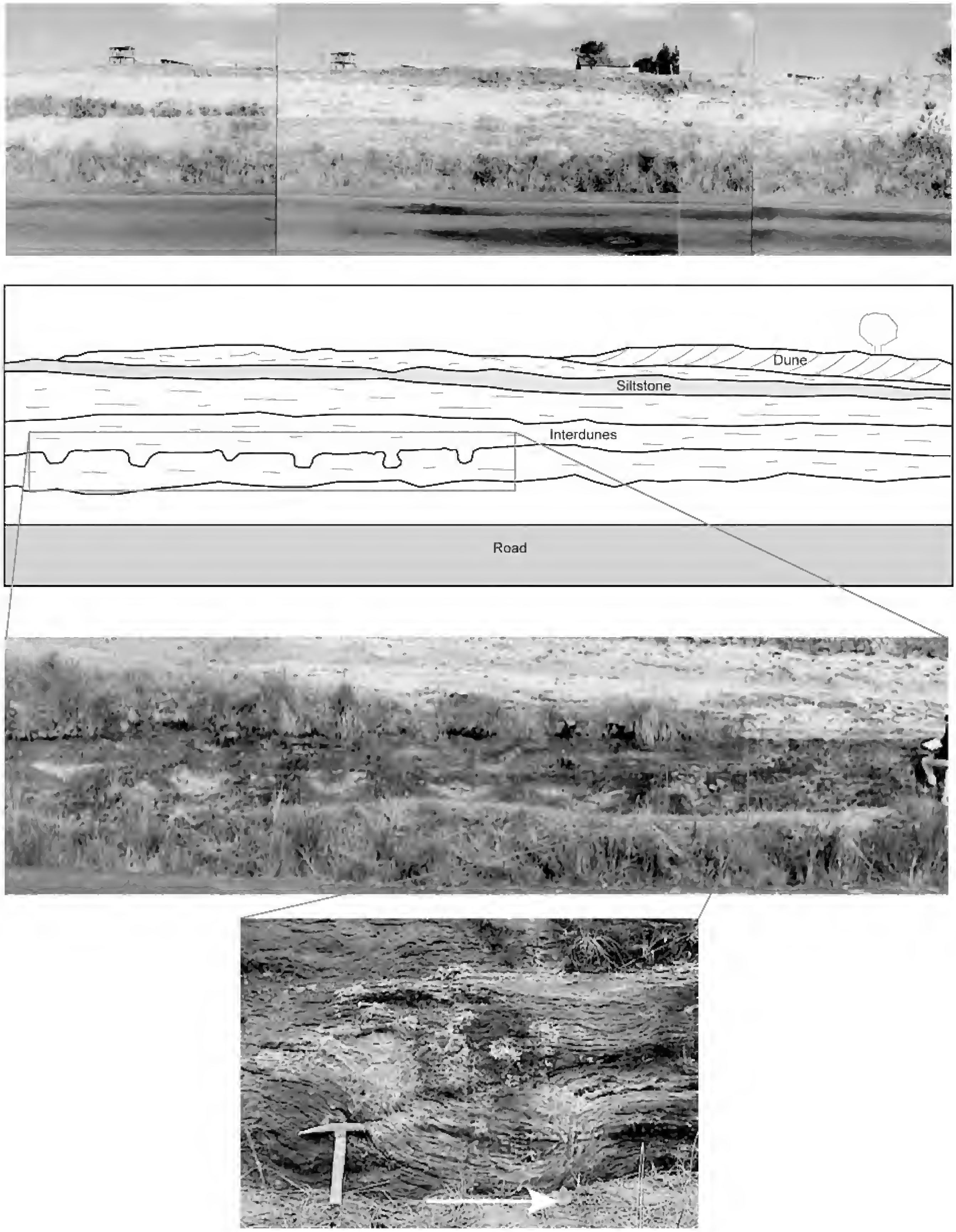


Fig.5- Outcrop in section with a sauropod trackway. The arrow shows that the animal was moving to west.

The footprints are about 50cm wide and the undertracks reach around 45cm in depth. The deformation of the stratification inside the footprints is clearly asymmetric. A deeper portion is always present at the right side of each footprint, which resulted from the pressure created by the anterior portion of the foot during the step. This spatial orientation indicates that the animal was moving from East to West (left to right in figure 5). The direction of the wall is slightly different from that of the trackway, so that the footprints gradually come out from the wall. Indeed, the last footprint of the trackway (SLCP 07) can be partially seen in section, showing its rounded shape (Fig.6). The absence of additional footprints in the western portion of the outcrop leads us to conclude that this trackway represents successive steps of the left foot of the animal. Regarding the trackways that occur on the surface of the outcrop, probably the footprints were produced by the pes overlapping those of the *manus*. The distance between successive footprints in this trackway (length of pace) is 1.20m, while in the surface trackways the lengths of the paces are 1.3m (for the right trackway = North, Fig.7) and 1.4m for the other (Fig.8).

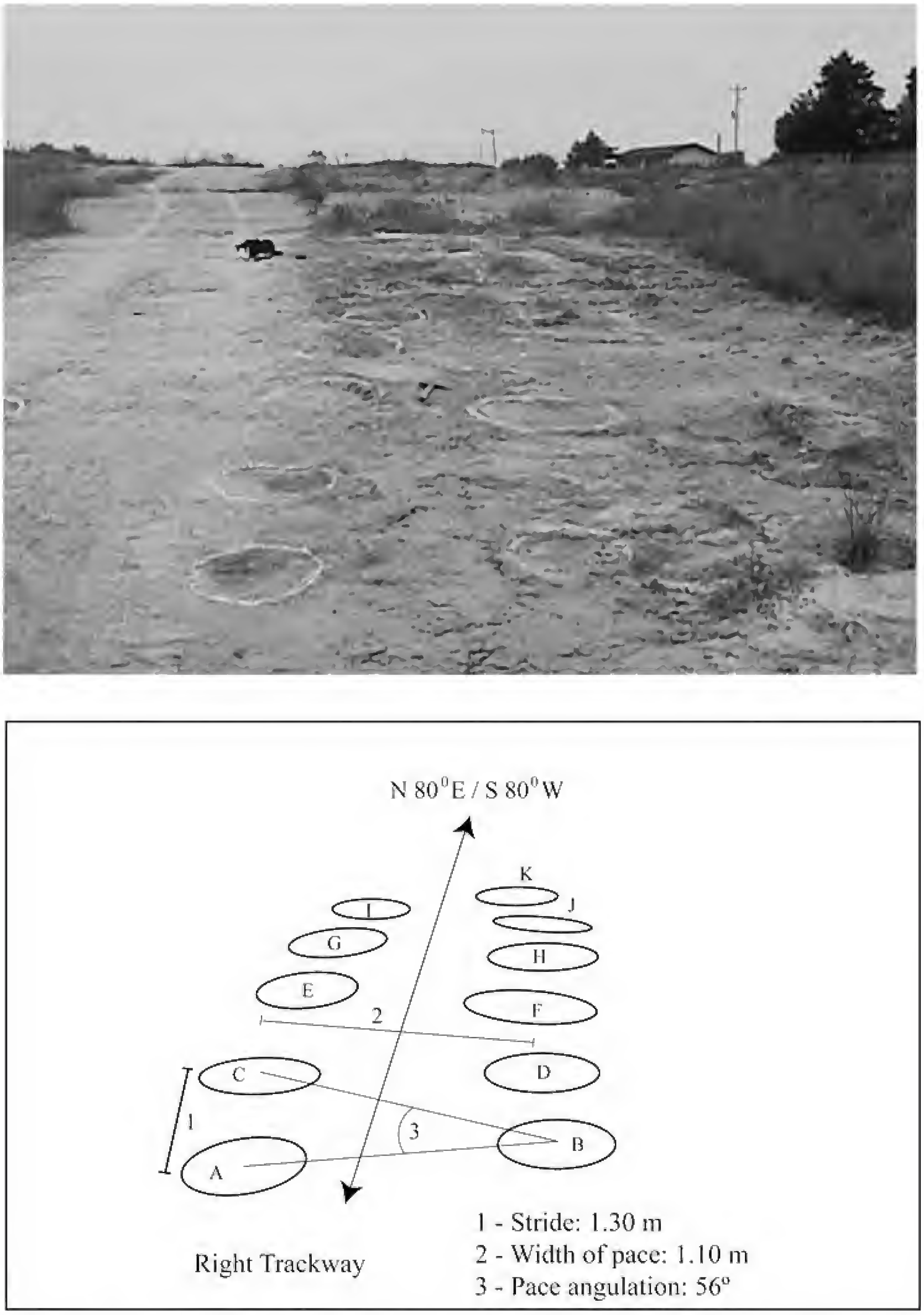
In the upper portion of the outcrop, represented by eolian dunes, another footprint can be seen in section. But it is too poorly preserved to permit a classification.

The second fossiliferous outcrop found in the Guará Formation (RSSJ) is situated in a dirt road west of the town of Rosário do Sul, near the Sanga do Jacaré creek. This outcrop is composed only of paleodunes, whose palaeocurrents are directed eastward. A trackway composed of two three-toed theropod footprints can be observed – in surface view and in section (Fig.9) –, oriented up the foresets of one of the dunes. In section, slide structures formed during this climbing can be clearly seen. These footprints were initially visible only in section, but an excavation was made to expose them in plan. It revealed that these footprints are tridactyl, with marks of sharp claws at their ends. They measure about 17cm in length. This morphology indicates that these footprints were made by a theropod and the size of the footprints suggests that it was no bigger than an extant ostrich.

In the upper level of this same outcrop several ribbons of massive sandstone can be observed crossing the sets of a palaeodune (Fig.10). These ribbons are lens-shaped in transverse section and have a regular width of about 20cm. The thickness of the ribbons range between 3 and 10cm and their lengths vary from 0.40m to 2.80m. These structures tend to be rectilinear, but some of them describe curves and at least one of them reveals a bifurcation (Fig.11). In some portions, these ribbons are covered by little blocks of stratified sandstones. The ribbons of massive sandstones are here interpreted as the floor of burrows, while the stratified blocks evidently represent the collapse of parts of the roof inside the burrows. The size and shape of these burrows is compatible with excavations done by small reptiles or mammals (Miller *et al.*, 2001), as can be illustrated by the extant *Ctenomys* sp. (the "tuco-tuco"), that builds extensive tunnels in the coastal eolian dunes at the South of Brazil.

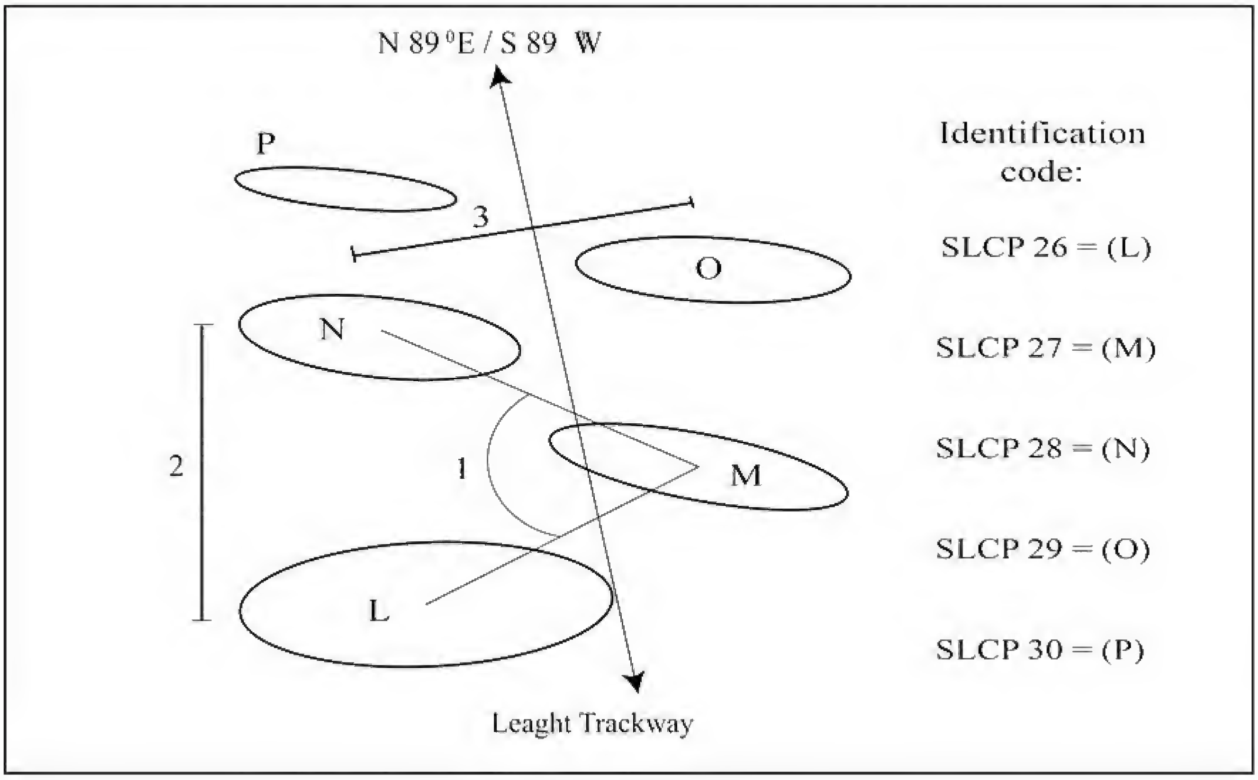
A third fossiliferous outcrop (RSCT) is also located in a dirt road, westward from Rosário do Sul city, near the Cerro Torneado hill. The basal layers of this outcrop are composed of palaeodunes with palaeocurrents directed to North, while its upper portion reveals a sequence of eolian sand sheets that are totally bioturbated by superimposed trackways. Footprints and trackways can be viewed both in section and on the surface. It was possible to identify at least three trackways of bipedal animals, two of theropods and one of an ornithopod.


Fig.6- Sauropod footprint in section, gradually come out of the wall.



Identification Code: SLCP 11 = (A) SLCP 12 = (B) SLCP 13 = (C)
SLCP 14 = (D) SLCP 15 = (E) SLCP 16 = (F) SLCP 17 = (G)
SLCP 18 = (H) SLCP 19 = (I) SLCP 20 = (J) SLCP 21 = (K)

Fig.7- North sauropod trackway with respective measurements (Leonardi *et al.*, 1987).



1 - Pace angulation: 107°
2 - Stride: 1,50m
3 - width of pace: 0.60m

Fig.8- South sauropod trackway from the outcrop SLCP with respective measurements (LEONARDI *et al.*, 1987).

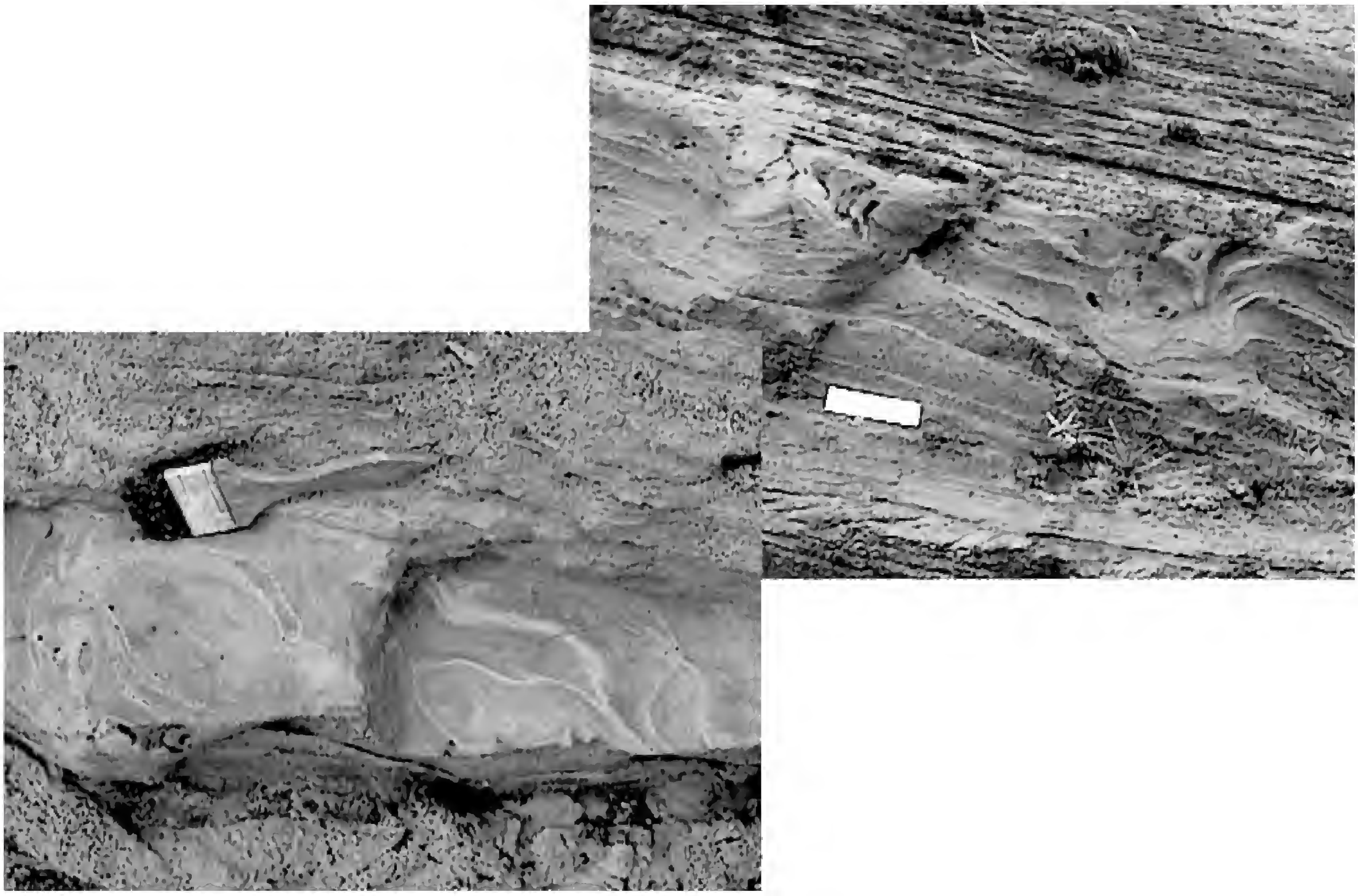


Fig.9- Theropod footprints in section and in surface view.

Fig.10- Burrow with 2.80m of length and 20cm of width.

Theropod footprints can be distinguished from those of ornithopods by the shape of the heel, the larger length of the fingers and for the presence of marks of claws (Fig.12), but they don't allow a distinction between a coelurosaur or carnosaur pattern.

The first RSCT trackway, made by a theropod, is directed to southwest and has footprints 35cm in length and 26cm in width. The step angle is 148° and the length of the stride is 110cm (Fig.13). This theropod would have been about 3m height. The second trackway, attributed to a theropod too, is directed to the northeast and has footprints 22cm in length and 15cm in width (Fig.14). The length of the stride is 75cm and the step angle is 175°. The only trackway from the RSCT outcrop that could surely be attributed to an ornithopod (Fig.15) is directed to North, its step angle is 155° and the length of the stride is 120cm. All the footprints are poorly preserved and don't stand out from the surface. Only the outlines of the deformations produced in the sand by the steps can be distinguished. At the margins of the road, about 50cm of this eolian sand sheet sequence can be observed in section showing that almost all its internal layers are completely bioturbated by superimposed footprints. It suggests a frequent transit of animals in that region at the time of the deposition of the layers.

A fourth tracksite was found near the Touro Passo stream, in Rosário do Sul Town (RSTP). This outcrop is represented by a succession of eolian and lacustrine sediments. In the eolian dunes some invertebrate traces were found, but the preservation was not good enough to permit a classification. However, in the eolian sand sheets, in section and surface, rounded footprints are clearly visible. The diameter of the footprints is about 45cm and the distance between them around 1m, while the depth varies between 15cm and 30cm. These footprints are very similar to those described at the first tracksite, which also leads us to classify them as middle-sized sauropods.

Finally, in the west of Rosário do Sul city, near to the Granja Santa Vitória (RSGV), another tracksite reveals a layer of eolian sand sheets, about 30cm thick, totally disturbed by dinosaur footprints. Some of them can be seen in section and others on the surface. One of the footprints is 25cm long and 23cm wide and shows well defined outlines. The heel has a "U" shape and no claw trace in the toes, which leads us to attribute it to a bipedal ornithopod about 2m in height.

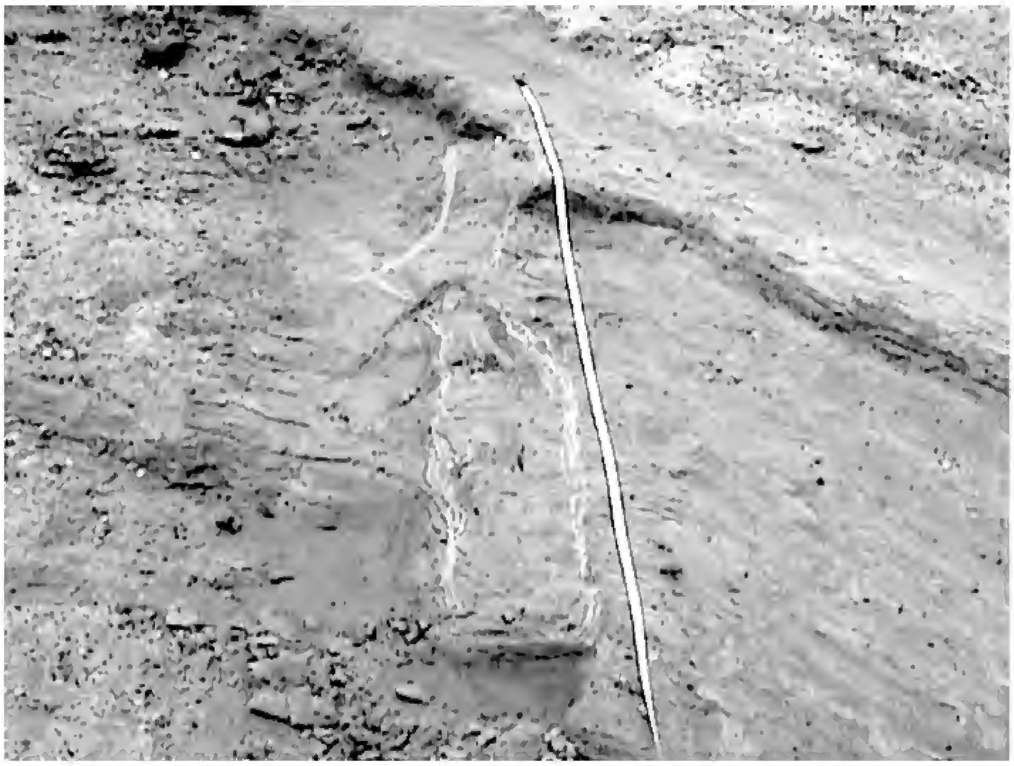
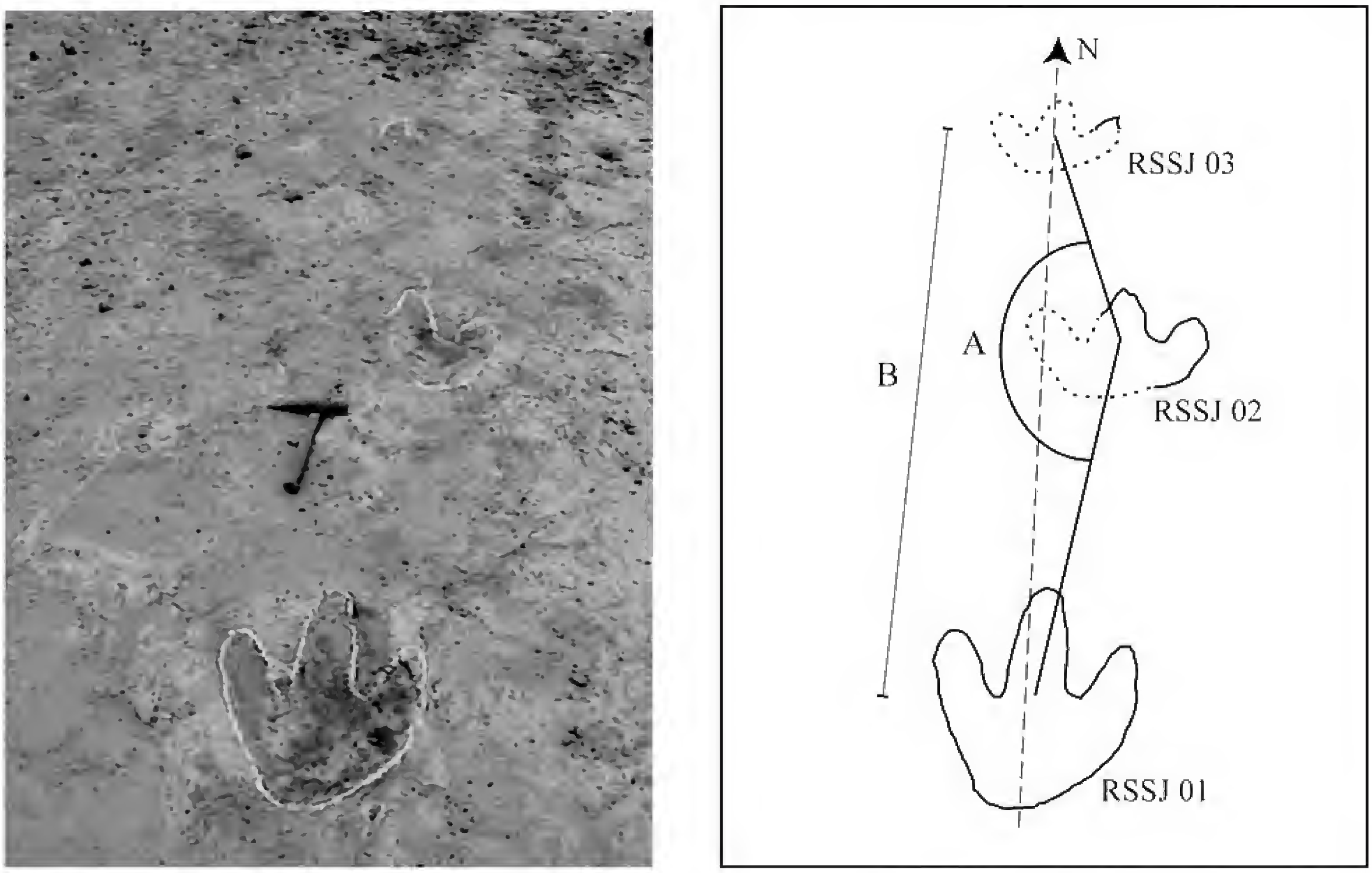


Fig.11- Bifurcated burrow from outcrop RSSJ.

Fig.12- Theropod footprint from outcrop RSCT.

DISCUSSION

Regarding to the dinosaur footprints, based on track morphology, we inferred sauropods (or, less probably, prosauropods), theropods, and ornithopods. We recognize that poor preservation makes trackmaker identification difficult. So our inferences presented below, are tentative. These three kinds of footprints don't occur together in any of the outcrops. In the outcrop RSSJ there are only theropod footprints, while in SLCP only sauropod footprints are present. In RSCT outcrop we infer associated theropods and ornithopods, but no sauropods. Some of the theropod footprints in RSSJ and RSCT have similar sizes and shapes, but the poor preservation does not allow us to infer a direct correlation. From this we get that there is no direct evidence of an association between the sauropods (prosauropods?) and the other groups, but we assume such a temporal coexistence based on the modest thickness of the Guará Formation as a whole (about 200m) and its internal homogeneity, specially regarding to the eolian facies, where the footprints occur. But even accepting the coexistence of these three groups of dinosaurs, it does not provide any precise chronostratigraphic information. Such an association could as easily be Upper Triassic as Cretaceous. However, the palaeocurrents measured in the fluvial layers of the Guará Formation point to S/SW, while the whole Triassic package from Rio Grande do Sul State shows paleocurrents directed to N/NE.



A - Pace Angulation : 148°
B - Stride : 110 cm

Fig.13- Theropod trackway with respective measurements (LEONARDI *et al.*, 1987).

It is, therefore, not possible to infer such a structural change in the basin occurring during the end of the Triassic. So, the Guará Formation could not have been deposited at that time.

On the other hand, the overlaying Botucatu Formation has a minimum age of 132m.y. (SCHERER, 2000). It decreases (but does not exclude) the possibility of a Lower Cretaceous age for the Guará Formation.

There is no Late Jurassic record of dinosaur's footprints for South America, in order to compare it with that from Guará Formation. The shape and size of some theropod footprints from Guará Formation are roughly similar to those found in the Cretaceous of Argentina (Rio Limay Formation, Albian to Cenomanian) and Brazil (Sousa Formation, Lower Cretaceous), but it is not conclusive.

The other fossils found in the Guará Formation, including the burrows of vertebrates and invertebrates, also do not furnish any usefull chronostratigraphic information.

So, the assumption of a Late Jurassic age for the Guará Formation is still tied to the lithostratigraphic correlation with the Tacuarembó Formation (SANTA-ANA & VEROSLAVSKY, 2003; SCHERER & LAVINA, 2005) from Uruguay. Concerning the biostratigraphic criteria, still no shared fossils are known for these units.

CONCLUSIONS

During the time of the Guará Formation sedimentation, in the west of Rio Grande do Sul State, a diversity of dinosaurs coexisted, probably including sauropods, theropods,and ornithopods, whose footprints and trackways were registered in the eolian facies of the Guará Formation.

Fig.14- Theropod trackway with 22cm of length and 15cm of width.

The depositional environment associated with the Guará Formation was relatively dry as evidenced by the eolian sedimentation, mainly dunes and eolian sand sheets.

Footprints and trackways are present only in the eolian facies including dunes and sand sheets. This reduces the anatomic details of tracks that can be preserved.

The ichnofossils does not allow us to establish a precise age for the Guará Formation. An association of theropods, ornithopods, and sauropods dinosaurs could be either Triassic as Cretaceous. The main direction of the palaeocurrents measured in the fluvial layers of the Guará Formation (to South) is totally different from that one from the Triassic package (to N-NE) from Rio Grande do Sul State. It is, therefore, not possible to imagine such a structural change in the basin occurring during the end of the Triassic. So, the Guará Formation could not have been deposited at that time.

The Late Jurassic age here proposed as most probable for the Guará Formation is also supported by the lithostratigraphic correlation with the Tacuarembó Formation from Uruguay, although no common taxa have yet been found in these two units. This study may encourage more detailed studies in the Guará Formation that can provide well-preserved vertebrate ichnofossils to improve the knowledge of those tracks.

Fig.15- Ornithopod trackway with footprints about 43cm of length and 34cm of width.

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