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

VOL.LXVI
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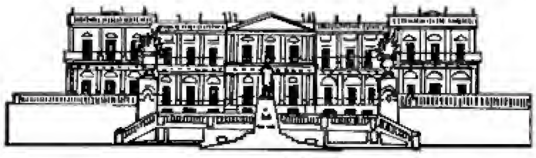

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Janeiro/Março
2008

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II LATIN AMERICAN CONGRESS OF VERTEBRATE PALEONTOLOGY - VOLUME 2

The Second Latin American Congress of Vertebrate Paleontology (II CLPV) was held from August 10th to 12th in Rio de Janeiro, Brazil. More than 220 contributions were received and 211 ended up being published in the abstract volume of the meeting. The Organizing Committee made it possible that complete papers be submitted to the Arquivos do Museu Nacional, the most traditional scientific publication of Brazil. The first volume was published in the Arq. Mus. Nac., v. 65 n. 4 and with the present publication, we conclude the activities of the II CLPV. A total of 29 contributions was accepted, ranging from research on fishes to taphonomical studies. There are also some papers on Paleontological Tourism, in the present volume, a field that has a great potential in Latin America and hopefully will be fostered in the next years.

The Organizing Committee also wants to thank the valuable help of the referees as follows: Antonio Carlos Sequeira Fernandes (Museu Nacional, Universidade Federal do Rio de Janeiro), Átila Augusto Stock da Rosa (Universidade Federal de Santa Maria), Bernardo Javier González Riga (Universidad Nacional de Cuyo; Centro Regional de Investigaciones Científicas y Tecnológicas), Castor Cartelle Guerra (Pontifícia Universidade Católica de Minas Gerais), Christopher Bennett (Fort Hays State University), Christopher Brochu (University of Iowa), Cibele Schwanke (Universidade do Estado do Rio de Janeiro), Claudia Tambussi (Museo de La Plata), Dana Biasatti (National High Magnetic Field Laboratory and Florida State University), David Lovelace (University of Wyoming, Big Horn Basin Foundation), David Weishampel (The Johns Hopkins University), Diego Pol (Museo Paleontológico Egidio Feruglio), Douglas Riff (Universidade Estadual do Sudoeste da Bahia), Édio Ernest Kischlat, Felipe Vasconcellos (Instituto de Geociências, Universidade Federal do Rio de Janeiro), Gisele Mendes Lessa del Giudice (Universidade Federal de Viçosa), Gustavo Oliveira (Museu Nacional, Universidade Federal do Rio de Janeiro), Herculano Alvarenga (Museu de História Natural de Taubaté), Ismar de Souza Carvalho (Instituto de Geociências, Universidade Federal do Rio de Janeiro), John Maisey (American Museum of Natural History), Jonathas Bittencourt (Universidade de São Paulo - Ribeirão Preto), Jorge Calvo (Centro Paleontológico Lago Barreales, Universidad Nacional del Comahue), Leila Maria Pessoa (Instituto de Biologia, Universidade Federal do Rio de Janeiro), Leonardo dos Santos Ávilla (Universidade Federal do Estado do Rio de Janeiro), Lílian Paglarelli Bergqvist (Instituto de Geociências, Universidade Federal do Rio de Janeiro), Marcelo Trotta (Museu Nacional, Universidade Federal do Rio de Janeiro), Marco Brandalise de Andrade (Universidade Estadual Paulista/University of Bristol), Maria Claudia Malabarba (Pontifícia Universidade Católica do Rio Grande do Sul), Maria Magdalena Perini (Centro Paleontológico Lago Barreales, Universidad Nacional del Comahue), Maria Teresa Alberdi (Museo Nacional de Ciencias Naturales), Marise Sardenberg Salgado de Carvalho (Companhia de Pesquisa de Recursos Minerais), Martin Lockley (University of Birmingham), Mauro José Cavalcanti (Universidade do Estado do Rio de Janeiro), Max Langer (Universidade de São Paulo - Ribeirão Preto), Michael Holz (Universidade Federal do Rio Grande do Sul), Nicholas Czaplewski (University of Oklahoma), Patrícia Gonçalves Guedes (Museu Nacional, Universidade Federal do Rio de Janeiro), Paulo Marques Machado Brito (Universidade do Estado do Rio de Janeiro), Reinaldo José Bertini (Universidade Estadual Paulista - Rio Claro), Renata Guimarães Netto (Universidade do Vale do Rio dos Sinos), Rita de Cássia Tardin Cassab (Museu de Ciências da Terra, Departamento Nacional de Produção Mineral), Romain Amiot (Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology), Sebastián Apesteguía (Museo Argentino de Ciencias Naturales Bernardino Rivadavia), Susan Evans (University College London), Taissa Rodrigues (Museu Nacional, Universidade Federal do Rio de Janeiro), Valéria Gallo (Universidade do Estado do Rio de Janeiro), and Zulma Gasparini (Universidad Nacional de La Plata).

We would also acknowledge PETROBRAS, the main sponsor of this meeting, and the following institutions and scientific societies: Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ), Universidade Federal do Rio de Janeiro (UFRJ), Academia Brasileira de Ciências (ABC), Departamento Nacional de Produção Mineral (DNPM), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Fundação Universitária José Bonifácio (FUJB), Society of Vertebrate Paleontology (SVP), Sociedade Brasileira de Paleontologia (SBP), Asociación Paleontológica Argentina (APA), Sociedad Paleontológica de Chile (SPACH), and Sociedad Mexicana de Paleontología. The companies Varig and Rio Othon Palace Hotel were also very important for the success of this meeting.

The Organizing Committee also thanks Dr. Sergio Alex Kugland de Azevedo, Director of the Museu Nacional for all support, and Ulisses Caramaschi, Miguel Angel Monné Barrios, Lia Ribeiro and Thiago Macedo Santos of the Publication Committee of the Museu Nacional.

We hope that you enjoy both volumes.

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

II CONGRESSO LATINO-AMERICANO DE PALEONTOLOGIA DE VERTEBRADOS - VOLUME 2

O Segundo Congresso Latino-americano de Paleontologia de Vertebrados (II CLPV) foi organizado entre 10 e 12 de agosto na cidade do Rio de Janeiro, Brasil. Mais de 220 contribuições foram recebidas das quais 211 acabaram sendo aceitas para o volume de resumos do evento. A Comissão Organizadora tornou possível que trabalhos completos fossem submetidos para os Arquivos do Museu Nacional, a revista científica mais tradicional do país. O primeiro volume (Arq. Mus. Nac., v. 65 n. 4) já foi publicado e com a presente publicação nós concluímos os trabalhos do II CLPV. Um total de 29 contribuições foi aceito, variando desde pesquisas sobre peixes até estudos tafonômicos. Também foram publicados, no presente volume, trabalhos sobre Turismo Paleontológico, um campo que possui grande potencial na América Latina e para o qual esperamos ter contribuído para o seu desenvolvimento nos anos vindouros.

A Comissão Organizadora gostaria de agradecer a importante ajuda dos revisores como segue: Antonio Carlos Sequeira Fernandes (Museu Nacional, Universidade Federal do Rio de Janeiro), Átila Augusto Stock da Rosa (Universidade Federal de Santa Maria), Bernardo Javier González Riga (Universidad Nacional de Cuyo; Centro Regional de Investigaciones Científicas y Tecnológicas), Castor Cartelle Guerra (Pontifícia Universidade Católica de Minas Gerais), Christopher Bennett (Fort Hays State University), Christopher Brochu (University of Iowa), Cibele Schwanke (Universidade do Estado do Rio de Janeiro), Claudia Tambussi (Museo de La Plata), Dana Biasatti (National High Magnetic Field Laboratory and Florida State University), David Lovelace (University of Wyoming, Big Horn Basin Foundation), David Weishampel (The Johns Hopkins University), Diego Pol (Museo Paleontológico Egidio Feruglio), Douglas Riff (Universidade Estadual do Sudoeste da Bahia), Édio Ernest Kischlat, Felipe Vasconcellos (Instituto de Geociências, Universidade Federal do Rio de Janeiro), Gisele Mendes Lessa del Giudice (Universidade Federal de Viçosa), Gustavo Oliveira (Museu Nacional, Universidade Federal do Rio de Janeiro), Herculano Alvarenga (Museu de História Natural de Taubaté), Ismar de Souza Carvalho (Instituto de Geociências, Universidade Federal do Rio de Janeiro), John Maisey (American Museum of Natural History), Jonathas Bittencourt (Universidade de São Paulo - Ribeirão Preto), Jorge Calvo (Centro Paleontológico Lago Barreales, Universidad Nacional del Comahue), Leila Maria Pessoa (Instituto de Biologia, Universidade Federal do Rio de Janeiro), Leonardo dos Santos Ávilla (Universidade Federal do Estado do Rio de Janeiro), Lílian Paglarelli Bergqvist (Instituto de Geociências, Universidade Federal do Rio de Janeiro), Marcelo Trotta (Museu Nacional, Universidade Federal do Rio de Janeiro), Marco Brandalise de Andrade (Universidade Estadual Paulista/University of Bristol), Maria Claudia Malabarba (Pontifícia Universidade Católica do Rio Grande do Sul), Maria Magdalena Perini (Centro Paleontológico Lago Barreales, Universidad Nacional del Comahue), Maria Teresa Alberdi (Museo Nacional de Ciencias Naturales), Marise Sardenberg Salgado de Carvalho (Companhia de Pesquisa de Recursos Minerais), Martin Lockley (University of Birmingham), Mauro José Cavalcanti (Universidade do Estado do Rio de Janeiro), Max Langer (Universidade de São Paulo - Ribeirão Preto), Michael Holz (Universidade Federal do Rio Grande do Sul), Nicholas Czaplewski (University of Oklahoma), Patrícia Gonçalves Guedes (Museu Nacional, Universidade Federal do Rio de Janeiro), Paulo Marques Machado Brito (Universidade do Estado do Rio de Janeiro), Reinaldo José Bertini (Universidade Estadual Paulista - Rio Claro), Renata Guimarães Netto (Universidade do Vale do Rio dos Sinos), Rita de Cássia Tardin Cassab (Museu de Ciências da Terra, Departamento Nacional de Produção Mineral), Romain Amiot (Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology), Sebastián Apesteguía (Museo Argentino de Ciencias Naturales Bernardino Rivadavia), Susan Evans (University College London), Taissa Rodrigues (Museu Nacional, Universidade Federal do Rio de Janeiro), Valéria Gallo (Universidade do Estado do Rio de Janeiro), e Zulma Gasparini (Universidad Nacional de La Plata).

Também agradecemos a PETROBRAS, o principal patrocinador deste congresso, e as seguintes instituições e sociedades científicas: Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ), Universidade Federal do Rio de Janeiro (UFRJ), Academia Brasileira de Ciências (ABC), Departamento Nacional de Produção Mineral (DNPM), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Fundação Universitária José Bonifácio (FUJB), Society of Vertebrate Paleontology (SVP), Sociedade Brasileira de Paleontologia (SBP), Asociación Paleontológica Argentina (APA), Sociedad Paleontológica de Chile (SPACH) e Sociedad Mexicana de Paleontología. As empresas Varig e Rio Othon Palace Hotel também foram muito importantes para o sucesso deste evento.

A Comissão Organizadora também agradece ao Dr. Sergio Alex Kugland de Azevedo, Diretor do Museu Nacional por todo o apoio e a Ulisses Caramaschi, Miguel Angel Monné Barrios, Lia Ribeiro e Thiago Macedo Santos da Comissão de Publicação do Museu Nacional.

Esperamos que aproveitem os dois volumes.

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

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MORPHOLOGICAL AND ANATOMICAL OBSERVATIONS ABOUT *MARILIASUCHUS AMARALI* AND *NOTOSUCHUS TERRESTRIS* (MESOEUCROCODYLIA) AND THEIR RELATIONSHIPS WITH OTHER SOUTH AMERICAN NOTOSUCHIANS[1]

(With 19 figures)

MARCO BRANDALISE DE ANDRADE[2,3]
REINALDO J. BERTINI[2]

ABSTRACT: The phylogenetic relationship of the notosuchians *Mariliasuchus amarali* (Campanian; Bauru Group) and *Notosuchus terrestris* (Santonian; Neuquén Group) is revised. Morpho-anatomical evaluation of *Mariliasuchus* in the current bibliography indicate close relationship with *Notosuchus*, while cladistic analysis either related *Mariliasuchus* to *Candidodon itapecuruense* (Albian/eo-Cenomanian; São Luis-Grajaú Basin), as part of the phylotaxon Candidodontidae, or to *Comahuesuchus brachybuccalis* (Santonian; Neuquén Group). Comparative study of specimens shows similarities on the palate, choanae, dentition, retroarticular process, and other structures from *Mariliasuchus* and *Notosuchus*, supporting the original classification as a Notosuchidae. Preliminary phylogenetic analysis sets these taxa as sister-groups. Reevaluation of a previously published phylogenetic analysis from other authors provides further support for the *Mariliasuchus+Notosuchus* clade. The current work indicates that *Mariliasuchus* is a Notosuchidae, refuting its allocation as a Candidodontidae. The influence of character construction and the definition of Notosuchia are discussed.

Key words: *Mariliasuchus*. *Notosuchus*. *Candidodon*. Notosuchia. Cretaceous.

RESUMO: Observações morfológicas e anatômicas sobre *Mariliasuchus amarali* e *Notosuchus terrestris* (Mesoeucrocodylia) e suas relações com outros notosúquios sulamericanos.

As relações filogenéticas entre os notosúquios *Mariliasuchus amarali* (Campaniano; Grupo Bauru; Brasil) e *Notosuchus terrestris* (Santoniano; Grupo Neuquén; Argentina) são revisadas. A avaliação morfo-anatômica de *Mariliasuchus* na bibliografia corrente indica parentesco próximo com *Notosuchus*, enquanto análises cladísticas tanto relacionam *Mariliasuchus* a *Candidodon itapecuruense* (Albiano-eo-Cenomaniano; Bacia de São Luis-Grajaú), como parte do táxon Candidodontidae, ou com *Comahuesuchus brachybuccalis* (Santonian; Grupo Neuquén). Estudo comparativo de espécimes traz novas informações sobre palato, coanas, dentição, processo retroarticular e outras estruturas de *Mariliasuchus* e *Notosuchus*, suportando a classificação original como Notosuchidae. Análise filogenética preliminar posiciona estes taxons como grupos-irmãos. Reavaliação de análise filogenética previamente publicada por outros autores fornece evidência adicional para um clado *Mariliasuchus+Notosuchus*. O trabalho presente indica que *Mariliasuchus* é um Notosuchidae, refutando a sua alocação em Candidodontidae. A influência da construção de caracteres e a definição de Notosuchia são discutidas.

Palavras-chave: *Mariliasuchus*. *Notosuchus*. *Candidodon*. Notosuchia. Cretáceo.

INTRODUCTION

The Cretaceous of South America is rich in many species of fossil crocodylomorphs, especially the Mesoeucrocodylia (BERTINI, 1993; BERTINI *et al.*, 1993; BERTINI & CARVALHO, 1999; KELLNER & CAMPOS, 1999; CARVALHO & BERTINI, 2000; LEANZA *et al.*, 2004; ANDRADE, 2005; CANDEIRO *et al.*, 2006). Among the South-American forms, several fossil taxa constituted highly adapted terrestrial crocodylians, with lateral orbits

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and oreinrostral snout (*e.g.*, *Araripesuchus, Lomasuchus, Peirosaurus*), frequently showing short rostrum and specialized dentition (*e.g.*, *Candidodon, Comahuesuchus, Uruguaysuchus*). *Notosuchus terrestris* and *Mariliasuchus amarali* are two special examples of Mesoeucrocodylia, sharing several characteristics with each other (*e.g.*, maxillo-palatine fenestrae, single terminal nares, elongated glenoid fossa, triangular choanae, fenestrated quadrate). They are usually referred as notosuchians, although definition of this group has been extensively debated (Gasparini, 1971; Buffetaut, 1981, 1982; Benton & Clark, 1988; Clark, 1994; Ortega *et al.*, 2000; Sereno *et al.*, 2001; Andrade, 2005; Zaher *et al.*, 2006) and divergences on its composition and range occur. *Notosuchus* and *Mariliasuchus* are among the most common fossil crocodylians from Argentina and Brazil respectively, with several specimens collected. Nevertheless, only a fraction of the specimens from both taxa were properly described (Woodward, 1896; Gasparini, 1971; Bonaparte, 1991; Carvalho & Bertini, 1999; Zaher *et al.*, 2006). Though both *Mariliasuchus* and *Notosuchus* were previously related to other notosuchians in morpho-anatomical studies, their close phylogenetic relationship has not been always recognized. The objective of this paper is to compare morphological features of *Notosuchus terrestris* and *Mariliasuchus amarali*, discuss some of the characters uniting these notosuchians and explore the relations of these species with other South American notosuchians.

THE FOSSIL CROCODYLIAN *NOTOSUCHUS* FROM PATAGONIA

Notosuchus terrestris Woodward, 1896 (Fig.1) is one of the first species of fossil crocodylomorphs to be described from South America, which was the focus of many studies during the last century (Woodward, 1896; Saez, 1957; Gasparini, 1971; Bonaparte, 1991; Pol, 1999, 2005; Martinelli, 2003; Andrade, 2005; Fiorelli, 2005; Andrade *et al.*, 2006). Several specimens, from the Upper Cretaceous of the Neuquén Basin, Bajo de La Carpa Formation, are distributed throughout paleontological collections from Argentina, such as MACN, MLP, MUCPv-UNC/"Proyecto Dino" and MPCA. The material available includes cranial and postcranial remains, composing an impressive group of more than 40 specimens, all from Patagonia (Argentina). There are several reconstructions of *Notosuchus terrestris* available from published works, where different interpretations show the lack of consensus on the morphology of the species (Fig.1).

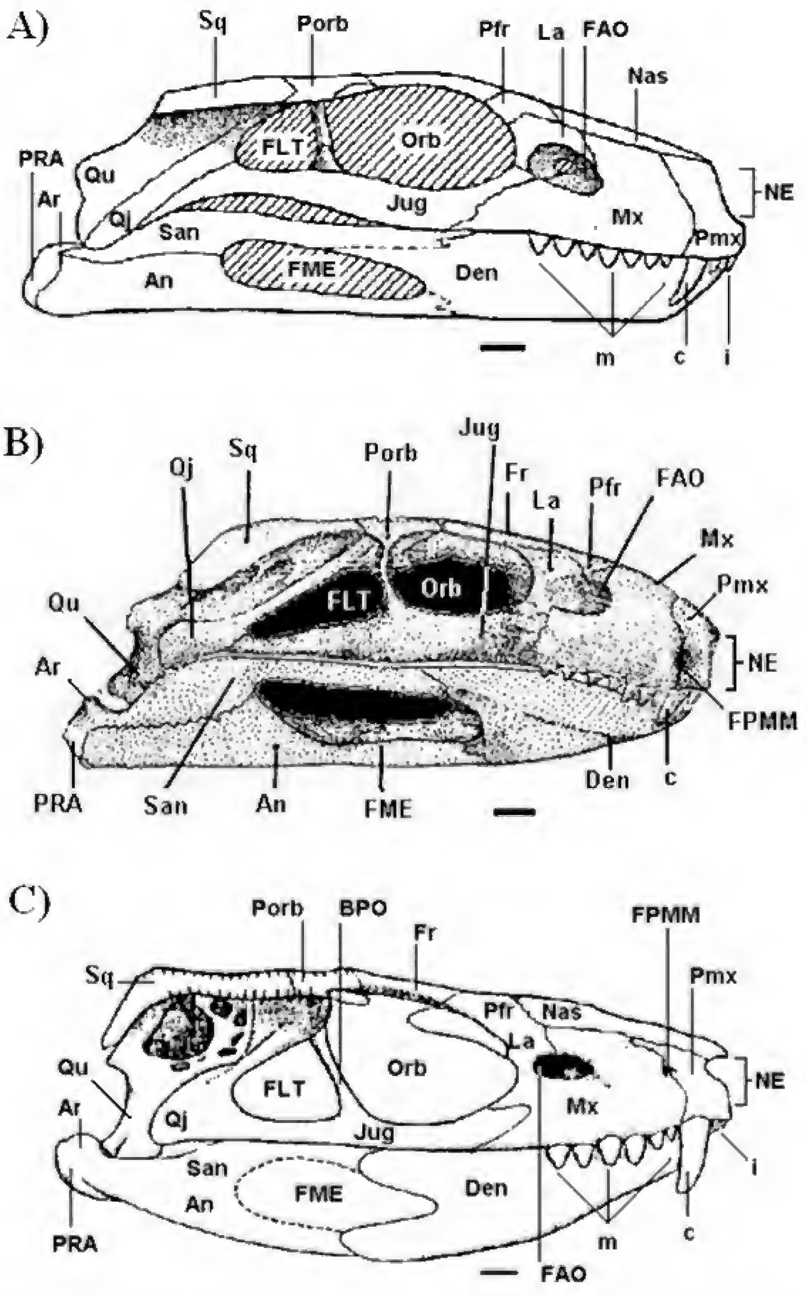

Fig.1- *Notosuchus terrestris*, as reconstructed by different authors; A) reconstruction based on MLP 64-IV-16-5, lectotype, from Price (1959); B) reconstruction based on MLP 64-IV-16-5, from Gasparini (1971); C) reconstruction based on the MACN-Pv-N specimens, from Bonaparte (1991). Note the differences on the reconstruction of the rostral region, antorbital fenestra, dentition, quadrate surface, general morphology of the mandible and retroarticular process. Bar = 10mm.

The Family Notosuchidae Dollo, 1914 was originally erected to *Notosuchus terrestris* alone, defined then as a Mesosuchia Huxley, 1875. The new species was very different from any other known fossil crocodylomorph described until the first half of the Twentieth Century. A second species, *Notosuchus lepidus*, was posteriorly described by Saez (1957) based on two poorly preserved specimens (MLP 64-IV-16-1, MLP 64-IV-16-2), which was subsequently considered as a junior synonym to *N. terrestris* by Gasparini (1971). The work of Gasparini (1971) extended the observations on *Notosuchus* and included the genus in the Infra-Order Notosuchia, along with *Araripesuchus* and *Uruguaysuchus*. In this work, specimens from the original collection of the La Plata Museum were reorganized and a new number assigned to them. Gasparini (1971) also elected a lectotype for *N. terrestris*, as the original description referred to the specimens as a group.

The development of the cladistic methods allowed a revision of general phylogenetic relationships, and works ranging main groups of crocodylomorphs (Benton & Clark, 1988; Clark, 1994) assigned *Notosuchus* to the Mesoeucrocodylia. Bonaparte (1991) described additional materials in detail (MACN–Pv–N–22, MACN–Pv–N–23, MACN–Pv–N–24), providing valuable information on the species. Based on the structures of the basicranium and the perforated quadrate, Bonaparte (1991) suggested that *Notosuchus* could be related to the protosuchian lineage. Even though there is a huge variation upon the topologies obtained for Crocodylomorpha (Wu *et al.*, 1995; Wu & Sues, 1996; Gomani, 1997; Pol, 1999, 2003, 2005; Buckley *et al.*, 2000; Ortega *et al.*, 2000; Martinelli, 2003; Sereno *et al.*, 2003; Carvalho *et al.*, 2004; Pol & Norell 2004a, 2004b; Andrade, 2005; Fiorelli, 2005; Fiorelli & Calvo, 2005; Pol & Apesteguia, 2005; Turner & Calvo, 2005; Jouve *et al.*, 2006; Turner, 2006; Zaher *et al.*, 2006; Larsson & Sues, 2007; Lauprasert *et al.*, 2007), all subsequent phylogenetic studies support *Notosuchus* as a Mesoeucrocodylia. Substantial new information was provided by Pol (1999, 2005), who contributed to the understanding of *Notosuchus* describing new postcranial remains (MACN–Pv–RN–1037), showing the relevance of this type of data for the study of crocodylomorph evolution. Furthermore, several other specimens exist, as reported by the unpublished works of Andrade (2005) and Fiorelli (2005), providing a huge amount of new and important data.

Phylogenetic relationships proposed and published for *Notosuchus terrestris* relate the species to several other notosuquians and sebecosuchians, in a series of different hypothesis, most of them supported by only a few other works. Closer relationships with other notosuchians include *Malawisuchus mwakasyungutiensis* Gomani, 1997 (as in Wu & Sues, 1996; Gomani, 1997; Sereno *et al.*, 2001, 2003; Larsson & Sues, 2007; Lauprasert *et al.*, 2007), *Sphagesaurus huenei* Price, 1950 (as in Martinelli, 2003) and *Uruguaysuchus* (as in Jouve *et al.*, 2006). It is also related to comahuesuchids (Turner, 2004, 2006; Turner & Calvo, 2005), although these authors included *Anatosuchus* in this clade (as in Sereno *et al.*, 2003; *contra* Martinelli, 2003; Andrade *et al.*, 2006). A closer relationship with sebecosuchians is presented by Ortega *et al.* (2000) and Carvalho *et al.* (2004), where *Notosuchus* is depicted by as the basalmost Ziphosuchia, along with *Libycosuchus*, baurusuchids and other sebecosuchians.

Other different hypothesis includes mixed relationships with notosuchians and sebecosuchians. Buckley *et al.* (2000) included *Notosuchus* in the same clade along with *Libycosuchus* and a subgroup composed by *Uruguaysuchus*, *Simosuchus* and *Malawisuchus*. In a much broader framework (Pol, 1999, 2003; Pol & Norell 2004a, 2004b; Pol & Apesteguia, 2005), *Notosuchus* is considered a sister-group to a branch composed by *Comahuesuchus*, *Baurusuchus*, *Bretesuchus*, *Iberosuchus*, *Chimaerasuchus* and *Sphagesaurus*. Zaher *et al.* (2006) further add *Mariliasuchus* to this list.

Although it is difficult to extract a common sense upon the mixture of results presented by these various frameworks, in a broader view most works agree that *Notosuchus* relates closely to Comahuesuchidae, Sphagesauridae, Baurusuchidae and Bretesuchidae (Pol, 1999, 2003; Ortega *et al.*, 2000; Martinelli, 2003; Pol & Norell 2004a, 2004b; Pol & Apesteguia, 2005; Zaher *et al.*, 2006). Main problems and alternative relationships obtained may be regarded, for most cases, as the result of differential absence of certain taxa from each analysis.

The Brazilian notosuchid from Marília

Mariliasuchus amarali Carvalho & Bertini, 1999 is another South American species, described from the Upper Cretaceous of the Bauru Group, Brazil (Fig.2). *Mariliasuchus* was extensively described by Carvalho & Bertini (1999), Andrade (2005), Vasconcellos & Carvalho (2005, 2006), Andrade *et al.* (2006) and Zaher *et al.* (2006), all focusing on cranial features and most also addressing its relationships with other notosuchians.

Most descriptive details published can be seen in Zaher *et al.* (2006), but also in Andrade *et al.* (2006) for specific focus on the choanae. Vasconcellos & Carvalho (2005, 2006) studied the ontogeny of *Mariliasuchus* and other works (Carvalho *et al.*, 2004; Fiorelli, 2005) included the species in broad phylogenetic analysis of crocodylomorphs.

Mariliasuchus is well represented in Brazilian paleontological collections (UFRJ-DG, IGCE-UNESP/ Rio Claro, MN-UFRJ, and MUZUSP). As for *Notosuchus*, the large number of specimens contributes to the knowledge of this taxon. Nevertheless, until most recently the holotype was the only specimen with a published description (Carvalho & Bertini, 1999). The holotype is truly a juvenile, which can be inferred by its small size, proportionally large orbits (Vasconcellos & Carvalho, 2005, 2006; Zaher *et al.*, 2006) and the unfused interfrontal suture (as in Carvalho & Bertini, 1999; p.93, fig.7). A few new specimens (UFRJ-DG-56-R, UFRJ-DG-105-R, UFRJ-DG-106-R) were reported by Vasconcellos & Carvalho (2005, 2006) and others (MN 6298-V, MN 6756-V, MZSP-PV-50, MZSP-PV-51) were addressed by Zaher *et al.* (2006). MN 6756-V is figured in Azevedo *et al.* (2004). As previously mentioned by Zaher *et al.* (2006), the MN specimens have an intermediate size between the holotype and the MUZUSP specimens and also possibly constitute semi-adult individuals. In an unpublished work, Andrade (2005) introduced three specimens that can be considered as semi-adults, which are briefly presented here.

Mariliasuchus was initially identified as a Notosuchidae through anatomical comparison (Carvalho & Bertini, 1999). The first phylogenetic analysis including the species (Carvalho *et al.*, 2004) proposed a closer relationship with *Candidodon itapecuruense* Carvalho & Campos, 1988, from the São Luis-Grajaú Basin (Itapecuru Group, Lower Cretaceous; Rossetti, 2001). Andrade (2005), Fiorelli (2005) and Marconato (2006), in unpublished works, also included *Mariliasuchus* in a phylogenetic analysis, obtaining a closer relationship with *Notosuchus*. Phylogenetic hypothesis by Zaher *et al.* (2006) presented *Mariliasuchus* as the sister-group of *Comahuesuchus brachybuccalis* Bonaparte, 1991, from the Neuquén Basin (Bajo de la Carpa Formation, Upper Cretaceous; Leanza *et al.*, 2004), Argentina.

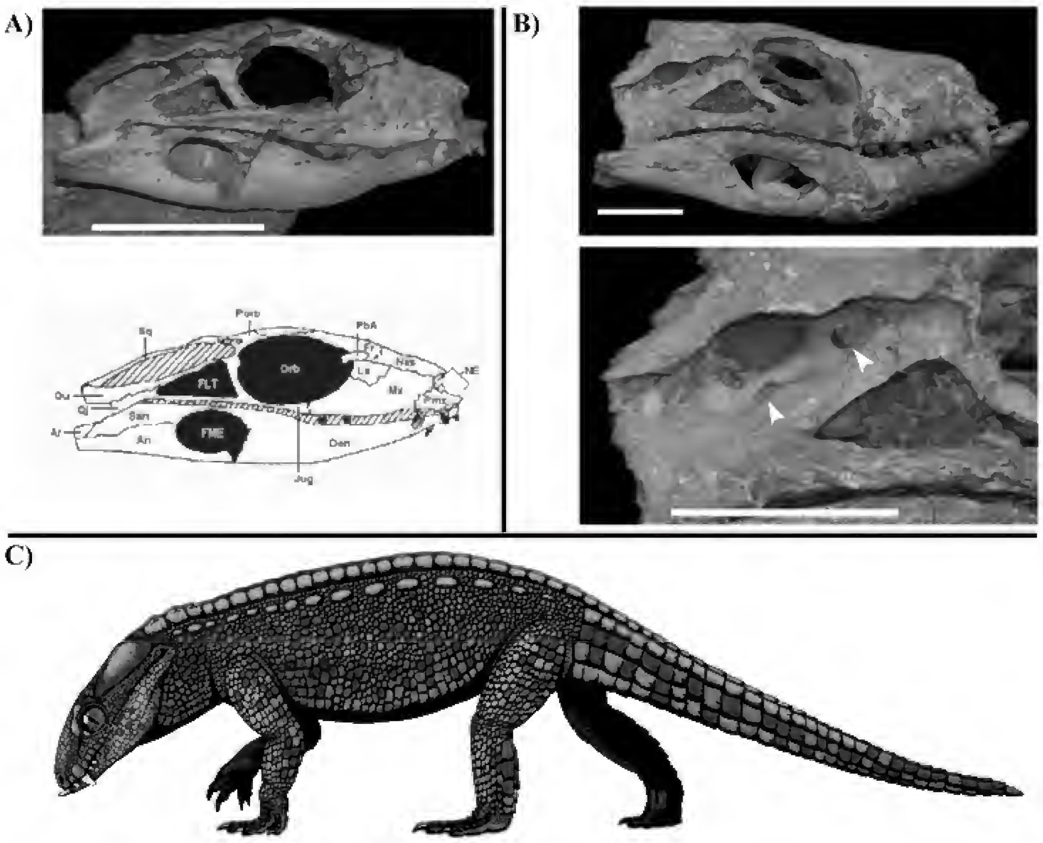

Fig.2- Main aspects of *Mariliasuchus amarali*: A) UFRJ-DG-50-R, holotype, a juvenile specimen; B) mature specimen UFRJ-DG-106-R, showing a detail of the quadrate surface; C) paleoartistic reconstruction of *Mariliasuchus*. Note white pointers, showing quadrate fenestrae. Bar = 20mm. (UFRJ-DG-50-R drawing adapted from Carvalho & Bertini, 1999; C - by Felipe Alves Elias).

Carvalho *et al.* (2004) chose to include *Mariliasuchus* in the then defined phylotaxon Candidodontidae. Nevertheless, *Candidodon* lacks several morphological characteristics of *Mariliasuchus* (Andrade, 2005; Zaher *et al.*, 2006). The general set of characteristics seems to indicate that *Candidodon* may be more similar to Uruguaysuchidae (*sensu* Gasparini, 1971), although with a single naris (Nobre & Carvalho, 2002). The lack of morphological information on the skull of *Candidodon* clearly introduces a problem, especially regarding the relationship of palatine and choanal elements, as stated by Andrade *et al.* (2006). The phylogenetic relationships obtained in posterior studies indicate that *Mariliasuchus*, *Notosuchus*, *Comahuesuchus* and possibly *Sphagesaurus* are closely related (Andrade, 2005; Fiorelli, 2005; Zaher *et al.*, 2006).

The recently published phylogenetic study by Zaher *et al.* (2006) shows *Mariliasuchus* as sister-group to *Comahuesuchus*, an exclusive relationship supported by several characters (*e.g.*, jugal foramen present, maxilla reaching the orbit, anterior procumbent alveoli). The relevance of these characters and their occurrences in other taxa is still open to debate, as suggested by other works (Martinelli, 2003; Andrade, 2005).

Geological Settings

Both *Notosuchus* and *Mariliasuchus* have a reasonably common geological provenance. They are Upper Cretaceous notosuchians that inhabited different areas of Central to Southern South-America. Although these areas were distant, they represent cratonic structures rather than marine sediments. In both cases, the sedimentary units are interpreted as semi-arid environments, suggesting a similar ecologic background. While the geological settings for *Notosuchus* are fairly known, there is some disagreement on *Mariliasuchus* specific settings.

Notosuchus terrestris specimens come from an extensive area in Patagonia (Fig.3), from at least two localities (Neuquén and Rio Negro provinces), housed by many institutions (MACN, MLP, MPCA, MUCPv-UNC). *Notosuchus* is found in deposits of the Bajo de La Carpa Formation, which is part of the Rio Colorado Subgroup and the Neuquén Group, Neuquén Basin (Woodward, 1896; Gasparini, 1971; Bonaparte, 1991; Leanza *et al.*, 2004). The age of the Bajo de la Carpa Formation is most probably Santonian (Leanza *et al.*, 2004). These sediments are usually composed of fine to coarse grained reddish to whitish sandstones,

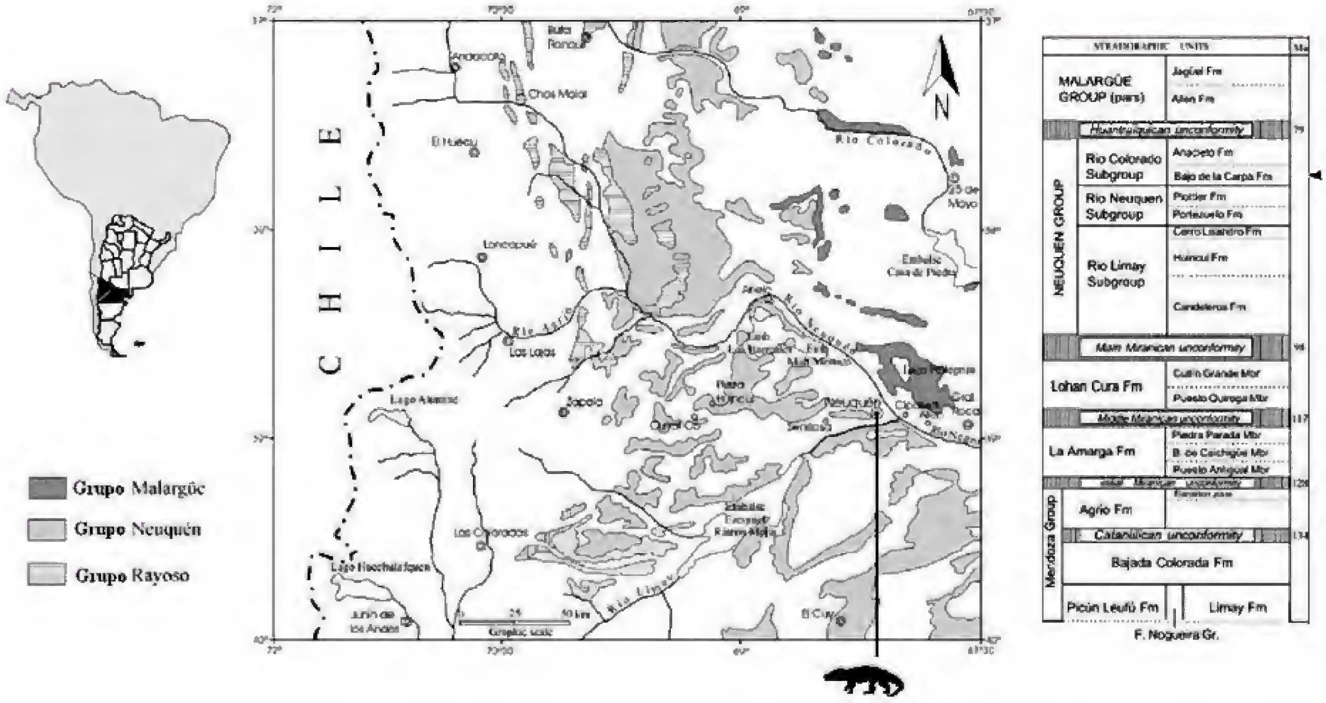

Fig.3- Geographical distribution and stratigraphical range of *Notosuchus terrestris*. The stratigraphical diagram (right) shows the Cretaceous geological units of the Neuquén Basin in the Neuquén Province, and the position of the Bajo de La Carpa Formation (modified from Leanza *et al.*, 2004).

with carbonatic nodules and mudstone lenses (Leanza *et al.*, 2004; Andrade, 2005; Candeiro & Martinelli, 2006).

Mariliasuchus amarali comes from the Upper Cretaceous of Bauru Group (*sensu* Batezelli *et al.*, 2003), Southwestern Brazil (Fig.4). The specific geological settings for this species have become controversial, mostly because a new terminology has been adopted for the Bauru Group sediments. All specimens come from the vicinities of Marília City (São Paulo State, Brazil) (Carvalho & Bertini, 1999, 2000; Vasconcellos & Carvalho, 2005, 2006; Zaher *et al.*, 2006), collected from at least four sites (Nava, 2004). The holotype and the URC specimens come from Rio do Peixe outcrop, close to the Peixe River (Carvalho & Bertini, 1999, 2000; Andrade, 2005). Most authors refer to the sediments as the lower layers of the Adamantina Formation (Carvalho & Bertini 1999, 2000; Kellner & Campos, 1999; Dias-Brito *et al.*, 2001; Vasconcellos & Carvalho, 2005; Candeiro *et al.* 2006) but these have been recently recognized as a distinct formation. The lower Adamantina layers, where there is a predominance of siltic matrix over sandstone, are now considered a part of the Araçatuba Formation (Batezelli, 1998, 2003; Batezelli *et al.*, 1999, 2003; Fernandes *et al.*, 2003; Nobre & Carvalho, 2006). Vasconcellos & Carvalho (2006) not only recognize the current model, but also consider the difficulties in the determination of the limits between units. These authors identified the provenance of the specimens as near the contact between the Araçatuba and Adamantina formations. Zaher *et al.* (2006) also recognize the occurrence of the Araçatuba Formation at Rio do Peixe area, but identify the provenance of the fossil material as the upper levels of the Adamantina Formation, closer to the contact with the Marília Formation.

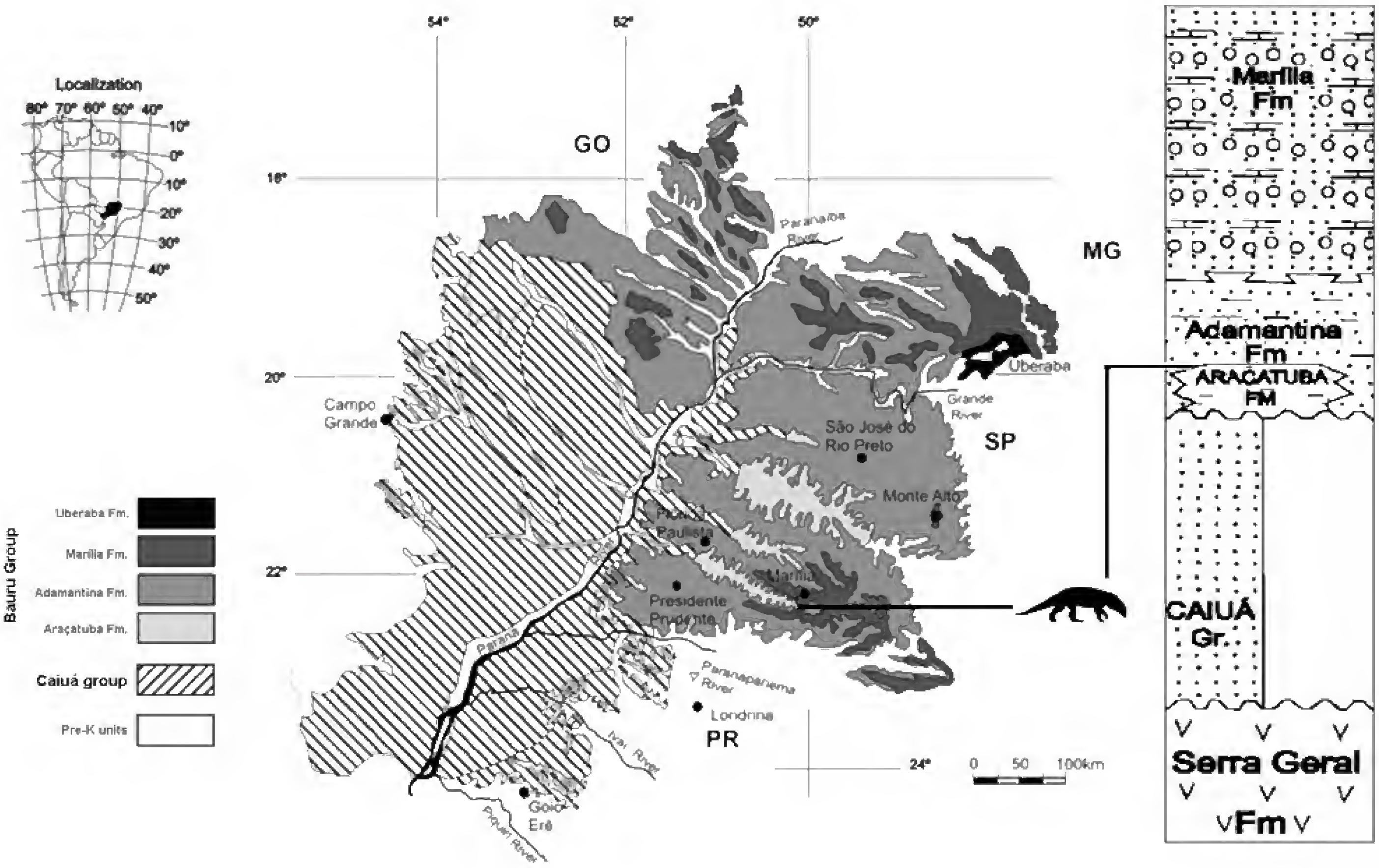

Fig.4- Geographic and stratigraphic range of *Mariliasuchus amarali* within the Bauru Group, Southeastern Brazil. Type-locality indicated, at the vicinities of Marília. The lithological column (right) shows the distribution of the Cretaceous geological units in the State of São Paulo, and the relative position of the Araçatuba Formation. Note that the Bauru Group extends over a large area, including the states of Goiás (GO), Minas Gerais (MG), Paraná (PR) and São Paulo (SP). (Map compiled from Fernandes & Coimbra, 1996; Batezelli, 1998; lithological column modified from Batezelli, 2003).

Actually, as the Araçatuba and Adamantina formations interbed, and were probably synchronic, it is possible that *Mariliasuchus* remains may eventually be recovered from both the Araçatuba and the Adamantina formations. This idea is supported by NAVA's (2004) statement that specimens were not found in a single site. However, the occurrence of *Mariliasuchus* in the upper levels of the Adamantina Formation is yet to be properly reported, especially including material from other outcrops.

The sediments of the Araçatuba Formation are usually composed of greenish to brownish mudstones, interbedded with fine-grained sandstone lenses. *Mariliasuchus* material usually comes from such lenses and, as in the case of URC•67, can be associated with carbonatic nodules. The Araçatuba Formation may be positioned over deposits of either the Caiuá Group (probably middle Cretaceous) or the older basaltic Serra Geral Formation (Lower Cretaceous), depending on the area of occurrence. It is always overlaid by the sediments of the Adamantina Formation (Bauru Group), and although its extension is not small, only a minor part is exposed on the surface (PAULA E SILVA *et al.*, 2003).

Further debate also exists on the age of the Upper Cretaceous deposits from the Bauru Group. DIAS-BRITO *et al.* (2001) argue for a Turonian-Maastrichtian age for the Bauru Group, with a Campanian depositional hiatus, indicating an early age for the Araçatuba Formation sediments, possibly Turonian. The proposal by DIAS-BRITO *et al.* (2001) is widely adopted (VASCONCELLOS & CARVALHO, 2005, 2006; NOBRE & CARVALHO, 2006; ZAHER *et al.*, 2006). Nevertheless, the existence of several gradational contacts between the Adamantina and Marília formations is widely recognized (BATEZELLI, 1998, 2003; BATEZELLI *et al.*, 1999, 2003; ZAHER *et al.*, 2006), which implies that a Campanian depositional hiatus is unlikely to occur.

Correlations based on charophytes, ostracods and vertebrates (GOBBO-RODRIGUES *et al.*, 2000a, 2000b, 2000c; GOBBO-RODRIGUES, 2001; SANTUCCI & BERTINI, 2001) indicate that the Araçatuba Formation was most probably Campanian (Fig.4), rather than Turonian. Although the age attributed for *Mariliasuchus* is similar for ZAHER *et al.* (2006) (Campanian-Maastrichtian), it should be noticed that both models represent different interpretations of the data available. ZAHER *et al.* (2006) follows the basic correlation model proposed by DIAS-BRITO *et al.* (2001) without the Campanian hiatus, and considers that *Mariliasuchus* comes from the upper Adamantina layers. We consider that *Mariliasuchus* comes from the Araçatuba Formation, and follow the GOBBO-RODRIGUES (2001) model for age correlation.

Other notosuchians possibly related with either *Notosuchus* or *Mariliasuchus* come from a similar broad geological background. *Candidodon itapecuruense* was found in deposits of the São Luis-Grajaú Basin (Brazil), previously included in the Parnaiba Basin (ROSSETTI, 2001). The structure of its sedimentary units is under revision. *Candidodon* was previously referred to as from the Itapecuru Formation, but this unit was redescribed as a Group and divided into other units (ROSSETTI, 2001). The specimens probably come from the lower layers of the Itapecuru Group, currently referred to 'undifferentiated unit' by ROSSETTI (2001). Palinologic data from correlated localities (Guariba and Querru outcrops) suggest a meso-Albian age (Lower Cretaceous) for *Candidodon* (PEDRÃO *et al.*, 1993; CARVALHO & BERTINI, 2000). *Comahuesuchus brachybuccalis* was found in the Bajo de la Carpa Formation (Neuquén Basin, Upper Cretaceous, Argentina). Considering the geological settings, *Comahuesuchus* and *Sphagesaurus* are notosuchians that share the stratigraphic range of both *Notosuchus* and *Mariliasuchus*. *Comahuesuchus* also shares the same geographical provenance of *Notosuchus*, while *Sphagesaurus* share a similar geographical provenance with *Mariliasuchus*.

ABBREVIATIONS

Institutional. IGCE-UNESP, Instituto de Geociências e Ciências Exatas, Universidade Estadual Paulista, Rio Claro, Brazil; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MN-UFRJ, Museu Nacional, UFRJ, Rio de Janeiro, Brazil; MPCA, Museo "Carlos Ameghino", Cipoletti, Argentina; MUCPv, Museo de la UNC, Neuquén, Argentina; MUZUSP, MZSP, Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil; UFRJ, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; UFRJ-DG, Departamento de Geologia, UFRJ, Rio de Janeiro, Brazil; UNC, Universidad Nacional del Comahue, Neuquén, Argentina; URC, Museu "Paulo Milton Barbosa Landim", IGCE-UNESP, Rio Claro, Brazil.

Anatomical. An, angular; Ar, articular; Boc, basioccipital; Bes, basiesphenoid; BPO, postorbital bar; c, caniniform; Den, dentary; Eoc, exoccipital; Ept, ectopterygoid; FAO, antorbital fenestra; FLT, laterotemporal fenestra; FME, external mandibular fenestra; FMP, maxilo-palatine fenestra; FPMM, premaxilla-maxilla foramen; Fr, frontal; FSO, suborbital fenestra; FST, supratemporal fenestra; i, incisiform; Jug, jugal; La, lachrymal; m, molariform; Mx, maxilla; Na, nasal; NE, external naris; NI, internal naris (choana); Orb, orbit; Pal, palatine; Par, parietal; PbA, palpebral (anterior); Pfr, prefrontal; pm, premolariform; Pmx, premaxilla; Porb, postorbital; PRA, retroarticular process; Pt, pterygoid; Qj, quadrate-jugal; Qu, quadrate; San, surangular; SIC, interchoanal septum; Sp, splenial; Sq, squamosal; Sy, symphysis.

MATERIAL, PRESERVATION, AND VARIABILITY

Studied material

A small number of specimens of *Mariliasuchus amarali* (URC R•67, URC R•68, URC R•69) was studied in the IGCE-UNESP Collection (Rio Claro *Campus*, Brazil), but also from MN-UFRJ (Rio de Janeiro, Brazil). The specimens were composed mostly by cranial material, although URC R•67 also has well preserved cervical vertebrae and ribs. In contrast, a representative number of specimens from *Notosuchus terrestris*, comprising no less than 45 individuals, was studied from the collections of MACN, MLP and MPCA, all from Argentina. Most specimens included only cranial material, although MACN-Pv-RN-1037 also preserves postcranial elements. Furthermore, other species were observed, including most of the existing specimens of *Comahuesuchus*. A complete list of specimens of notosuchians included in this study can be seen in Appendix 1.

Preservation

Most specimens of *Notosuchus* and *Mariliasuchus* show some degree of deformation and thus a few aspects of the morphology could not be taken from a single specimen. This can be related to differences observed in both notosuchians and must not be confounded with intraspecific variability. The material from both species may be broken, incomplete, deformed, showing eroded surfaces and delicate structures are missing. However, it was possible to recognize that specimens of *Mariliasuchus* are usually better preserved than those of *Notosuchus*. Particularly in *Notosuchus*, no single specimen has shown a really good preservation throughout the entire skull, considering the studied material. Examples of structures clearly identified in *Mariliasuchus*, but not easily seen in *Notosuchus* due to preservation problems, are the medial borders of the maxillo-palatine fenestrae, the interchoanal septum and teeth ornamentation. Furthermore, a greater number of *Mariliasuchus* specimens include associated (or even articulated) postcranial remains.

Most specimens of *Notosuchus* include at least some degree of deformation (MACN-Pv-RN-1041, MACN-Pv-RN-1046, MACN-Pv-RN-1048, MACN-Pv-RN-1118, MACN-Pv-RN-1119, MPCA-Pv-789, MPCA-Pv-791) and two (MACN-RN-1037, MACN-Pv-RN-1041) have a broken rostrum (thrusted downwards). The lectotype, MLP 64-IV-16-5, has an abnormally enlarged antorbital fenestra due to preservation problems (Fig.1B) and most of the skull surface suffered from either abrasion or corrosion, lacking most of the original ornamentation. Although the right fenestra is altered, the left antorbital fenestra is smaller, with a different morphology and smooth borders, as in MACN-Pv-N-24 (see Bonaparte, 1991). This specific problem was previously addressed by Woodward (1896) himself. On the other hand, the most complete specimen regarding presence of elements is MACN-Pv-RN-1037, which includes most of the skull and mandibles, cervical and dorsal vertebra and anterior appendicular remains, these described by Pol (2005). Other two specimens (MACN-Pv-RN-1041, MACN-Pv-RN-1045) include skulls that can be considered as reasonably preserved. Several partial specimens, despite damaged, are especially valuable (MACN-Pv-N-22, MACN-Pv-N-23, MACN-Pv-N-24, MACN-Pv-N-43, MACN-Pv-RN-1038, MACN-Pv-RN-1039, MACN-Pv-RN-1040, MLP-64-IV-16-1, MLP-64-IV-16-6, MLP-64-IV-16-11, MLP-64-IV-16-13, MLP-64-IV-16-14, MLP-64-IV-16-15, MLP-64-IV-16-16, MLP-64-IV-16-23, MLP-64-IV-16-24). Though partial remains, these specimens provide a lot of quality information as some of them are beautifully preserved, showing sutures and details that are often not evident in more complete specimens, as previously pointed out by Andrade *et al.* (2006) for *Sphagesaurus* and *Stratiotosuchus*.

Although the *Mariliasuchus* material shows good preservation, specimens are not free from problems. URC R•67 is a most complete set of skull and mandible, including cervical vertebrae and ribs, with the skull showing dorsoventral deformation. URC R•68 is a partial rostrum and mandible, including the right side of the rostrum and dental series, as well as most of the right hemimandible and the symphyseal part of the left hemimandible, showing no identifiable deformation. Though the specimen is broken and constitutes only a part of a skull, each element shows an exquisite preservation. URC R•69 includes only the occipital surface and the left quadrate, but most other elements were destroyed. MN 6298-V lacks the mandible and does not preserve the left posterior elements of the skull. MN 6756-V is mostly complete, with a well preserved set of skull and mandible. In ZAHER *et al.* (2006; p.7, 2nd column, lines 8-15), the identification of MN specimens is changed, as MN 6298-V is identified as MN 6756-V and vice versa (as also in AZEVEDO *et al.*, 2004).

Lateral compression can be identified in the MN specimens and UFRJ-DG-105-R, due to the deformation of the suborbital fenestrae. Although UFRJ-DG-105-R and UFRJ-DG-106-R are partial skulls, they are well preserved and include the mandible. UFR-DG-56-R is poorly preserved and was subject to severe deformation. MUZUSP specimens may be the most complete and better preserved, as described by ZAHER *et al.* (2006), although MZSP-PV-50 shows a reasonable amount of damage on the dorsal surface of the rostrum (ZAHER *et al.*, 2006; p.9; Fig.5). UFRJ-DG-56-R and URC R•69 are badly damaged skulls (VASCONCELLOS & CARVALHO, 2006; ANDRADE, 2005) and information on these specimens should be considered with caution.

VARIATION AMONG SPECIMENS AND TRUE INTRASPECIFIC VARIABILITY

Differences in the morphology are the basis for the erection of new fossil species. However, morphological evidence for a new taxon should be constant and allow the recognition of each species, provided the relevant structures are preserved. Differences in the morphology are often regarded as evidence of new species, but not all structures show a constant morphology and, thus, can be regarded as suitable evidence supporting the recognition of different species. Intraspecific variability constitutes a simpler explanation and very common source of morphological differences among individuals in extant taxa. Furthermore, preservation may be an important factor to be considered regarding fossil groups (HOLZ & SCHULTZ, 1998; HOLZ & SOUTO-RIBEIRO, 2000; HOLZ & SIMÕES, 2002). In fossil taxa the reduced sample of specimens is often a problem, as continuous variable characters may appear to be distinct discrete states and discrete states of a character may not be represented in the sample.

Notosuchus and *Mariliasuchus* constitute exceptions in the study of fossils, as the elevated number of specimens contributes to the identification of minor population differences, which may occur within one species or the other. For *Notosuchus*, both ANDRADE (2005) and FIORELLI (2005) identified variability on the morphology of the parietal, which was considered as related to sexual dimorphism. In *Mariliasuchus*, ZAHER *et al.* (2006) identified variability in the development of ornamentation, presence (or absence) frontal medial ridge, parietal width between the supratemporal fenestra and teeth implantation.

Regarding *Mariliasuchus*, the occurrence of ornamentation and frontal ridge may be easily misinterpreted due to preservation. The presence of ornamentation, even if regarded to be of biological origin, may also interfere with the development of the frontal ridge. It is thus preferable not to consider a particular hypothesis to explain this variability, while a broader range of specimens awaits description. In *Notosuchus*, differences are often the result of poor preservation. Good examples include: (i) the description of *Notosuchus lepidus*, based in damaged and partially reconstructed specimens (GASPARINI, 1971); (ii) the reinterpretation of the palatine-ectopterygoid contact by MARTINELLI (2003), which the suture is positioned in the palatine bar, medially to the taphonomic features previously regarded as the suture. In both cases, characters involved are not truly variable. Instead, the poor preservation prevented the correct identification of the morphology. In *Notosuchus*, further disagreement between previous published studies affects several aspects of the morphology, such as the orientation of the retroarticular process, general profile of the mandible, elongation of the symphysis, presence of teeth ornamentation and interchoanal septum (Fig.1).

TRUE VARIABILITY

Despite problems of preservation, true variability can be identified in *Notosuchus* and *Mariliasuchus*, whenever selected specimens are taken. In *Notosuchus*, true variability mostly relates to the parietal morphology, which is discussed below. In *Mariliasuchus*, this applies at least to parietal width and teeth implantation.

ZAHER *et al.* (2006) suggested that the *Mariliasuchus* specimen with wider parietals (MZSP-PV-51) may constitute a different species, but preferred to assume either sexual dimorphism or individual variation to explain differences. Teeth implantation is also variable, as maxillary and mandibulary teeth may be oblique or not oblique (ZAHER *et al.*, 2006). As in *Notosuchus* and *Sphagesaurus*, oblique implantation only affects middle and posterior teeth and is always present as a paramesial rotation of the crown. The good preservation of specimens indicates that they are unlikely to reflect taphonomic bias and there is no evidence suggesting an ontogenetic trend toward obliquely implanted teeth. Thus, populational variation is currently the simplest explanation. Other aspects of the variability in *Mariliasuchus* have been explained as the result of ontogenetic changes (Vasconcellos & Carvalho, 2005, 2006), as discussed below.

It should be noticed that, currently, no particular difference could be linked to any other variable character, layer or site of collection, either in *Mariliasuchus* or *Notosuchus*. This indicates there seems to be no particular population in space and time sharing a set of characters that could justify the identification of distinct populations. Variability has been explained as the result of other biological aspects of these species (ontogeny, sexual dimorphism, individual differences within the population) or even preservation (Andrade, 2005; Fiorelli, 2005; Vasconcellos & Carvalho, 2005, 2006; Zaher *et al.*, 2006). Furthermore, the common paleogeographic and stratigraphic provenance of specimens does not support the existence of new species within each genera.

Ontogenesis and developmental stages of the specimens

An important aspect already recognized on the intraspecific variability refers to ontogenesis. Most specimens of *Notosuchus* are adults (Andrade, 2005), with a small proportion of young (MLP-64-IV-16-24) and sub-adult (MACN-Pv-N-43, MLP-64-IV-16-7, MLP-64-IV-16-8) individuals among the specimens studied (±8.5%). In *Mariliasuchus* this proportion is more expressive (±50%), considering the total specimens officially reported. The most relevant specimen on ontogenetic studies may be the holotype UFRJ-DG-50-R, which is currently the smallest specimen, widely recognized as the youngest individual (Carvalho & Bertini, 1999; Vasconcellos & Carvalho, 2005, 2006; Zaher *et al.*, 2006). The URC and the MN specimens show an intermediate size, bigger than the holotype and smaller than MZSP-PV-50. Among them, MN 6756-V is the smallest and URC R•68 is the largest specimen (Tab.1). Recognition of this difference between the *Mariliasuchus* and *Notosuchus* samples is important, because the ontogeny can be a source of morphological variability, especially in the sample of *Mariliasuchus*. The same argument can barely apply for the studied specimens of *Notosuchus*, as only a low percentage of them are not adult specimens.

Vasconcellos & Carvalho (2005, 2006) demonstrated that significant changes occur during the development of *Mariliasuchus*. These includes the caudal displacement of the mandibular and laterotemporal fenestrae, as well as an increment of size of the supratemporal and laterotemporal fenestra, with implications in the proportional volume of muscles associated with these fenestrae. Nonetheless, the study does not clarify most changes affecting characters used in phylogenetic studies. Furthermore, although ontogenetic changes are reasonably described for *Mariliasuchus*, they are virtually unknown for *Notosuchus*. The description of young specimens may be particularly important to allow comparison and improve understanding on the evolution and development of notosuchians.

Problems of interpretation of the dental formula

Both in *Notosuchus* and *Mariliasuchus*, an important problem affecting the comprehension of variability regards the interpretation of the dental formula. In *Mariliasuchus*, the original description (Carvalho & Bertini, 1999) accounted for three premaxillary teeth, at least three maxillary teeth and at least two mandibulary teeth. Of these, the third (and last) premaxillary tooth was a hypertrophied caniniform. Although this constitutes poor information, teeth were simply not accessible in the specimen, which was preserved with jaws in occlusion and attempts to free the mandible would have inflicted damage to the material. The unpublished work of Andrade (2005) further extends the information on the dental formula, confirming three teeth on the premaxilla, the third one been the hypertrophied caniniform, six maxillary and nine mandibulary teeth. Zaher *et al.* (2006) provide an alternative interpretation for the dental formula, with four premaxillary (the last one been the first postcaniniform) and five maxillary teeth. All works agree with nine teeth in the mandible.

Dentition is difficult to access in *Notosuchus*, as the overall preservation is poor and most specimens with reasonably complete skulls have the mandible in occlusion, preventing access to the teeth. Nevertheless, the oblique implantation was only well represented by Woodward (1896; Plate II) and is beautifully exposed in several MLP partial specimens (MLP-64-IV-16-1, MLP-64-IV-16-6, MLP-64-IV-16-7, MLP-64-IV-16-11, MLP-64-IV-16-13, MLP-64-IV-16-16, MLP-64-IV-16-23). Woodward (1896; as Gasparini; 1971; Bonaparte, 1991) originally considered two small cylindrical teeth (incisiforms) in the premaxilla, and a possible third small tooth preceding them, below the naris. The presence of this anteriormost tooth is confirmed in MACN-Pv-RN-1038 and MACN-Pv-RN-1040, while the same area is not reasonably preserved in other specimens. These incisiforms were followed by a well developed caniniform tooth, robust and long-rooted (Woodward, 1896; Gasparini, 1971; Bonaparte, 1991), also in the premaxilla. The first postcaniniform tooth from the upper series was considered by Woodward (1896) and Gasparini (1971) as pertaining to the maxilla. Bonaparte (1991; p.36, 2nd§) describes the first post-caniniform as of difficult identification, as in lateral view it seemed to be related to the maxilla, and in palatal view it could be related to the premaxilla. Eventually, Bonaparte (1991; p.43, 1st§) refers to it for the first time as part of the premaxillary series, although representing it as a maxillary tooth (Bonaparte, 1991; fig.3, p.33; fig.5, p.37). The following teeth would comprise six elements, according to Woodward (1896) and Gasparini (1971), but Bonaparte (1991) suggested their number could reach up to 10 teeth. The number of mandibulary elements is probably 10 (Woodward, 1896; Gasparini, 1991) despite problems of preservation, which suggest a similar number for the complete upper series.

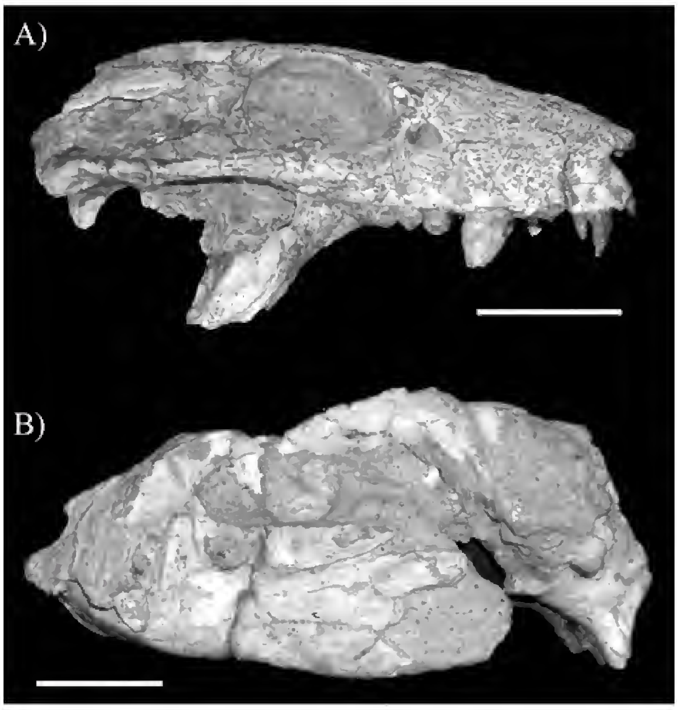

Fig.5- Cranial material from other species of notosuchians, which have been related to *Mariliasuchus* by previous cladistic analysis. A) right side of the skull of *Candidodon itapecuruense* UFRJ-DG-114-R, a referred specimen; B) left side of the skull of *Comahuesuchus brachybuccalis* MUCPv-202, holotype. Bar = 20mm.

TABLE 1. Summary of *Notosuchus* and *Mariliasuchus* specimens considered in this study, showing general state of the material and completeness.

Feature	*Notosuchus* specimens	*Mariliasuchus* specimens
Specimens including cranium and postcranium	MACN-Pv-RN-1037, MPCA-Pv-789	MN 6756-V, MZSP-PV-50, MZSP-PV-51, **UFRJ-DG-50-R**, UFRJ-DG-106-R, URC R•67
Non-adult specimens	MACN-Pv-N-43, MLP-64-IV-16-7, MLP-64-IV-16-8, MLP-64-IV-16-24	MN 6298-V, MN 6756-V, **UFRJ-DG-50-R**, URC R•67, URC R•68, URC R•69
Badly crushed skulls	MACN-Pv-RN-1046, MACN-Pv-RN-1048	UFRJ-DG-56-R
Partial skulls, including rostrum or rostrum and symphysis preserved	MACN-Pv-N-24, MACN-Pv-N-43, MACN-Pv-RN-1038, MACN-Pv-RN-1039, MACN-Pv-RN-1040, MLP-64-IV-16-6, MLP-64-IV-16-11, MLP-64-IV-16-15, MLP-64-IV-16-16, MLP-64-IV-16-23, MLP-64-IV-16-24	URC R•68
Partial skulls, including rostrum, orbits and skull table	MACN-Pv-N-23, MACN-Pv-N-107, MACN-Pv-RN-1046, MACN-Pv-RN-1048, MACN-Pv-RN-1118, MACN-Pv-RN-1119, MLP-64-IV-16-1, MLP-64-IV-16-2, MLP-64-IV-16-7, MLP-64-IV-16-8, MLP-64-IV-16-31, MPCA-Pv-789/1, MPCA-Pv-791	UFRJ-DG-56-R
Skulls mostly preserved	MACN-Pv-RN-1037, MACN-Pv-RN-1041, MACN-Pv-RN-1045, MLP-64-IV-16-3, **MLP-64-IV-16-5**	MN 6298-V, MN 6756-V, MZSP-PV-50, MZSP-PV-51, UFRJ-DG-50-R, UFRJ-DG-105-R, UFRJ-DG-106-R, URC R•67
Sample	46 (45 studied)	13 (8 studied)

Type specimens in bold.

As seen above, there is disagreement on the interpretation of distribution of dental elements in the premaxilla and maxilla of both *Mariliasuchus* and *Notosuchus*. Here, the first postcaniniform is considered as originally pertaining to the maxillary series, following the traditional descriptions of *Mariliasuchus* (Carvalho & Bertini, 1999) and *Notosuchus* (Woodward, 1896; Gasparini, 1971), but also based on the studied specimens, as described below.

Morphological Comparison of *Mariliasuchus* and *Notosuchus*

Mariliasuchus amarali and *Notosuchus terrestris* were considered similar species by Carvalho & Bertini (1999), who present a general comparison with several other mesoeucrocodylians. This comparative analysis focuses on the morphology of both species, along with *Candidodon itapecuruense* Carvalho & Campos, 1988 and *Comahuesuchus brachybuccalis* Bonaparte, 1991. *Candidodon* and *Comahuesuchus* were considered respectively by Carvalho *et al.* (2004) and Zaher *et al.* (2006) the sister group of *Mariliasuchus*. Though most of these species are extensively described in the bibliography, it should be noticed that information on the skull of *Candidodon* is limited (Carvalho, 1994; Nobre & Carvalho, 2002), lacking detailed interpretation of sutures.

Rostrum and general features of the skull – The general proportions of the skull are similar (Fig.6), with rostrum length as short as the postorbital region. The general shape of the skull is mostly similar for *Notosuchus* and *Mariliasuchus*, where the rostrum is small but clearly distinguishable from the rest of the skull. This can better be seen in adult specimens. In *Notosuchus*, the limits of the rostrum are not so evident in younger specimens (MACN-Pv-N-43, MLP-64-IV-16-7, MLP-64-IV-16-24), and the same happens in the case of *Mariliasuchus* holotype. Subadult specimens of *Mariliasuchus* (URC R•67, MN 6298-V, MN 6756-V) show evident rostrum limits, but less evident than in MZSP specimens, which are adults. Both in *Notosuchus* and *Mariliasuchus*, the source of variability is most likely ontogenetic (see Vasconcellos & Carvalho, 2005, 2006, for *Mariliasuchus* ontogenetic development). Neither *Candidodon* nor *Comahuesuchus* show similar characteristics, though the rostrum of the last is extremely short (Bonaparte, 1991). In both cases, the rostrum fits gradually to the skull. In the different specimens of *Comahuesuchus*, there seems to be no particular straightening of the rostrum, and MOZ-P-6131 (the biggest specimen; Martinelli, 2003) show a wide rostrum, as the other smaller specimens.

Mariliasuchus and *Notosuchus* have the same type of ornamentation (Fig.7), characterized by irregular sulcation. This ornamentation develops on the skull, although mainly over the rostrum. This type of ornamentation is not exclusive to them and can be found also in baurusuchids and *Comahuesuchus*, among others. Ornamentation composed by subpolygonal pits, on the other hand, is usually seen in neosuchians, peirosaurids and *Araripesuchus* (Benton & Clark, 1988; Clark, 1994; Ortega *et al.*, 2000), but also in *Candidodon*.

In *Notosuchus, Mariliasuchus, Comahuesuchus* and *Candidodon* the nares are single and terminal. Though in *Comahuesuchus* they were considered as 'inset' (Sereno *et al.*, 2003), this was related to a preservation problem on the specimens described by Bonaparte (1991). Description of MOZ-P-6131 shows that *Comahuesuchus* have a truly terminal naris (Martinelli, 2003). Nasals have a similar general profile in *Notosuchus, Mariliasuchus* and *Comahuesuchus*, but not in *Candidodon*. In the first three notosuchians, the nasals contribute anteriorly to the naris and widen posteriorly near the contact with the lachrymals, straightening again at the contact with the frontal. In dorsal view, this triangular to rhomboidal profile is common to *Sphagesaurus*, but is apparently absent from *Candidodon* (Andrade, 2005). Other mesoeucrocodylians usually have straight nasals, with paralleled lateral borders, including *Araripesuchus, Anatosuchus* and most neosuchians. Thalattosuchians constitute an exception, as they also have triangular nasals (Andrews, 1913).

Further similarities can be seen between *Notosuchus, Mariliasuchus* and *Comahuesuchus*. As in Bonaparte (1991), *Notosuchus* shows a small anterior projection of the nasals over the naris (Fig.6). The structure is preserved in several specimens (MACN-Pv-N-24, MACN-Pv-RN-1037, MACN-Pv-RN-1038, MACN-Pv-RN-1040, MACN-Pv-RN-1041, MACN-Pv-RN-1119, MLP-64-IV-16-1, MLP-64-IV-16-5, MLP-64-IV-16-6, MLP-64-IV-16-22, MPCA-Pv-791). The projection itself has a triangular outline, extending slightly over the naris, but not exceeding the mesial border of the premaxilla. Vasconcellos & Carvalho (2005) have already pointed out the possible presence of a small anterior projection of the nasals in *Mariliasuchus*, without the development of an internarial bar. The structure was considered present in UFRJ-DG-105-R and also probably in the holotype. Zaher *et al.* (2006) ignored the occurrence of the structure, but

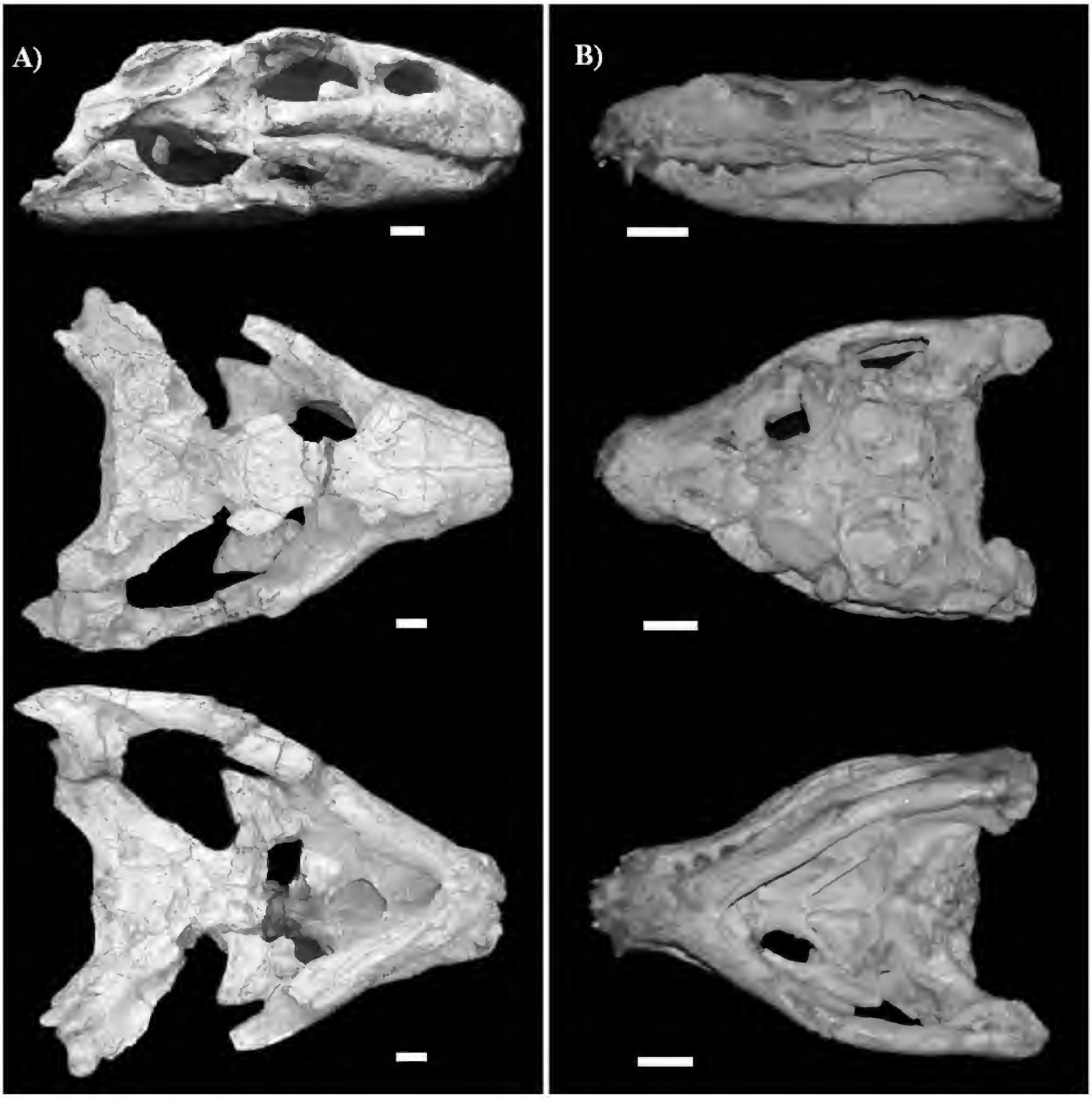

Fig.6- Cranial material of studied specimens, in lateral, parietal and palatal views, showing main similarities between *Notosuchus* and *Mariliasuchus* and main problems of preservation: A) *Notosuchus terrestris* MLP-64-IV-16-5, lectotype, with an abnormally enlarged antorbital fenestra and damaged areas of the skull; B) *Mariliasuchus amarali* URC R•67, with dorsoventral compression. Note the almost triangular outline of the skulls in parietal and palatal views. Bar = 10 mm.

it can be identified at least in MZSP-PV-50. Examination of URC R•67, URC R•68 and the MN specimens allows the recognition of this projection, as originally proposed (Fig.7). The nasal projection is indeed small, not reaching or surpassing the anteriormost (mesial) process of the premaxilla and showing a general outline of a wide triangle, as in *Notosuchus*. *Comahuesuchus* also show the same projection, as seen in MUCPv-202 and MOZ-P-6131 (Bonaparte, 1991; Martinelli, 2003).

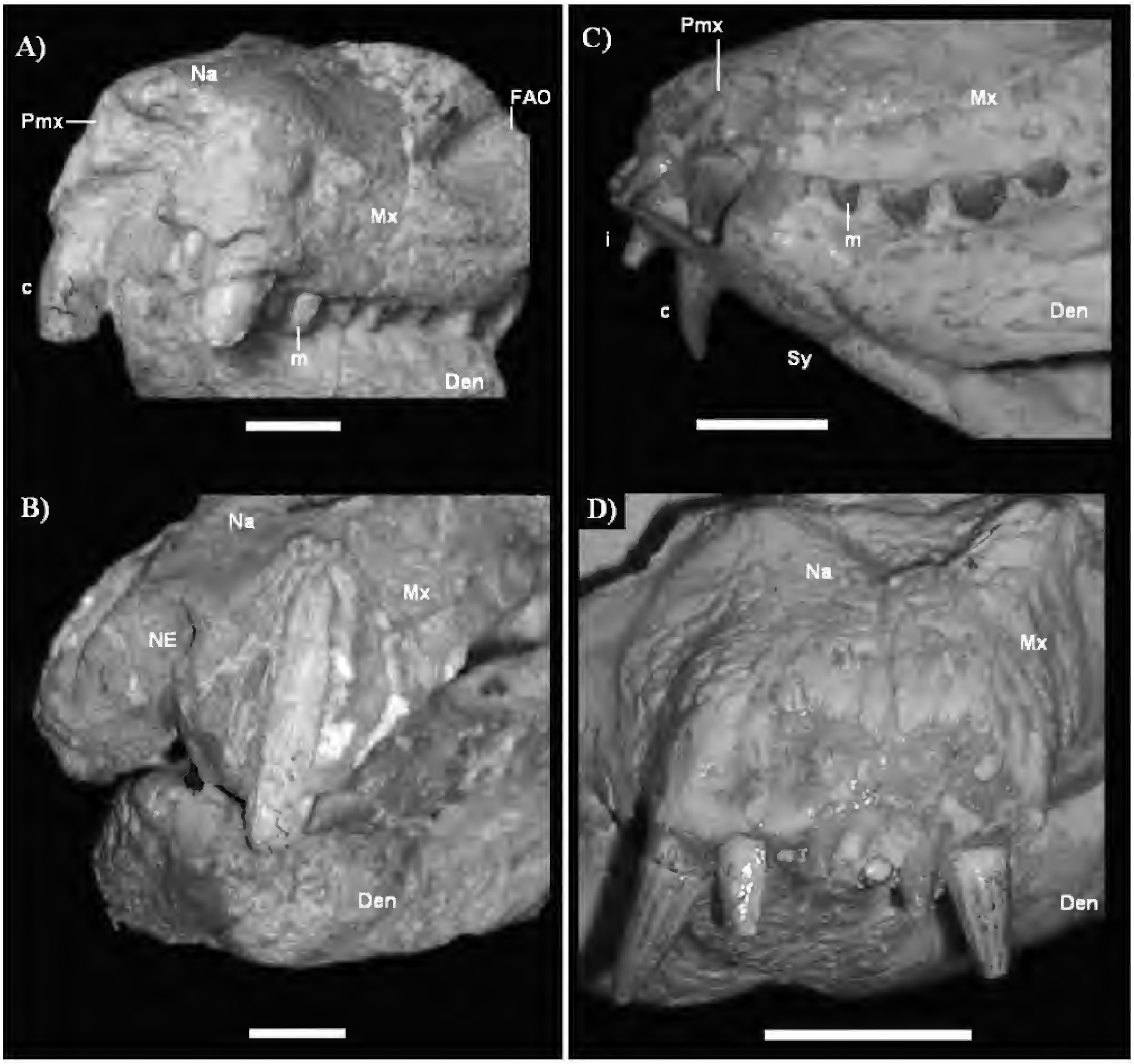

Fig.7- Cranial material of studied specimens, showing the rostrum and its characteristics: A) *Notosuchus terrestris* MACN-Pv-N-24, in anterolateral view; B) MLP-64-IV-16-31(206), in anterolateral view, where the abrasion of the premaxilla exposed the major part of the root from the hypertrophied caniniform; C) *Mariliasuchus amarali* URC R•67, in ventrolateral view, showing the anteriormost dentition and the symphysis; D) *M. amarali* URC R•67, in frontal view, with nasals projecting over the naris in a triangular outline. Note the development of the dorsal part of the premaxilla, lateral to the external naris, which supports the root of the hypertrophied caniniform. Bar = 10 mm.

Palpebrals are poorly preserved in most notosuchians. In *Notosuchus* the presence of two elements over each eye can be verified in a few specimens (MACN-Pv-N-107, MACN-Pv-RN-1037, MACN-Pv-RN-1119, MPCA-Pv-789). The anterior palpebral is elongated and possibly slightly curved, supported mesially by the prefrontal. The posterior palpebral is short and thick, supported by the post-orbital. Palpebrals can be seen in several specimens of *Mariliasuchus*, including URC R•67 and MN 6756-V. In URC R•67, both palpebrals are present on the left side of the specimen, and in MN 6756-V both anterior and the right posterior palpebrals are preserved. The anterior palpebral is elongated and curved, tapering posteriorly as in *Notosuchus*. The posterior palpebral is subtriangular, widening posteriorly at the contact with the postorbital. Both structures are ornamented and show a gracile laminar structure. In *Candidodon*, only one palpebral is registered, with a morphology very similar to *Notosuchus* and *Mariliasuchus*. Palpebrals are not preserved in *Comahuesuchus*.

JUGAL – Jugal sutures are difficult to be observed in *Notosuchus*, either due to the presence of ornamentation or to abrasion. Nevertheless, it is broadly accepted that the anterior ramus exceeds the orbit and reaches the ventral end of the lachrymal (GASPARINI, 1971; BONAPARTE, 1991, 1996). The anterior ramus is inclined ventrally, as its anterior end is positioned in a more ventral position than the central body of the jugal. The distal end of the posterior ramus is not so easily identified, and BONAPARTE (1991, 1996) did not included this contact in his reconstruction. Nevertheless, in a few specimens (MACN-Pv-RN-1037, MACN-Pv-RN-1048 and MLP-64-IV-16-7) the distal end exceeds de distal end of the laterotemporal fenestra, as in GASPARINI (1971). The jugal ascending process takes part on the postorbital bar. This structure is gracile and is often not preserved (or poorly preserved), displaced from its original position. ZAHER *et al.* (2006; character 142) consider the postorbital bar of *Notosuchus* as vertical and the jugal posterior ramus as not exceeding the laterotemporal fenestra, but none of the well preserved specimens evaluated showed such features. Whenever the postorbital bar is reasonably preserved (MACN-Pv-RN-1037, MACN-Pv-RN-1041, MACN-Pv-RN-1045), it shows to be posteromedially inclined, with its lower end (jugal ascending process) positioned anteriorly and externally to its upper end (postorbital descending process).

In *Mariliasuchus* the jugal anterior process also extends at least to the anterior border of the orbit, slightly exceeding it (*contra* CARVALHO & BERTINI, 1999). Nevertheless, it does not extend dorsally and does not meet the lachrymal, as reported by ZAHER *et al.* (2006). As a consequence, the maxilla reaches the anteroventral border of the orbit (ANDRADE, 2005; ZAHER *et al.* (2006). The anterior jugal ramus is also inclined ventrally, as in *Notosuchus*. The postorbital bar (with participation of the ascending jugal ramus) is inclined posteromedially and the posterior jugal ramus extends posterior to the laterotemporal fenestra, as described by ZAHER *et al.* (2006). Over the lateroventral surface of the anterior ramus, close to the contact with the maxilla, there is an evident neurovascular foramen, anteriorly directed (ANDRADE, 2005; ZAHER *et al.*, 2006). The foramen is present in all specimens preserving the ramus and can also be identified in *Sphagesaurus* (ANDRADE, 2005), as well as in *Comahuesuchus* (MARTINELLI, 2003; ANDRADE, 2005; ZAHER *et al.* 2006), but it is absent from *Notosuchus* and *Candidodon*.

In *Comahuesuchus*, the jugal anterior ramus extends dorsally and contacts the lachrymal, preventing the maxilla from reaching the orbit, as in *Notosuchus*. This can be seen in MACN-Pv-N-31 and MOZ-P-6131, as reported by MARTINELLI (2003; *contra* ZAHER *et al.*, 2006). As in *Notosuchus* and *Mariliasuchus*, the anterior jugal ramus seems to be inclined ventrally. In *Candidodon* the jugal does not show inclination of the anterior ramus, but the posterior ramus seems to exceed the laterotemporal fenestra and the postorbital bar, partially preserved on the right side of UFRJ-DG-114-R. The postorbital bar has the same posteromedial inclination found in *Notosuchus*, *Mariliasuchus* and most Mesoeucrocodylia (NOBRE & CARVALHO, 2002).

SKULL TABLE – In *Notosuchus*, the parietal surface is mostly narrow and can be defined as a parietal crest, though it does not project dorsally from the skull table and shows a flattened dorsal surface. From its anterior end, the parietal crest develops posteriorly towards the occipital, where it widens and creates part of a broad, crown-like structure, slightly deeper in its center (WOODWARD, 1896; GASPARINI, 1971; BONAPARTE, 1991). The crown-like structure is located between the fenestrae and the occipital border, at the parietal-postparietal suture. In *Mariliasuchus*, the surface cannot be characterized as a crest but, as in *Notosuchus*, it is flat and shows at least some degree of ornamentation. In *Comahuesuchus* the parietal surface is reasonably wide, but still narrower than the frontal. In *Candidodon*, the parietal and the frontal are subequal in width, a quite different condition from *Mariliasuchus*, *Notosuchus* and also *Comahuesuchus*. Currently, only *Notosuchus* and *Mariliasuchus* show variability on the morphology of the parietal, though the reduced number of specimens of *Comahuesuchus* and *Candidodon* prevents statements on the variability within these notosuchian clades.

QUADRATE – In *Notosuchus* the quadrate medial dorsal surface is fenestrated in both sides (GASPARINI, 1971; BONAPARTE, 1991), which can be easily identified on MACN-Pv-N-22, MACN-Pv-RN-1037 and MACN-Pv-RN-1048 (Fig.8). MLP-64-IV-16-3 (not MLP-64-IV-16-1, as reported by GASPARINI, 1971) also preserves the quadrate structure and shows such fenestration. These perforations are also present in the MUCPv specimens (FIORELLI, 2005). Furthermore, reconstruction by RUSCONI (1933) suggests the presence of perforations in an unidentified specimen. The fenestration does not follow a specific pattern and morphology can show small differences even in the same individual, as fenestrae may vary slightly in number, size and position. Most other specimens have the quadrate surface not preserved or covered with matrix. Among all skulls where the quadrate is visible and preserved, only MLP-64-IV-16-5(253) and MLP-64-IV-16-31(206) do not show the quadrate fenestrae (Woodward, 1896). These MLP specimens, although composed of entire skulls, show a poor quality of preservation, lacking several structures and details (*e.g.* pos-orbital bar, interchoanal septum, maxillo-palatine fenestrae, palpebrals). It is possible that these specimens may be anomalous, but the scarceness of material without the fenestration and their preservation highly suggests that differences are taphonomic. It seems clear that the fenestrated quadrate was the rule for *N. terrestris*, as this situation is present in a far greater number of well preserved specimens. Furthermore, other specimens (MACN-Pv-N-22, MACN-Pv-N-23, MACN-Pv-RN-1045, MLP-64-IV-16-30), where the quadrate is severely broken, show that this element was highly pneumatic. In *Mariliasuchus*, quadrate fenestrae were identified by Zaher *et al.* (2006) in MZSP-PV-50, as also in UFRJ-DG-106-R (Fig.2). Other specimens do not preserve the region or it is filled with sediment. No other mesoeucrocodylian shows similar quadrate fenestrae, though it should be stated that these fenestrae reached an extreme development in *Notosuchus*.

The quadrate distal end of *Notosuchus* shows an articular condyle with double articulation (Woodward, 1896; Ortega *et al.*, 2000) and the same can be seen in *Mariliasuchus* (Andrade, 2005; Zaher *et al.*, 2006). The medial head is larger than the lateral one, which can be verified at least in the MN, MZSP and UFRJ-DG specimens. In URC R•67 the medial head is not as evident, and the texture of the surface suggests that the bone is slightly damaged in this area. In URC R•69 the medial condyle of the right quadrate is also damaged, but the occurrence of two distinct heads is evident. It is possible that the condition shown by these URC specimens is the result of an incomplete ossification and presence of cartilage in younger individuals, combined with poor preservation. Nobre & Carvalho (2002) describe the quadrate condyle of *Candidodon* with an opposite morphology, with the lateral head larger and rounder, while the medial head is smaller, showing a flatter acute profile. The same profile can be seen in eusuchians. In *Comahuesuchus*, the quadrate condyles are not preserved.

Palate, choanae, and pterygoid – In *Notosuchus*, the naso-oral fenestra (=incisive foramen, *foramen incisivum*) is recognizable also in a few specimens (MACN-Pv-RN-1037, MACN-Pv-RN-1038, MACN-Pv-RN-1041), due to its position on the palate and the fact that most specimens are preserved with the mandibles in occlusion. The premaxillary-maxillary suture is also not accessible in palatal view, due to the presence of matrix and/or symphysis. Thus, the position of the foramen relative to the premaxillary-maxillary suture could not be accurately determined in almost all specimens. This can only be seen in MACN-Pv-RN-1040, where the naso-oral foramen can be accessed from the naris.

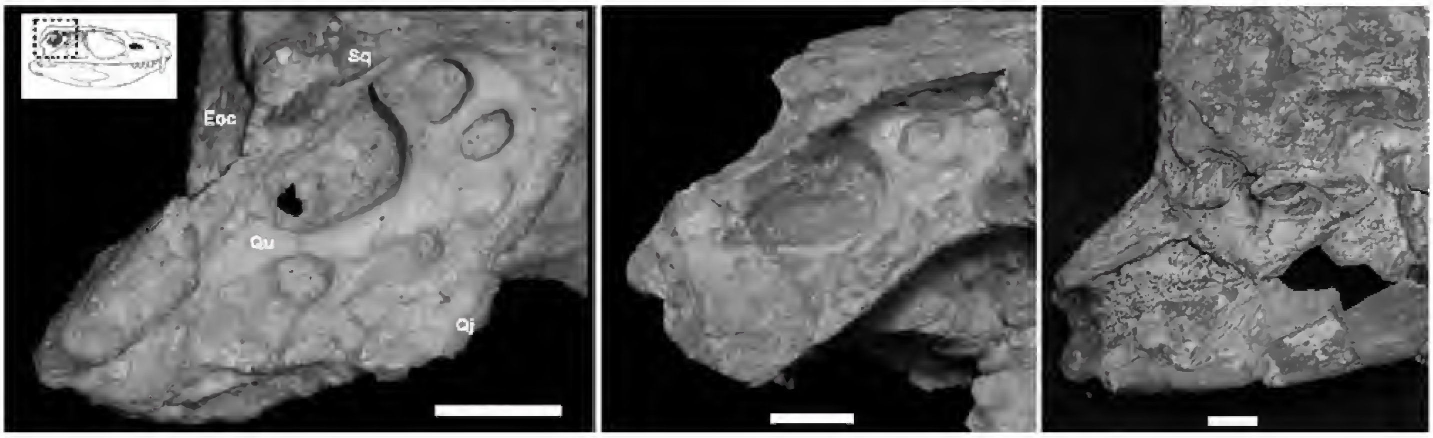

Fig.8- Right quadrate surface in *Notosuchus terrestris*, from specimens MACN-Pv-N-22 (left; dorsolateral view), MACN-Pv-RN-1037 (center; lateral view) and MACN-Pv-RN-1048 (right; dorsal view), showing the characteristic pattern of fenestration. Bar = 10 mm. (skull adapted from Bonaparte, 1991).

It shows a subelliptical profile, similar to a teardrop, and it seems to be limited to the premaxillae. In *Mariliasuchus* the naso-oral fenestra is also hardly accessible, and only four specimens have the area properly exposed. Of these, three specimens (MN 6298-V, MN 6756-V, URC R•68) show an irregular foramen delimited between the premaxilla and the maxilla sutures, while the last, MZSP-PV-50, seems to lack this structure (as reported by Zaher *et al.*, 2006). Reasons for this can be either taphonomic or ontogenetic, and further material is needed to investigate if adult specimens, as MZSP-PV-50, show any trend toward the closure of this structure. Though *Mariliasuchus* and *Notosuchus* show a very different morphology on the naso-oral fenestra, the structure (and the medial surface of the anterior palate) is not preserved either in *Candidodon* or in *Comahuesuchus*, preventing further comparison.

Among mesoeucrocodylians, only *Mariliasuchus* and *Notosuchus* have maxillo-palatine fenestrae (=palatine fenestrae). They constitute small fenestrae positioned near the medial line of the palate (Fig.9), at the suture between palatine and the maxilla (ventral ramus). These structures were identified for the first time by Woodward (1896), in *Notosuchus*. Ever since its original description, the presence of these fenestrae has been widely recognized (Gasparini, 1971; Bonaparte, 1991; Martinelli, 2003; Andrade, 2005; Fiorelli, 2005). Maxillo-palatine fenestrae are almost invariably broken in *Notosuchus*, and this pair of structures appears to be a single one in all specimens studied. Nevertheless, these fenestrae are preserved in MLP-64-IV-16-3 (Woodward, 1971; Gasparini, 1971) and may eventually be observed in other specimens. The anterior borders of these fenestrae do not surpass the fifth pair of teeth anteriorly or the seventh pair, posteriorly.

In *Mariliasuchus*, the recognition of the maxillo-palatine fenestrae came rather later to the description of this taxon. This is due because the holotype has the ventral surface obliterated by rock matrix and it could not be observed in the original description (Carvalho & Bertini, 1999). Maxillo-palatine fenestrae can be seen in URC R•67, URC R•68 (Andrade, 2005), UFRJ-DG-106-R (Vasconcellos & Carvalho, 2005) and also in the MN-UFRJ and MUZUSP specimens (Zaher *et al.*, 2006). In most cases, the actual borders are well preserved, including their medial margins. URC R•68 is an exception and shows only the right fenestra, as the left portion of the palate is not preserved. In UFRJ-DG-105-R the bone surface at the maxilla-palatine contact seems to be damaged and the fenestrae are therefore not clearly visible (as figured in Vasconcellos & Carvalho, 2005). The fenestrae do not surpass the fifth maxillary pair of teeth anteriorly or the sixth pair (last pair) posteriorly.

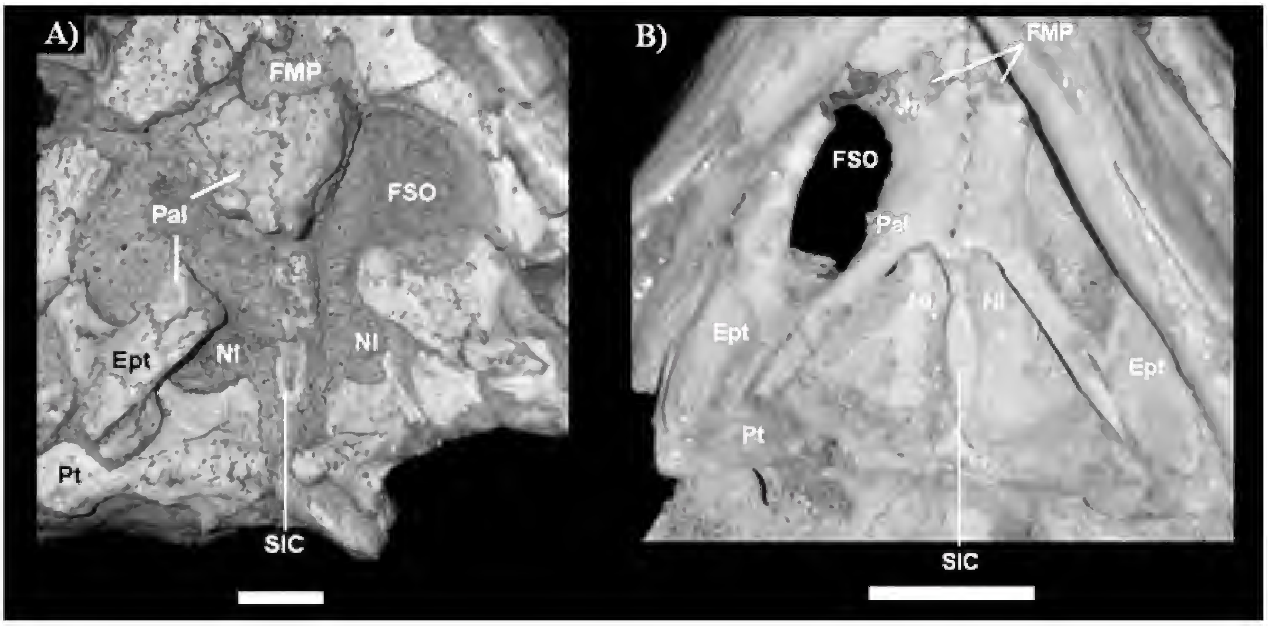

Fig.9- Palatal view of studied material, showing the choanae and perichoanal structures: A) *Notosuchus terrestris* MACN-Pv-RN-1038; B) *Mariliasuchus amarali* URC R•67. Note the the general morphology of the choanae, as the presence of maxillo-palatine fenestrae and interchoanal septum. Bar = 10 mm.

Neither *Candidodon* nor *Comahuesuchus* have these fenestrae or similar structures on the palate (Bonaparte, 1991; Nobre & Carvalho, 2002; Martinelli, 2003), though the area is preserved.

In *Notosuchus* the choanae are ample and triangular (Fig.9), as in Woodward (1896), showing a fragile interchoanal septum (Andrade *et al.*, 2006). The septum is represented, but not commented, by Gasparini (1971; p.90, Plate III-B). Specimens evaluated by Bonaparte (1991) do not preserve the structure. In fact, the MLP series and most of the MACN material do not preserve choanal regions at all, providing no clue to the existence of this structure or to the actual shape of the internal naris. Nevertheless, the interchoanal septum can be identified in MACN-Pv-RN-1038, as an almost complete lamina. Furthermore, MACN-Pv-RN-1045 shows a posterior end of the septum, while MPCA-Pv-789 shows an anterior end. In *Mariliasuchus* choanae are also ample and triangular (Fig.9), as shown by Andrade *et al.* (2006), Zaher *et al.* (2006) and figured by Andrade (2005) and Vasconcellos & Carvalho (2005, 2006). A thin interchoanal septum divides the choanae, as seen in URC R•67 (Andrade, 2005), UFRJ-DG-105-R (Vasconcellos & Carvalho, 2005), MN and MZSP specimens (Zaher *et al.*, 2006). In UFRJ-DG-106-R the septum is incomplete and only its posterior end is preserved (Vasconcellos & Carvalho, 2005). As discussed by Andrade *et al.* (2006), *Comahuesuchus* shows an ample triangular internal naris (Martinelli, 2003), which is consistent with the morphology observed in *Notosuchus, Mariliasuchus* and a few other notosuchians, but the septum itself was not preserved. As observed by Andrade *et al.* (2006), the morphology of the choanae figured by Nobre & Carvalho (2002) for *Candidodon* is rather different from *Mariliasuchus* and *Notosuchus*. This is however an artifact of preservation, since the skull UFRJ-DG-114-R is laterally compressed and the configuration of the pterygoids and the shape of the suborbital fenestra suffered from dramatic deformation. Therefore, the choanae of *Candidodon* still awaits proper characterization.

In *Notosuchus*, the palatine-ectopterygoid contact is of difficult recognition, which is located at the anterolateral border of the choanae (Martinelli, 2003; Andrade *et al.*, 2006). At this point, the palatine posterior process and the ectopterygoid medial process meet, creating a bar that separates the choana from the suborbital fenestra, which can be clearly observed only in MACN-Pv-RN-1038 and MACN-Pv-RN-1040 (Martinelli, 2003; Andrade *et al.*, 2006). In *Mariliasuchus* the situation is rather different from *Notosuchus* (Andrade, 2005; Andrade *et al.*, 2006; Zaher *et al.*, 2006), as the palatine posterolateral processes are long, extending toward the triple contact with the ectopterygoid and the pterygoid, posterior to the suborbital fenestra and lateral to the choanae, as in URC R•67 (Andrade, 2005; Andrade *et al.*, 2006), UFRJ-DG-105-R, UFRJ-DG-106-R (Vasconcellos & Carvalho, 2005), MN and MZSP specimens (Zaher *et al.*, 2006). This contact isolates the pterygoid from the suborbital fenestra. The palatine processes constitute the anterolateral borders of the choanae, with no participation of the ectopterygoid whatsoever. The condition found in *Comahuesuchus* (Martinelli, 2003) truly resembles the one in *Mariliasuchus* and *Sphagesaurus* (Andrade *et al.*, 2006), with palatine and ectopterygoid meeting posteriorly to the suborbital fenestra. The pattern observed in *Notosuchus*, where the palatine and ectopterygoid meet at the palatine bar, can only be seen in baurusuchids (Martinelli, 2003; Andrade *et al.*, 2006; Pinheiro *et al.*, 2008). Nevertheless, in all these cases (including *Sphagesaurus* and baurusuchids), the pterygoid is extensively isolated from the suborbital fenestra. *Candidodon* seems to show a palatine bar, but sutures on this region are still undescribed and it is impossible to state if the palatines have true posterolateral projections, or if the anterolateral borders of the choanae are composed by either the ectopterygoid or the pterygoid (Andrade *et al.*, 2006). Despite de limited information on the taxon, the description by Nobre & Carvalho (2002) seems to suggest that there was no palatine-ectopterygoid contact and the pterygoid reached the posterior end of the suborbital fenestra.

The pterygoid wings (=pterygoid flanges) of *Notosuchus* are usually referred as well developed, as in Woodward (1896) and Gasparini (1971), but they are truly small, when compared to other groups. The pterygoid wings are mostly horizontal and the general structure is robust, though the wings thicken toward the lateral borders and get progressively thinner at the posterior ones. These features can be verified in several specimens of *Notosuchus* (MACN-Pv-RN-1037, MACN-Pv-RN-1041, MACN-Pv-RN-1045, MLP-64-IV-16-5, MLP-64-IV-16-7, MLP-64-IV-16-31, MPCA-PV-789/1). In *Mariliasuchus* the pterygoid wings are also proportionally small, and are similar to the ones in *Notosuchus*. These structures are preserved at least in URC R•67, MN 6756-V, MZSP-PV-50, UFRJ-DG-106-R and also partially in MN 6298-V and UFRJ-DG-105-R. However, it should be noticed that both URC R•67 and MN 6756-V show an evident compression, altering the inclination of the ventral flanges. As a character, the pterygoid wings are in fact often coded as small (*e.g.*, Andrade, 2005, character 90; Zaher *et al.*, 2006, character 166). In *Comahuesuchus*, pterygoid wings are poorly preserved.

Nevertheless, they are reasonably small and robust, basically similar to what can be observed in *Notosuchus* and *Mariliasuchus* (Martinelli, 2003; p.562, fig.2). In *Candidodon*, on the other hand, specimen figured by Nobre & Carvalho (2002), shows well developed wings, mostly vertical in orientation. This inclination is however likely to be the result of taphonomic deformation, as UFRJ-DG-114-R is laterally compressed.

Mandible – Whenever the mandible is present in specimens of *Notosuchus*, there are parts missing or deformation. There is no reasonably preserved mandible isolated from the skull, which makes the observation of characters related to the element and its dentition especially problematic. The anterior part of the mandible is constituted by the symphysis, which is concave dorsally (as in Bonaparte, 1991, 1996). Well preserved symphysis showing the inclination upwards (Fig.10) can be seen in specimens with no dorsoventral compression (MACN-Pv-N-24, MACN-Pv-N-43, MACN-Pv-N-107, MACN-Pv-RN-1037, MACN-Pv-RN-1038, MACN-Pv-RN-1039, MACN-Pv-RN-1040, MACN-Pv-RN-1119, MLP-64-IV-16-7, MLP-64-IV-16-24, MLP-64-IV-16-31). In the middle section of the mandible there is a smooth coronoid process, creating an evident dorsal convexity (Woodward, 1896; Gasparini, 1971). In the posterior region of the mandible, the retroarticular process is directed posteroventrally (Woodward, 1896; Gasparini, 1971; *contra* Bonaparte, 1991). In *Mariliasuchus*, at least MN 6756-V and the MZSP specimens have mostly complete mandibles freed from the skull. URC R•68 also shows most of the middle and anterior right hemimandible. In both *Notosuchus* and *Mariliasuchus*, the mandible follows the same general profile. However, it is widely recognized that in *Mariliasuchus* the symphyseal part of the mandible is mostly horizontal (Carvalho & Bertini, 1999; Andrade, 2005; Zaher *et al.*, 2006), while in *Notosuchus* it is inclined dorsally (Woodward, 1896; Bonaparte, 1991; Andrade, 2005). The coronoid process is also present in *Mariliasuchus* and the retroarticular process is directed posteroventrally (Carvalho & Bertini, 1999; Andrade, 2005; Zaher *et al.*, 2006). In *Comahuesuchus* there seems to be a coronoid process, but preservation is imperfect and confirmation must await the description of further specimens. Nevertheless, the profile of the mandible is reasonably different, as the anterior portion of the mandible is wide, shovel-like (Bonaparte, 1991; Martinelli, 2003). In *Candidodon* the only mandible known is distorted and does not show details, although it is possible to recognize that the symphyseal section is narrow and elongated, as in *Notosuchus* and *Mariliasuchus* (Carvalho, 1994).

In *Notosuchus*, the splenials meet medially. In ventral view, the splenials reach ventrally, marginally taking part of the symphysis. They neither extend anteriorly, nor get fused. At the mandibular ramus, the splenials contribute to the medial border at least to the three posteriormost mandibular alveoli (MACN-Pv-RN-1038, MLP-64-IV-16-13). In *Mariliasuchus*, the splenials relate to the mandible in the same manner. Nevertheless, it is possible to recognize that the splenial contributes to the last four mandibular alveoli (URC R•68, MN 6756-V and MZSP specimens).

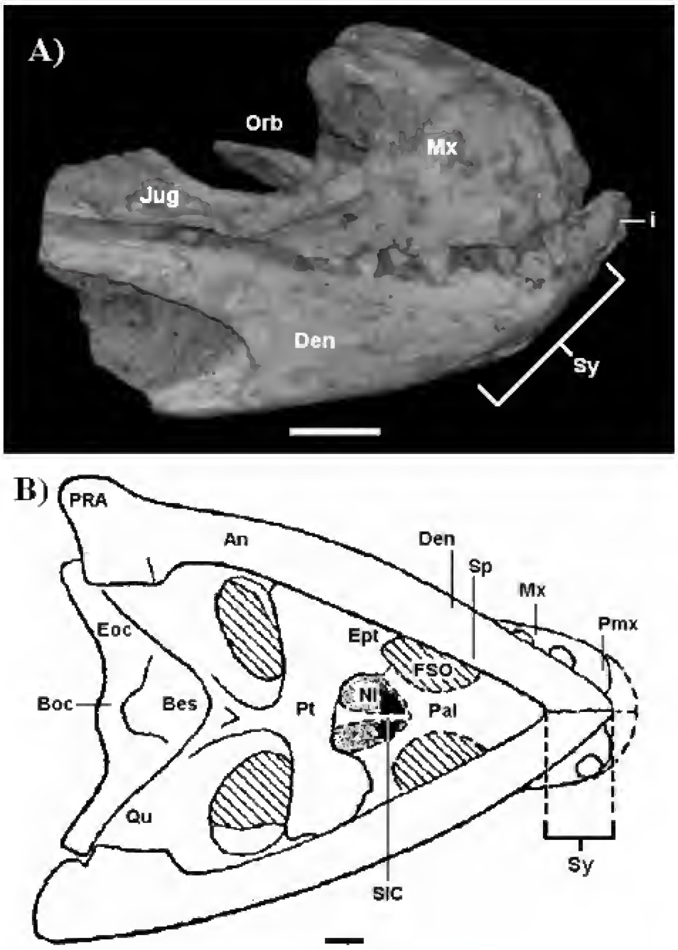

Fig.10- Length of the symphysis in *Notosuchus terrestris*: A) lateral view of the rostrum and mandible of MACN-Pv-N-43, showing the actual length of the symphysis; B) drawing of *N. terrestris* from Price (1959), showing the skull and mandible in ventral view, where the symphysis seems to be shorter than it really is. Reconstruction in "B" based on MLP-64-IV-16-5, lectotype. Note that the reconstruction does not show maxillo-palatine fenestrae, as these structures are not preserved in this specimen. Bar = 10 mm.

Although it is not possible to compare this pattern to the situation in *Candidodon* due to the poor preservation of the mandible, *Comahuesuchus* shows that at least the two posteriormost alveoli receive contribution of the splenial (Martinelli, 2003; p.566, fig.4).

One of the important aspects shown by the reevaluation of the specimens refers to the morphology of the symphysis, which is frequently described as short in *Notosuchus* and *Mariliasuchus* (Woodward, 1896; Price, 1959; Gasparini, 1971; Carvalho & Bertini, 1999; Pol, 2003; Zaher *et al.*, 2006), as in Protosuchia. This may occur with *Notosuchus*, as this species shows a symphysis inclined upwards, a characteristic observed in several specimens (MACN-Pv-N-24, MACN-Pv-N-43, MACN-Pv-N-107, MACN-Pv-RN-1037, MACN-Pv-RN-1038, MACN-Pv-RN-1039, MACN-Pv-RN-1040, MACN-Pv-RN-1046, MLP-64-IV-16-5 and MLP-64-IV-16-24 and MLP-64-IV-16-31). Available images and reconstructions in ventral/palatal view show an apparently small area of contact between the rami. Thus, the symphysis seems to represent a very small portion of the mandible length, a truly misleading situation (Fig.10). In MACN-Pv-RN-1048 the symphysis is horizontalized by severe dorsoventral compression and is clearly elongate. Furthermore, definition of the long symphysis is not straightforward and can be presented in a number of ways. Because in notosuchians the mandible may show proal/propalinal movement (Clark *et al.*, 1989; Wu *et al.*, 1995; Ortega *et al.*, 2000; Pol, 2003; Andrade, 2005; Zaher *et al.*, 2006), the position of the symphysis relative to the rostrum is variable, which gives a false idea as how posteriorly it extends. Some specimens of *Notosuchus* show a forward displacement of the mandible, and the symphysis does not cover most of the palate (*e.g.*, MACN-Pv-N-43, MACN-Pv-RN-1038, MACN-Pv-RN-1039, MACN-Pv-RN-1119). In other specimens, the symphysis is preserved in a slightly more recoiled position, and the symphysis ranges from the anterior border of the premaxilla almost to the anterior border of the maxillo-palatine fenestrae (*e.g.*, MACN-Pv-RN-1037, MACN-Pv-RN-1040, MACN-Pv-RN-1041, MLP-64-IV-16-7, MLP-64-IV-16-11, MLP-64-IV-16-23, MPCA-PV-789/1, MPCA-PV-791). Such displacement is expected, as it is widely agreed that *Notosuchus* was able of mandibular movements (Ortega *et al.*, 2000; Pol, 2003; Zaher *et al.*, 2006). Another similar aspect is that the mandible includes at least five pairs of teeth, as much as *Mariliasuchus* (Andrade, 2005; Zaher *et al.*, 2006) and *Sphagesaurus* (Pol, 2003; Andrade, 2005). Furthermore, in *Notosuchus*, *Mariliasuchus* and *Sphagesaurus* the teeth in the symphysis are disposed in parallel lines. Whenever a specimen of *Notosuchus* shows a different situation, it can be related to preservation problems, such as the deformation or loss of the first and more delicate section of the symphysis. *Comahuesuchus* shows a long symphysis, despite its shovel-like profile. Dental elements are disposed in a very different disposition though, and the symphysis supports at least nine pairs of teeth, set in an arched line. *Candidodon* has a long symphysis (Carvalho, 1994), which probably included parallel lines of teeth. Despite these notosuchians can be considered as having elongated symphysis, neither of these forms discussed above have the extremely elongated symphysis seen in longirostrine mesoeucrocodylians (*e.g.*, thalattosuchians, dyrosaurids, gavialids), which may include 10 or more pairs of teeth (Andrews, 1913; Benton & Clark, 1988; Clark, 1994; Jouve *et al.*, 2006; Pierce & Benton, 2006).

Both in *Notosuchus* and *Mariliasuchus* the glenoid fossa has a close similar morphology, anteroposteriorly elongated and with a general triangular shape, in dorsal view. The posterior margin is very low and poorly delimited (Woodward, 1896; Ortega *et al.*, 2000; Pol, 2003; Andrade, 2005; Zaher *et al.*, 2006). The elongated articular glenoid fossa must have allowed mandibular mobility (Clark *et al.*, 1989; Wu *et al.*, 1995; Ortega *et al.*, 2000; Pol, 2003; Andrade, 2005; Zaher *et al.*, 2006). Thalattosuchians and most neosuchians, on the other hand, have a well delimited posterior margin and are prived from proal/propalinal displacements of the mandible (Andrews, 1913; Benton & Clark, 1988; Clark, 1994; Jouve *et al.*, 2006; Pierce & Benton, 2006, Turner, 2006).

In the posterior region of the mandible of *Notosuchus*, the retroarticular process is directed posteroventrally (Woodward, 1896; Gasparini, 1971; *contra* Bonaparte, 1991), as in *Mariliasuchus* (Carvalho & Bertini, 1999). In both cases, the retroarticular process shows an ample and continuous single surface for muscle insertion (*musculus depressor mandibulae*), which faces medially, posteriorly and dorsally (Fig.11). This can be seen in a representative number of specimens of *Notosuchus* (MACN-Pv-RN-1037, MLP-64-IV-16-5, MLP-64-IV-16-31) and *Mariliasuchus* (URC R•67, MN 6756-V, UFRJ-DG-105-R, UFRJ-DG-106-R and the MUZUSP specimens).

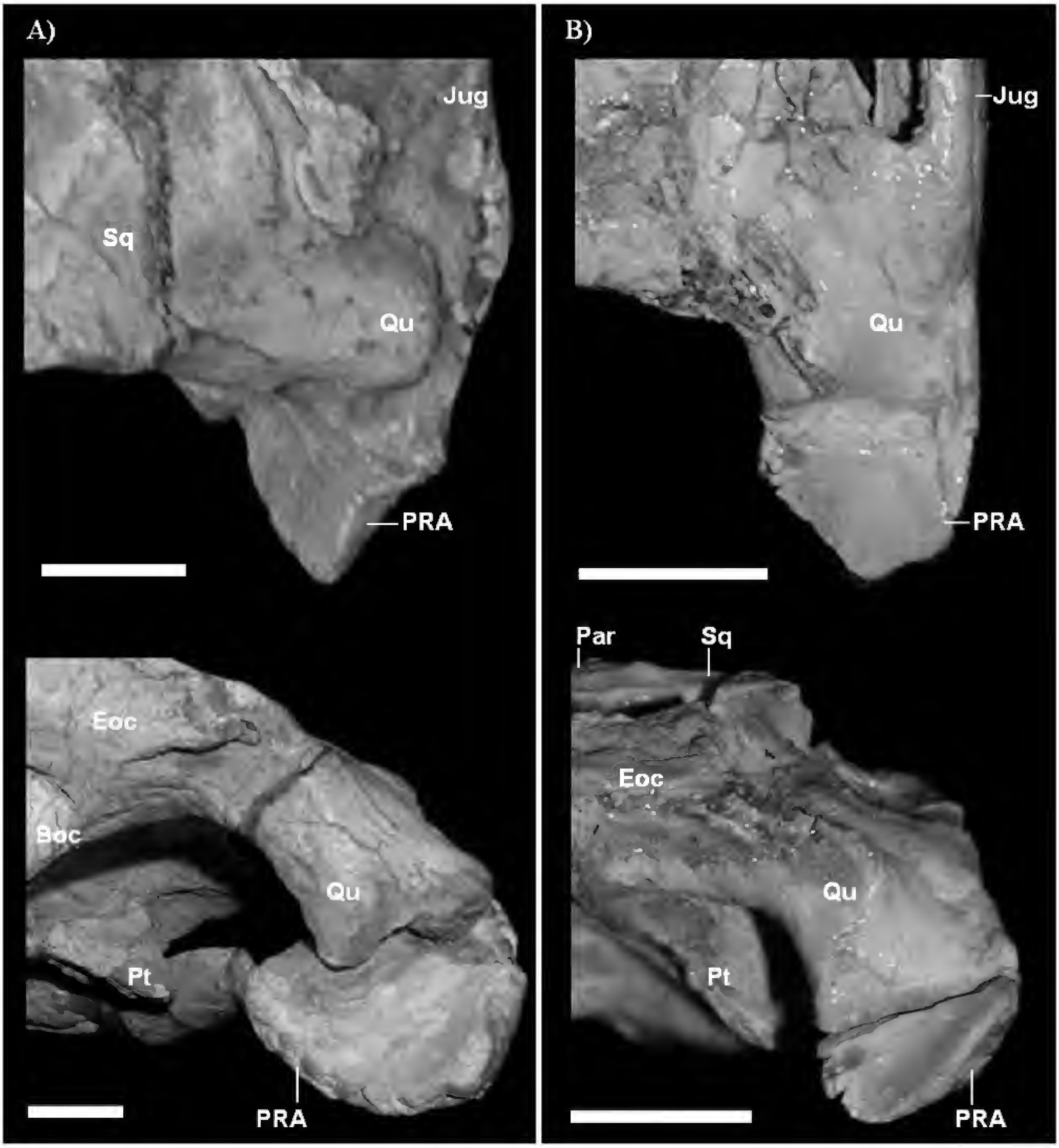

Fig.11- Parietal (top) and occipital views (bottom) of the right retroarticular process from studied specimens: A) *Notosuchus terrestris* MLP-64-IV-16-5, lectotype, where the distal end of the quadrate is broken and slightly twisted; B) *Mariliasuchus amarali* URC R•67, where the medial condyle is incompletely preserved. Bar = 10 mm.

The general shape of this surface is subcircular to subpolygonal, as long as wide. In general aspect, the articular apparatus of *Mariliasuchus* and *Notosuchus* resemble most of the other notosuchians, including the Baurusuchidae. This pattern is clearly different from the elongated and posterodorsally oriented retroarticular process found in Eusuchia, Thalattosuchia and *Sebecus* (Andrews, 1913; Colbert, 1946; Benton & Clark, 1988; Clark, 1994; Ortega *et al.*, 2000; Pierce & Benton, 2006). Furthermore, at least in eusuchians, thalattosuchians and most neosuchians the retroarticular process have not a single surface, but a lateral surface facing dorsally and a medial surface, facing medially and dorsally, separated by a longitudinal ridge (Andrews, 1913; Benton & Clark, 1988; Clark, 1994; Pierce & Benton, 2006).

Dentition – The dentition of *Notosuchus* includes three premaxillary incisiforms, one premaxillary hypertrophied caniniform, one small conic post-caniniform and at least six maxillary molariform teeth in the upper series. In the lower series, possibly 10-11 teeth were present. The first three pair of teeth are small conic and blunt incisiforms. The second and third pairs are preserved in several specimens, but the first pair can only be seen in MACN-Pv-RN-1038 and MACN-Pv-RN-1040. The following tooth is a hypertrophied caniniform, clearly identifiable in most specimens. The first postcaniniform tooth of *Notosuchus* is small and mostly conic, and it is morphologically similar to the premaxillary series, but also blunter and larger. This would allow its characterization as a premolariform tooth. The following teeth are all single cusped molariforms. The premaxilla does not extend far posteriorly to the hypertrophied caniniform, as seen in MACN-Pv-N-24. Specimens show that in most cases there are at least six crowns preserved per maxillae (*e.g.* MACN-Pv-N-24, left crowns from pairs 1-6; MACN-Pv-RN-1037, pairs 1-6 in both sides; MACN-Pv-RN-1038 both sides; MACN-Pv-RN-1040; MLP-64-IV-16-6, pairs 1-6, both sides; MLP-64-IV-16-22, teeth pairs 2 and 3-7 from the right side). A few specimens (MACN-Pv-RN-1041, MLP-64-IV-16-1, MPCA-Pv-789) preserve seven maxillary crowns or their remnants, including the first postcaniniform tooth. However, a posteroventral extension of the premaxilla is noticed at least in MLP-64-IV-16-1 and it is possible to consider that the first post-caniniform tooth occupies an intermediate position between premaxilla and maxilla. It is certain that the premaxilla at least takes part of the anterior alveolar border of the first postcaniniform, providing partial support for the tooth. Nevertheless, it was not possible to identify a single specimen where the premaxilla constituted the entire alveolus. This supports the traditional interpretation of four premaxillary and seven maxillary teeth (Woodward, 1896; Gasparini, 1971; *contra* Bonaparte, 1991). On the size of the maxillary dentition, the first maxillary tooth was smaller, but the rest of the series had approximately the same size, according to Woodward (1896). Gasparini (1971) considered that the teeth increased in size from the first to the fourth, and the last teeth were similar in size. Reconstruction by Bonaparte (1991) supports Woodward (1897), but shows that the second tooth was also not as developed as the following teeth. Examination of the specimens reveals that maxillary pairs 4-6 seems to be slightly more developed than pairs 2, 3 and 7, but the difference is not as evident as in other mesoeucrocodylians, such as *Araripesuchus*, *Uruguaysuchus* and *Baurusuchus*. Furthermore, development problems may interfere in the interpretation. Nevertheless, the first tooth (the first post-caniniform) is clearly smaller than the fourth tooth.

The dentition of *Mariliasuchus* shows similar number and arrange of teeth, with two premaxillary incisiforms, one premaxillary hypertrophied caniniform, one small conic post-caniniform and six maxillary molariform teeth in the upper series. There are nine teeth in the lower series. The first incisiform is mostly conic. The second premaxillary tooth is also small and conic, but as it is slightly curved it can also be characterized as a caniniform. These teeth are preserved at least in URC R•67 and the MUZUSP specimens, but not in URC-R•68 and the MN material. The third tooth is a hypertrophied caniniform, well preserved in most specimens. The first postcaniniform tooth of *Mariliasuchus* is small and mostly conic, but with a discrete distal curvature of the apex. The second postcaniniform tooth is also small, conical and slightly curved, indicating an intermediate between the anterior element and the following teeth. As described by Zaher *et al.* (2006), this tooth has the labial side more convex than the lingual side, as all posterior elements. Furthermore, it is stouter and blunter than the anterior teeth. Both the first and the second postcaniniform teeth can thus be characterized as premolariform teeth, due to its intermediate morphology between the typical caniniform and the molariform types.

The third and subsequent postcaniniform teeth are all clearly molariform. The fourth postcaniniform tooth is the most developed within the series, and the last element is clearly the smallest of the maxillary series. As in *Notosuchus*, the premaxilla also does not extend far posteriorly to the hypertrophied caniniform in lateral view, as observed in URC R•67, URC R•68 (Andrade, 2005) and the MN specimens, but also as reported for the holotype (Carvalho & Bertini, 1999). In URC R•68 it is possible to recognize that the premaxilla extend distally in ventral aspect, taking part of the anterior portion of the alveolus (Fig.12). This extension and the borderline participation can also be verified in Zaher *et al.* (2006; fig.9B, p.20) for MZSP-PV-51, and seems to be present in MZSP-PV-50 (Zaher *et al.*, 2006; fig.5, p.9). Nevertheless, Zaher *et al.* (2006) prefer to consider that the first postcaniniform is included entirely in the premaxilla. Though the first postcaniniform tooth is small, the premaxilla extension is not as high as it should be to produce an effective support, and the maxilla certainly plays an important role in bearing this element. Furthermore, there is no evidence supporting that the maxilla is entirely excluded from the alveolus. Despite differences of interpretation, it seems clear that divergences on the position of the first postcaniniform tooth are due to the same reasons in *Notosuchus* and *Mariliasuchus*. The first postcaniniform tooth is, in both cases, partially held by the premaxilla and the maxilla, is mostly conical and less developed than the surrounding elements of the upper series, showing an intermediate morphology between caniniform and molariform.

Regarding the mandibular dentition, observation of MACN-Pv-RN-1038 suggests 11 mandibulary teeth in an occluded position, with crowns pairs 1-2 (left side) mildly procumbent. MLP-64-IV-16-14 shows small right anterior mandibulary tooth (pair 2?) with an elliptic cross-section, congruent with the presence of procumbent anterior teeth. Other specimens do not preserve anterior teeth or do not show them, albeit it should be observed that the anterior section of the mandible is inclined upwards, and any tooth that occludes with the premaxillary series is expected to be slightly procumbent to adequately occlude with the ones in the upper series. Though *Notosuchus* provides only a limited amount of information on its mandibulary dentition, there is no evidence for caniniform teeth whatsoever, and the anterior teeth were incisiform, while posterior teeth were molariform. The skull with associated mandible MACN-Pv-RN-1038, the right hemimandible MLP-64-IV-16-13 and the partial skulls MLP-64-IV-16-1 and MLP-64-IV-16-22 (where matrix associated to the palate beautifully holds the cross-section of mandibulary crowns) seem to support at least 10 mandibulary teeth. In *Mariliasuchus* the mandibular dentition shows a better preservation than in *Notosuchus*, for all specimens analyzed. As in *Notosuchus*, no element of the mandibular series of *Mariliasuchus* can be characterized as a caniniform, due to the complete lack of medial/distal curvature of the apex (URC R•68, MN 6756-V, MUZUSP specimens). The first five elements are progressively more procumbent anteriorly.

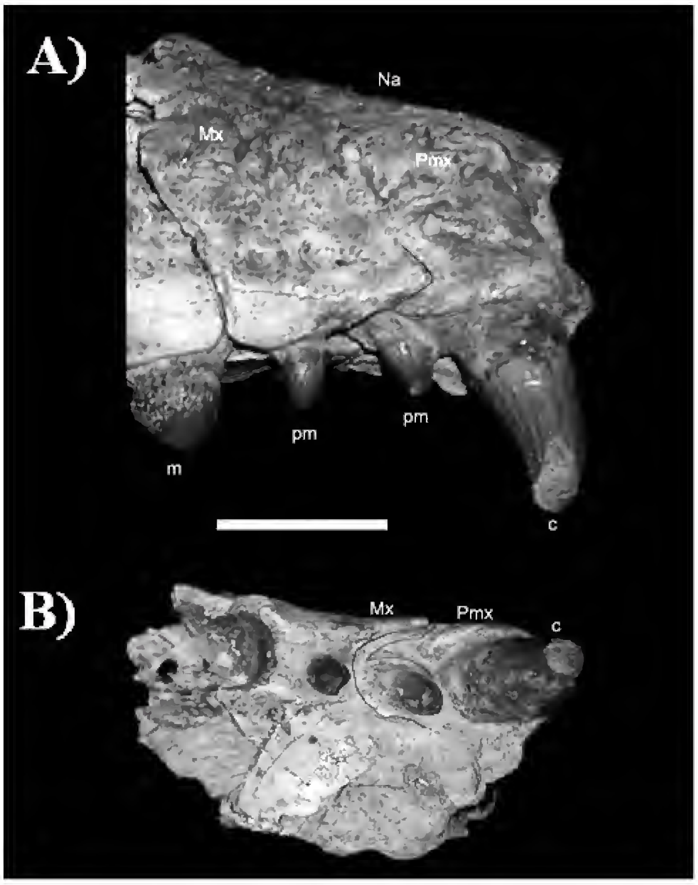

Fig.12- Anteriormost portion of the rostrum in *Mariliasuchus amarali*, specimen URC R•68, showing the contribution of the premaxilla and maxilla to the first maxillary alveolus: A) lateral view; B) palatal view. Dark lines represent the limits for each element, showing that the alveolus of the first postcaniniform receives contribution from both the premaxilla and the maxilla. Note the intermediate morphology shown by the first two postcaniniform teeth and also the evident molariform morphology shown by the third postcaniniform tooth. Bar = 10 mm.

The dentition is procumbent anteriorly, where the anteriormost elements are small and mostly conical (incisiform), and the postcaniniform teeth progress to a typical molariform pattern. There is no evident distinction though, as the fourth and fifth teeth from the lower series do not show either the typical incisiform or molariform morphology.

The morphology of the anteriormost mandibular dentition of *Mariliasuchus* is highly characteristic, because combines procumbent alveoli and straight anterior teeth. The result is that the crowns of the first pair of mandibulary teeth are almost horizontal. In *Notosuchus*, the anterior teeth are procumbent, but are not horizontal as in *Mariliasuchus*, as seen in MACN-Pv-RN-1038, MLP-64-IV-16-14. Furthermore, these specimens suggest the existence of a small toothless area at the anteriormost section of the mandible. The presence of this diastema between the right and the left series is not certain though, and observation of further material is needed to exclude taphonomic alteration.

An important aspect of the dental morphology of *Mariliasuchus* and *Notosuchus* is the peculiar occurrence of hypertrophied caniniforms in these clades, when compared to other notosuchians. Each of these caniniforms is particularly robust, tusk-like and firmly attached to the premaxilla, with roots extending through the maxillary bone to the upper part of the rostrum, where a thickened, well ornamented area can be identified (Fig.7). There is only a mildly enlarged caniniform in the premaxilla of *Candidodon* (Nobre & Carvalho, 2002), but it is not as developed as in *Mariliasuchus* and *Notosuchus*. The premaxillary dentition of *Comahuesuchus* does not show evidence of hypertrophied or even slightly enlarged teeth (Bonaparte, 1991; Martinelli, 2003). Truly hypertrophied caniniforms were certainly present in the premaxilla of *Sphagesaurus*, *Malawisuchus*, highly predaceous forms such as baurusuchids and other mesoeucrocodylians (Price, 1945; Gomani, 1997; Riff & Kellner, 2001; Pol, 2003), but are also absent from *Simosuchus* and thalattosuchians (Andrews, 1913; Buckley *et al.*, 2000). A more peculiar aspect of *Mariliasuchus* and *Notosuchus* is the lack of hypertrophied caniniforms from the maxilla. Such teeth are present in most mesoeucrocodylians and are usually compressed laterally, even acquiring a blade-like profile. The maxillary hypercaniniform is extremely well developed in *Candidodon* and baurusuchids (Riff & Kellner, 2001; Nobre & Carvalho, 2002). *Comahuesuchus* also shows a hypertrophied maxillary caniniform, although not as extremely developed as in the previous forms (Bonaparte, 1991; Martinelli, 2003). Well developed caniniforms can also be found in *Malawisuchus*, *Uruguaysuchus*, most eusuchians and several neosuchians (Benton & Clark, 1988; Clark, 1994). Nevertheless, such elements are absent from *Sphagesaurus*, *Chimaerasuchus*, *Simosuchus*, most thalattosuchians and longirostrine forms (Andrews, 1913; Wu & Sues, 1996; Buckley *et al.*, 2000; Pol, 2003). One pair of mandibulary hypertrophied caniniforms is also usually found in mesoeucrocodylians, as also in more basal groups of crocodylomorphs and in almost all eusuchian genera (Benton & Clark, 1988; Clark, 1994). Whenever present, they occlude where the premaxillary-maxillary suture lies. The only exception is *Comahuesuchus*, as in this form the mandibular hypercaniniform occupy a rather posterior position, fitting the paracanine fossa (Bonaparte, 1991; Martinelli, 2003). In *Candidodon* the condition is unknown, due to the preservation of the mandible. These caniniforms are only absent from *Mariliasuchus* and *Notosuchus*, as well as a few other clades (*Sphagesaurus, Chimaerasuchus*, longirostrine mesoeucrocodylians). In overview, only a few mesoeucrocodylians truly show the same pattern of disposition of hypertrophied caniniforms (i.e. restricted to the premaxilla, as in *Notoshuchus* and *Mariliasuchus*). These are *Sphagesaurus*, *Adamantinasuchus* and possibly *Chimaerasuchus*. In all other taxa, either there is no hypercaniniform at all (thalattosuchians, longirostrine forms) or there are hypertrophied caniniforms in the maxilla and the mandible.

Root morphology and teeth implantation – In *Notosuchus*, no tooth shows a basal crown constriction, although distinction between root and crown is evident (MACN-Pv-RN-1038). Roots, whenever exposed, were conic to elliptic in cross-section, and never divided. Woodward (1896; p.12, 1st§) found no successional tooth in the MLP series, which are not reported also by Gasparini (1971) or Bonaparte (1991). No single specimen studied shown reposition teeth, even though some specimens (*e.g.*, MACN-Pv-RN-1038, MLP-64-IV-16-31) had lingual or labial abrasions exposing roots of premaxillary and mandibulary teeth. In *Mariliasuchus*, middle and posterior teeth have a clear constriction identifying the limits between root and crown. Roots are undivided, what can be accessed in URC R•68. Reposition teeth have also never been reported in *Mariliasuchus*, and URC R•68 does not show any evidence of them. Oblique implantation can be observed in *Notosuchus* and

Mariliasuchus (Fig.13). This condition was observed for the first time by WOODWARD (1896), who identified oblique teeth in the maxilla of *Notosuchus*. Oblique teeth are always molariform and this can be better observed in the maxillae of MACN-N-22, MLP-64-IV-16-1, MLP-64-IV-16-6, MLP-64-IV-16-7, MLP-64-IV-16-11, MLP-64-IV-16-16, MLP-64-IV-16-22, MLP-64-IV-16-23 and MPCA-PV-789/1 (Fig.13). Oblique implantation on the dentary can be well observed in MLP-64-IV-16-13 (Fig.13B), but also in MLP-64-IV-16-1 and MLP-64-IV-16-22. Most of these specimens are fragmentary, but helpful to access the character. Oblique implantation is also present in *Mariliasuchus*, which can be easily observed in URC R•68. Nevertheless, oblique implantation is not present in all molariforms and certainly does not affect the premolariforms. Although there is intraspecific variability (ZAHER *et al.*, 2006), oblique implantation can easily be identified in at least a part of the postcaniniform teeth pairs 3-5 (URC R•68, MN and MUZUSP specimens) and mandibulary pairs 6-8 (URC R•68, MN 6756-V, MUZUSP specimens). None of the analyzed specimens lacks oblique teeth and these are present also in the MUZUSP specimens. The displacement is always paramesial and bilateral, affecting teeth with wear surfaces, indicating that this arrange is not accidental and due to a taphonomic bias. The occurrence of oblique implantation in *Mariliasuchus* and *Notosuchus* may only be compared to *Sphagesaurus*. In all other cases, teeth have a more common disposition, with carinae parallel to the maxillary/mandibulary alveolar margin. No single tooth of *Candidodon* shows oblique implantation whatsoever (NOBRE & CARVALHO, 2002), as in *Comahuesuchus*.

ORNAMENTATION, CARINAE, AND WEAR SURFACES – Ornamentation is present in *Mariliasuchus* teeth, constituting a series of well developed basal-apical undivided ridges in anterior teeth and a fabric of small anastomosed ridges over the teeth surface (ANDRADE, 2005; ANDRADE & BERTINI, 2005b; ZAHER *et al.*, 2006). Small true denticles constitute carinae, which develop on mesial and distal surfaces of middle and posterior teeth only, but never on the anterior teeth (ANDRADE & BERTINI, 2005b). ZAHER *et al.* (2006) prefers to consider these as small tubercles rather than true denticles, but without using scanning electronic microscopy. Both ANDRADE & BERTINI (2005b) and ZAHER *et al.* (2006) agree that these structures are tubercle-like and do not match the morphology found in ziphodont dentition. As identified by ANDRADE (2005) and ZAHER *et al.* (2006), anteroposteriorly elongated wear surfaces are present in maxillary and middle and posterior mandibulary teeth. These are inclined lingually and distally in maxillary teeth and labially and mesially in matching mandibulary elements. Wear surfaces can also be seen in the tips of the hypertrophied caniniform and the first postcaniniform tooth. In both cases, wear surfaces are subelliptical and face mesially and ventrally (ANDRADE, 2005). In *Notosuchus* the situation is more elusive, as just a few specimens preserve traces of the tooth surface.

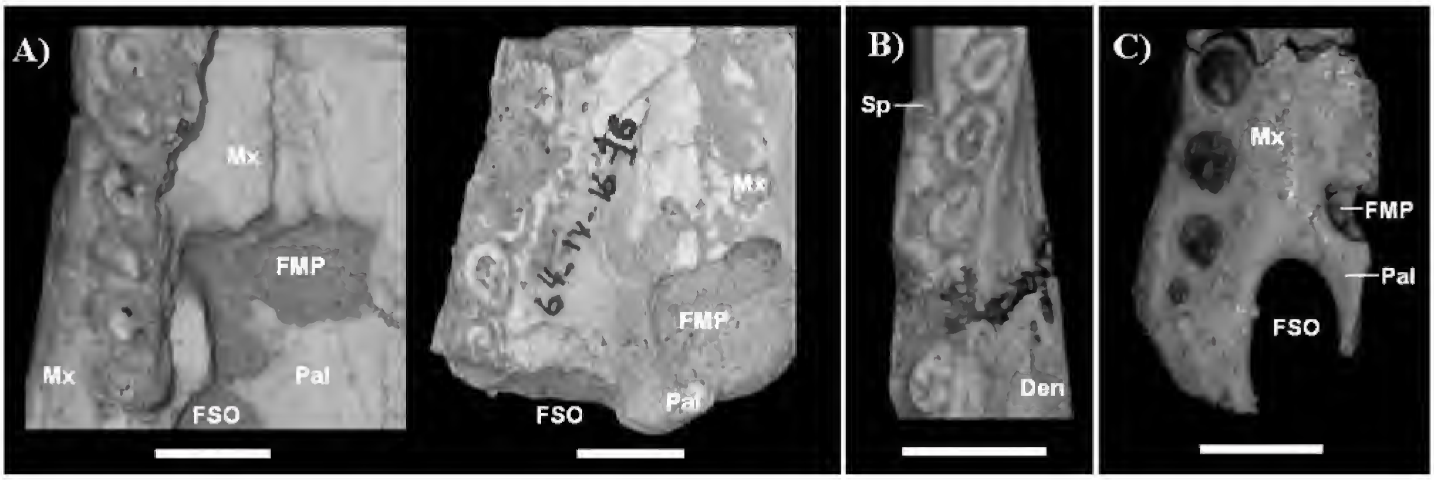

Fig.13- Cranial material of the specimens studied, showing the oblique implantation of the maxillary and dentary teeth: A) rostrum of *Notosuchus terrestris* in palatal view, specimens MLP-64-IV-16-1 (left) and MLP-64-IV-16-16 (right); B) *N. terrestris* MLP-64-IV-16-13, dorsal view of the right ramus of the mandible; C) *Mariliasuchus amarali* URC R•68, in palatal view. Bar = 10 mm.

The presence of ornamentation, carinae and wear surfaces needs further documentation and support. *Notosuchus* is usually considered as possessing carinae (Prasad & Broin, 2002; Zaher *et al.*, 2006, character 120). Woodward (1896) identified flutings in specimen 241 (Woodward, 1896; Pl.2, Fig.5), corresponding to ornamentation. Only MACN-Pv-N-23 preserves remnants of basal-apical ridges on the labial side of the fourth(?) and the sixth(?) maxillary crowns, from the right maxilla (Fig.14). These appear as undivided strong ridges, rather than the light anastomosed pattern seen in *Mariliasuchus*. Woodward (1896) recognized "a feeble crenulation" on the anterior edge of the seventh mandibulary tooth of specimen 200 (Woodward, 1896; p.12, 1st§; Pl.2, Fig.4a), but also on the distal face of the maxillary molariforms. This suggests the presence of denticulated carinae for *Notosuchus*, but the specimens are lost and no evidence truly supports this information. Nevertheless, Woodward's (1896) work is the first description of such features, matching posterior descriptions of denticulated carinae in other taxa and is highly unlikely to be biased. *Notosuchus* may also have shown wear surfaces, what is consistent with proal/propalinal jaw movents. According to Woodward (1896; p.12, 1st§) "the eight and tenth (maxillary) teeth seem to exhibit an outer oblique facette worn by opposing teeth from the upper jaw", in specimen 200. Once more, lack of preservation hinders the appropriate identification of these surfaces.

Both *Mariliasuchus* and *Notosuchus* show heterodonty in a peculiar pattern. The anteriormost teeth are small incisiforms and the last premaxillary tooth is a hypertrophied caniniform (Fig.7). The posterior elements of the upper series are followed by 1-2 teeth with intermediate morphology ("premolariforms"), and these are followed by molariform teeth that increase and then decrease in size posteriorly. Furthermore, the premaxilla and the maxilla contribute to the alveolus of the first postcaniniform tooth and to the support of this element, which is clearly not the case for either *Comahuesuchus* or *Candidodon*. In a broad view, the dentition of *Mariliasuchus* and *Notosuchus* resemble each other much more than to *Comahuesuchus* or *Candidodon*. In this last notosuchian an additional and important difference is that molariform teeth are cingulate and lack completely the denticulated carinae.

Fig.14- Tooth ornamentation in *Notosuchus terrestris* MACN-Pv-N-23. Note the presence of basal-apical undivided crests partially preserved on the labial surface of the fourth(?) and the sixth(?) molariforms from the right maxilla, indicated by white pointers.

Furthermore, in *Candidodon* there are at least three pairs of maxillary caniniforms, one of them clearly hypertrophied. In the premaxilla, the most developed tooth is proportionally not as developed as in *Notosuchus* and *Mariliasuchus*. In *Comahuesuchus* the teeth may be all single cusped, but there are no molariforms and hypertrophied caniniforms can only be found in the maxilla and posterior part of the mandible, exactly the opposite pattern shown by *Mariliasuchus* and *Notosuchus*. There is no evidence for ornamentation or carinae in the teeth of *Comahuesuchus* (Bonaparte, 1991), though preservation bias may have severely compromised observation of these features in the very few specimens known.

Comparative evaluation of the dentition shows that at least for this parameter, *Candidodon* and *Comahuesuchus* are not similar forms. *Sphagesaurus* shows to be a much better correlated. The dentition of this mesoeucrocodylian also shows only one pair of hypertrophied caniniforms in the premaxilla and none in the maxilla/mandible, predominance of molariform teeth, presence of obliquely implanted teeth, procumbent dentition in the anterior part of the mandible and all teeth single cusped and intensely ornamentated (Price, 1950; Pol, 2003; Andrade, 2005; Andrade & Bertini, 2007). In fact, the dentition of *Sphagesaurus* is much more similar to the dentition of *Notosuchus* and *Mariliasuchus* than the dentition of *Comahuesuchus* or *Candidodon*. The most important differences of *Sphagesaurus* from *Notosuchus* and *Mariliasuchus* are the absence of precaniniform teeth in the premaxilla, a more clearly distinction between caniniforms and molariforms and a more extreme paramesial rotation of middle and posterior teeth. Even though, in *Mariliasuchus*, *Notosuchus* and *Sphagesaurus* all the maxillary teeth are robust, ornamented, single cusped and distinctly modified to process food, rather than for prey capture. Furthermore, *Sphagesaurus* shows wear surfaces and was capable of anteroposterior mandibular movements (Pol, 2003). *Chimaerasuchus* also have most of these features, but the teeth are not as robust, showing multicusped wider crowns and lack ornamentation (Wu *et al.*, 1995; Wu & Sues, 1986). *Simosuchus* has spatulated teeth and broad jaws (Ortega *et al.*, 2000), but is hardly comparable to any other taxon. Most remaining mesoeucrocodylians show at least the anterior maxillary and middle mandibulary teeth caniniform curved, as in *Araripesuchus*, *Candidodon* and *Uruguaysuchus*.

Variable parietal morphology: a special case in Mesoeucrocodylia?

In *Notosuchus*, the parietal crest can be present in two forms (Fig.15). As in the *Notosuchus* lectotype, the crest widens progressively from its anterior end to the crown, producing an elongated triangular outline. On the other hand, the parietal crest can be narrow throughout and only widens very rapidly near its end, close to the crown, as in MACN-Pv-RN-1037. This creates a paddle-shaped, constricted crest with a subcircular crown. In the first morphological type, the crown and the crest are continuous, while in the second type the crown is completely distinct from the crest due to a constriction. Because of the relation between the crest and the supratemporal fenestra, in the paddle-shaped type of crest there is more area for muscular fibers to attach on the mesial border of the fenestra, though the difference is hardly noticeable. There is no correlation between the presence of this constriction (determining the paddle-shaped crest) with geographical and stratigraphical provenance, as the different morphologies are present in individuals of all collections. This constriction is also not related to preservation, as it occurs both in well preserved and poorly preserved specimens, and it cannot be related to ontogenesis, as it occurs in adult and semi-adult specimens.

These are discrete states present in *Notosuchus terrestris*, with no intermediate stages. The paddle shaped type of crest can be identified in approximately 50% of the specimens evaluated (Tab.2). Due to its bimodal distribution, the variability of parietal morphology may represent the first reasonable evidence for sexual dimorphism in mesoeucrocodylians. Nevertheless, a larger sample is desirable to support the hypothesis, and a more careful exploration of the subject is needed for *Notosuchus*.

As mentioned previously, Zaher *et al.* (2006) report variability in the morphology of parietal of *Mariliasuchus* MZSP-PV-51. Examination of specimens and observation of main bibliographic references (Vasconcellos & Carvalho, 2005, 2006; Zaher *et al.*, 2006) indicate that MN 6298-V, MZSP-PV-50, URC R•67 have a much narrower parietal, while MZSP-PV-51, MN 6756-V and UFRJ-DG-106-R show a proportionally wider surface. In all cases, the parietal surface is flat and the medial borders of the supratemporal fenestrae show the same curved profile.

Nevertheless, considering the number of specimens, it is not possible to evaluate if the variable character is truly discrete or may be part of a continuous series. Although the small sample is insufficient to avoid the risk of accidental distribution, it is possible that this represent another true example of sexual dimorphism in Notosuchia, as discussed by Zaher *et al.* (2006). If confirmed in both *Mariliasuchus* and *Notosuchus*, the occurrence of sexual dimorphism may constitute further evidence of close relationship between these species. Furthermore, the possible existence of this variability in these taxa suggests that other species of notosuchians might show the same trait.

PHYLOGENETICAL RELATIONSHIPS OF *MARILIASUCHUS AMARALI* AND *NOTOSUCHUS TERRESTRIS* WITH OTHER SOUTH AMERICAN NOTOSUCHIANS

METHODOLOGY APPLIED

A preliminary analysis focusing on notosuchians (Appendix 1) was carried out. The objective was to verify the relationships of *Notosuchus*, *Mariliasuchus*, *Candidodon* and *Comahuesuchus*. This analysis used characters from several previous contributions (Benton & Clark, 1988; Clark, 1994;

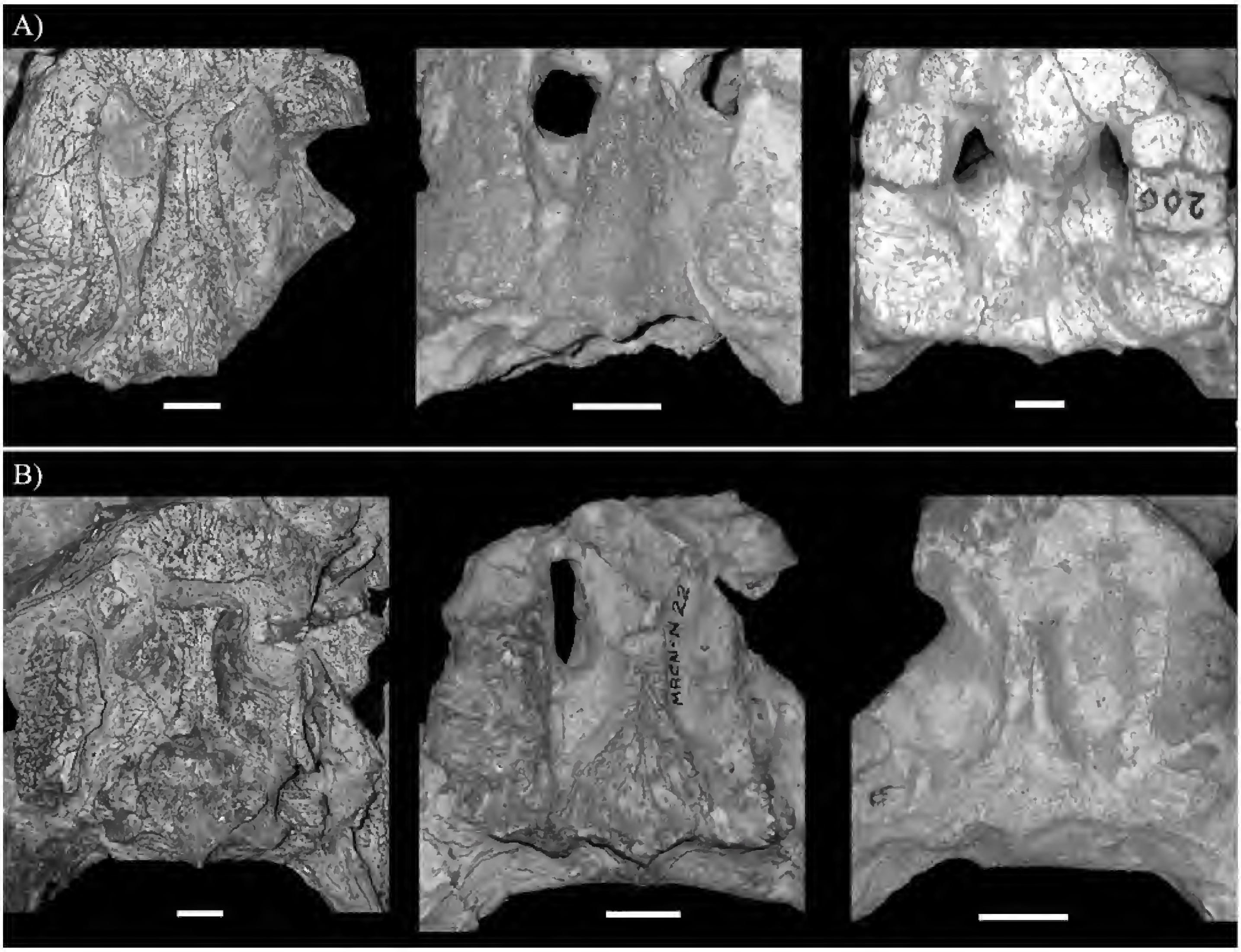

Fig.15- Morphological variation in the parietal of *Notosuchus terrestris*, in dorsal view. A) Triangular crest in MACN-Pv-RN-1045 (left), MACN-Pv-N-107 (center) and MLP-64-IV-16-31(206) (right); B) Paddle-shaped crest in MACN-Pv-RN-1048 (left), MACN-Pv-N-22 (center) and MLP-64-IV-16-8(209) (right). Note that both morphologies are present in material from Rio Negro (left) and Neuquén (center and right) provinces. Note also that both morphologies occur in MACN (center and left) and MLP (right) specimens. Bar = 10 mm.

TABLE 2. Intra-specific variability in the morphology of the parietal crest in *Notosuchus terrestris*.

	TRIANGULAR CREST	PADDLE-SHAPED CREST
Rio Negro	MACN-Pv-RN-1045, MACN-Pv-RN-1119	MACN-Pv-RN-1037, MACN-Pv-RN-1041, MACN-Pv-RN-1048, MACN-Pv-RN-1118
Neuquen	MACN-Pv-N-23, MACN-Pv-N-107, MLP-64-IV-16-1, MLP-64-IV-16-3, MLP-64-IV-16-6, MLP-64-IV-16-31	MACN-Pv-N-22, MLP-64-IV-16-8, MLP-64-IV-16-10
Total	8	7

Note that (i) specimens from MACN and MLP show both types of crests; (ii) specimens from Rio Negro (MACN-Pv-RN) and Neuquén (all others) also show both types of crest.

WU & SUES, 1996; GOMANI, 1997; BUCKLEY *et al.*, 2000; ORTEGA *et al.*, 2000; MARTINELLI, 2003; POL, 2003; SERENO *et al.*, 2003), but also from the unpublished analysis of ANDRADE (2005) (Appendix 2). Baurusuchidae terminal includes information from *Baurusuchus pachecoi* and *Stratiotosuchus maxhechti*. *Uruguaysuchus* refers only to *U. aznarezi*, as *U. terrai* is considered a possible junior synonym to the former (ANDRADE, 2005; ANDRADE & BERTINI, 2005a). The matrix included 20 terminals and 183 characters (Appendix 3).

Phylogenetic analysis (HENNIG, 1966) was carried out with PAUP 4.0b10 (SWOFFORD, 2002), using heuristic search (10,000 replicates). All characters were treated as unordered, with equal weight, and assuming the shortest optimization possible between accelerated and delayed transitions. These options were adopted to avoid the influence of *a priori* assumptions in the analysis. The collapse option for zero length branch was applied. Bootstrap (FELSENSTEIN, 1985) and branch decay (BREMER, 1994) were used to evaluate the tree stability. Bootstrap used 200 replicates. Branch decay was calculated with the use of TreeRot (SORENSON, 1999).

Due to the preliminary character of this analysis, a second analysis using a different framework was done to support or disprove results presented here. The matrix presented by ZAHER *et al.* (2006) was selected because it included a larger number of terminals and a good representation of the notosuchian clades. The original matrix by ZAHER *et al.* (2006) was based on an extended version of POL & NORELL (2004b), with the addition of seven characters, composing a matrix with 46 terminals and 198 characters (Appendix 4). A preparatory analysis using the original dataset was done to check for potential problems, using the same options provided by ZAHER *et al.* (2006), including the exclusion of character 5. The analysis of the original dataset by ZAHER *et al.* (2006) failed to achieve the same results in all attempts, obtaining a strict consensus that is three steps shorter (655 steps, from originally 658 steps), but otherwise identical to the original topology. Alternate analysis of the same dataset shows that the original number of steps could only be achieved if the character 5 was included in the analysis, without alteration of the topology and recovering the same indexes presented by ZAHER *et al.* (2006). It was understood that the original dataset was performing appropriately, but it is possible that the original analysis shown by ZAHER *et al.* (2006) actually included character 5.

The original dataset was then modified according to morpho-anatomical observation of the specimens. This modified version of the dataset has undergone three steps of progressive modifications, to ensure adequate comparison with the original results. In the first step, the dataset was subject to a detailed revision focused on the data coding of *Notosuchus*, *Mariliasuchus*, *Comahuesuchus*, *Candidodon* and *Sphagesaurus* (Appendix 5). Revision of *Candidodon* included basic morphological information on cranial data, obtained from CARVALHO (1994) and NOBRE & CARVALHO (2002), but not used by ZAHER *et al.* (2006). Revision of other taxa followed the morpho-anatomical observations addressed in this study, also reducing the number of missing data, with minor corrections introduced to *Malawisuchus*, *Uruguaysuchus* and both *Araripesuchus* species (Appendix 5). Characters coded as ordered were also revaluated and a reduced list produced, with the exclusion of few characters (1, 3, 65, 67, 105, 107 and 143) that were not considered to be orderable. This dataset was then used to run an unordered analysis. Ordering and successive weighting were applied only to verify stability and increase resolution.

A second step used the modified matrix, from where characters were excluded to verify the influence of these components over the original topology presented by ZAHER *et al.* (2006). Only six characters were excluded, related to dentition (105, 107, 120, 192, 194) and jugal morphology (193) (Appendix 4). This dataset was then used to run an unordered analysis.

In the third step of the modified phylogenetic analysis by ZAHER *et al.* (2006), the information from the characters excluded in step two (105, 107, 120, 192, 194) was reintroduced with restructured characters (Appendix 6). This dataset (Appendix 7) was then used to run an unordered analysis.

Successive weighting (FARRIS, 1969) was applied to unordered analysis as an exploratory method, to evaluate the stability and the limits of the topology. Ordered analysis was used in the same way, to evaluate stability and congruence but only applied to a restricted number of characters, with the modified dataset from ZAHER *et al.* (2006). Bootstrap (100 replicates) was also used to evaluate tree stability only in the third (final) step of the second analysis.

ORDERING AND CHARACTER EXCLUSION FROM MODIFIED MATRIX OF ZAHER *ET AL.* (2006)

Besides general criticism eventually presented against the use of ordered series, Wagner parsimony (FARRIS, 1970) was considered inapplicable for seven characters (1, 3, 65, 67, 105, 107, 143) from ZAHER *et al.* (2006) (Appendix 4). With exception of taxa listed in Appendix 5: (i) the original coding applies for the first step of the second analysis; (ii) the original coding was completely excluded from the second and third steps; (iii) revised coding with corrected information was only used in the third step (Appendixes 6 and 7).

No data suggests that skull ornamentation (character 1) necessarily have to develop a grooved pattern (state 1) before showing a pitted pattern (state 2). The same applies to the general morphology of the rostrum (character 3), as platyrostral forms (state 3) may develop into broad oreinrostral (state 1) or nearly tubular forms (state 2), and forms with nearly tubular rostrum may develop from narrow oreinrostral (state 0) or platyrostral forms. The size and number of palpebrals (character 65) is poorly known for taphonomic reasons, as these elements can be easily lost in the burial process, and the ordering can only introduce an additional bias. The development of an antorbital fenestra (character 67) may be recognizable as few discrete states, but the difference between states 1-3 do not necessarily need to be linear. Apart from that, minor differences on the size of the fenestrae may be an artifact of preservation. Multistate characters referring to repetitive structures (*e.g.* vertebrae, teeth) should not be subject to ordering because the number of elements can be the result of deletions and additions in any point of the series (characters 105 and 107). The position of the ascending jugal process (=postorbital jugal process; character 143), which takes part in the postorbital bar, may be the result of the postorbital bar inclination or either the development/ shortening of the anterior or the posterior process, which hinders the ordering of states.

Characters excluded in the second step are mostly related to dentition, and are subject to a series of problems. Characters 105-107 referred to the number of teeth of the premaxilla and maxilla. Although widely used (*e.g.*, WU & SUES, 1996; ORTEGA *et al.*, 2000; POL & APESTEGUIA, 2005; ZAHER *et al.*, 2006), the number of teeth for a single element may not represent true homologous conditions. In fossil crocodylians, the reduction of the dental series can be the result of loss of anterior, middle or posterior elements, as in the case of number of vertebrae. Furthermore, the existence of an intermediate tooth in the upper series complicates interpretation and coding. The information was reintroduced as characters 200-202, considering the position of this intermediate tooth and the exclusive premaxillary and maxillary series as independent characters. Nevertheless, this set of characters is still not free from criticism, as it ignores changes in size and morphology throughout the series. Character 120, as originally published (ORTEGA *et al.*, 2000) refers to the presence of a carina in teeth. In fact, as explored by PRASAD & BROIN (2002), ANDRADE (2005) and ANDRADE & BERTINI (2005b), carinae show variation in morphology and distribution over the dental series, and two different situations are recognized here. The true ziphodont type of carina is present in anterior teeth of highly predaceous forms, and can also develop on posterior teeth. An alternate situation is present in other species, where carinae are completely absent from anterior teeth, but are present in posterior teeth and show a different morphology of denticles, possibly related to processing food. The information was reintroduced as character 204. Character 194 dealt on the presence of procumbent alveoli in the anterior dentition, thus avoiding morphological differences of teeth related to those alveoli. Procumbent dentition is probably related to functional aspects of feeding, but may have evolved multiple times from quite different conditions. In fact, the original coding ignores that, in most eusuchians (*e.g.*, *Gavialis*, *Crocodylus*) and several Mesoeucrocodylia, the alveoli are usually inclined anteriorly and teeth are procumbent, both in the mandible and in the premaxilla. This may not be so evident, as these teeth are often strongly curved caniniforms, and the apex is directed to the occluding plane rather than anteriorly. The alveoli and teeth, nonetheless, are inclined anteriorly. The information is reintroduced with character 205, with reference to dental morphology. Nevertheless, it should be stressed that the new coding still does not solve the problem of adequately representing this information, as inclined alveoli can occur in different sections of the jaws. Furthermore, deformation may easily introduce bias in the coding of this character.

Character not comprising the dentition relate to the jugal, lachrymal and maxilla. The contact between jugal and lachrymal (character 192) is usually present in Mesoeucrocodylia, excluding the maxilla from the orbit. The maxillary participation to the orbit was already pointed out by Andrade (2005; character 16) and is also present in *Malawisuchus* and *Uruguaysuchus*. As in Martinelli (2003) and Andrade (2005), the maxilla of *Comahuesuchus* does not take part of the orbit (*contra* Zaher *et al.*, 2006). The information was reintroduced with character 203. Character 193, the presence of an anteriorly directed enlarged neurovascular foramen on the jugal anterior ramus of some notosuchians (*Mariliasuchus, Comahuesuchus* and *Sphagesaurus*), was previously introduced by Andrade (2005; character 43). Furthermore, Andrade (2005) includes a third state covering the existence of small ventrally directed foramina (generally four) close to the contact with the maxilla, present in eusuchians. The information was reintroduced as character 199.

RESULTS

Preliminary analysis

Only a single most parsimonious tree was obtained from the preliminary analysis (Fig.16; Length = 468, CI = 0.4829, RI = 0.6372, RC = 0.3077, HI = 0.5171). The topology shows a well supported closest relationship between *Mariliasuchus* and *Notosuchus* (bootstrap = 85%; branch decay = 4), as proposed originally by Carvalho & Bertini (1999) and consistent with Notosuchidae. *Sphagesaurus huenei* also shows a close relationship, in a well supported unnamed clade including Notosuchidae (bootstrap = 82%; branch decay = 5). *Comahuesuchus* and *Chimaerasuchus* are successively more distant sister-groups, but lacking a good support (bootstrap < 60%; branch decay = 1). A larger group including these species and the Baurusuchidae shown to be only slightly better supported (bootstrap < 50%; branch decay = 2).

Candidodon lays as sister-clade of *Uruguaysuchus*, as part of a more basal notosuchian lineage (along with *Simosuchus* and *Malawisuchus*). The support for this group is poor (bootstrap < 50%; branch decay d•2). Nevertheless, the close relationship between *Candidodon* and *Mariliasuchus*, proposed by Carvalho *et al.* (2004), is extensively rejected. Partial corroboration of main aspects of this analysis is provided by further analysis based on Zaher *et al.* (2006). Furthermore, a few other aspects deserve attention. Notosuchia (*sensu* Sereno *et al.*, 2001) finds a strong support (bootstrap = 79%; branch decay = 5), but does not include *Anatosuchus* or *Araripesuchus*. Furthermore, these taxa are represented as related to the neosuchian lineage, a position reasonably well supported in both cases (bootstrap = 55%; branch decay = 3). The close relationship between *Comahuesuchus* and *Anatosuchus*, proposed by Sereno *et al.* (2003), is extensively rejected. *Sebecus* appear as the sister group of Eusuchia, a relationship that finds a strong support (bootstrap = 79%; branch decay = 5). Although there is a lack of other highly predatorial mesoeucrocodylian taxa within the analysis (*e.g.*, *Libycosuchus, Bergisuchus, Bretesuchus, Hamadasuchus, Pabweshi*), the results do not support Sebecosuchia or Ziphosuchia.

Second analysis

The preliminary analysis of Zaher *et al.* (2006) – Considering only the original matrix (with exclusion of character 5), the ordered analysis is more resolved than the unordered analysis (96 MPTs, 619 steps). The unordered analysis with the same dataset solves the relationship between *Notosuchus* and the other notosuchians, although leads to a poor resolution for Neosuchia (*sensu* Sereno *et al.*, 2001).

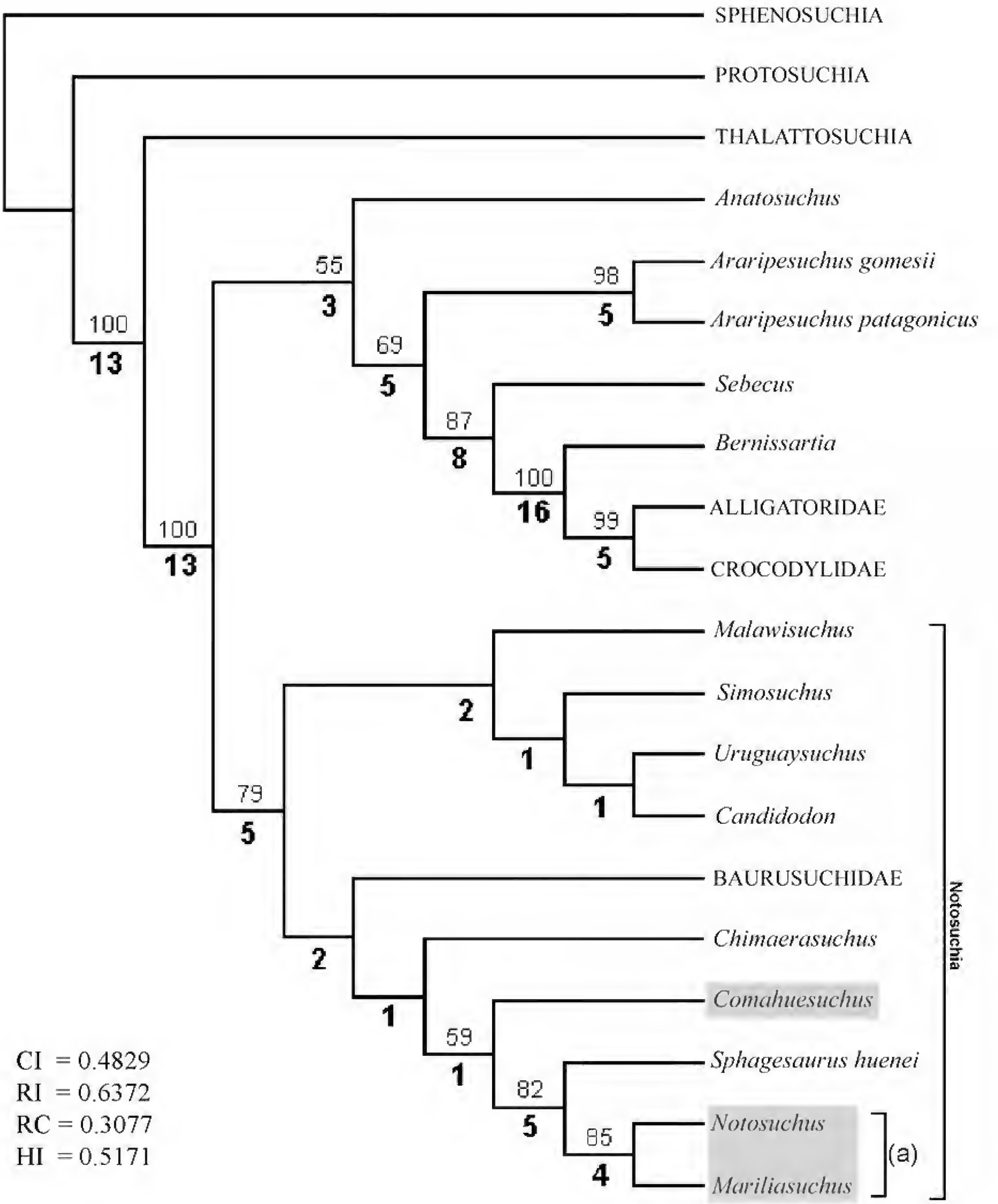

Fig.16- Single most parsimonious tree (468 steps) based on dataset by Andrade (2005), showing the position of Notosuchidae (a) within Notosuchia (*sensu* Sereno *et al.*, 2001). Support indicated for each node, showing bootstrap for values over 50% and branch decay (bold numbers) indexes. Note the position of *Notosuchus* in relation to *Mariliasuchus* and *Comahuesuchus*, indicated by the shaded areas, and the distant relationship with *Candidodon* and *Malawisuchus*.

In this analysis, *Notosuchus* remained as a sister-clade to *Mariliasuchus+Comahuesuchus*. Successive weighting of the unordered data confirms this relationship, with a slight increase of resolution inside Neosuchia.

FIRST STEP OF THE SECOND ANALYSIS – The result obtained from step one (Fig.17), where morphological information was corrected, solved the position of *Notosuchus* as sister-clade of *Mariliasuchus+Comahuesuchus*. In the strict consensus (95 MPTs, 615 steps), several polytomies are present (as in the unordered analysis of the original dataset). Ordering (22 MPTs, 629 steps) only improves the position of *Gavialis* and *Eutretauranosuchus*, while successive weighting enhances the resolution of basal neosuchian longirostrine forms (Teleosauridae, Dyrosauridae+*Sokotosuchus*). In all cases, *Sphagesaurus* figures as sister-group to *Chimaerasuchus*, representing a lineage associated to *Baurusuchus* and similar forms. *Candidodon* remains as sister-group to *Malawisuchus*, as in the original analysis, but *Simosuchus* appears as part of this lineage. *Uruguaysuchus* appears as a separated, more basal lineage within Notosuchia. *Araripesuchus* is shown as the basalmost group of Notosuchia (*sensu* SERENO *et al.*, 2001). The position of *Hylaeochampsa* remains unresolved relative to *Borealosuchus* and the extant crocodylians.

The result of this analysis shows that the information corrected is crucial to avoid incongruences that affect the position of *Notosuchus*. Ordering is an important element to improve resolution within Neosuchia, but successive weighting introduces more resolution, for this particular dataset.

SECOND STEP OF THE SECOND ANALYSIS – Step two verified the possible biased effect of a limited number of characters, by means of their exclusion. The unordered analysis (Fig.18) shows a similar strict consensus (76 MPTs, 583 steps) to the previous step, except for two noticeable changes: (i) an improvement in the relationships within Neosuchia; (ii) a shift in position between *Comahuesuchus* and *Notosuchus*, the later of which is then shown as sister-clade to *Mariliasuchus*. Ordered analysis (25 MPTs, 597 steps) and successive weighting do not change either the *Notosuchus+Mariliasuchus* exclusive relationship or the position of *Comahuesuchus*, but further improves resolution inside Neosuchia. In all cases, *Sphagesaurus* figures as sister-group to *Chimaerasuchus*, representing a lineage associated to *Baurusuchus* and similar forms. *Candidodon* appears as sister-group to *Malawisuchus+Simosuchus*. *Uruguaysuchus* remains as a separated, more basal lineage within Notosuchia. *Araripesuchus* figures as the basalmost group of Notosuchia. Also in all cases, *Hylaeochampsa* remains unresolved and atoposaurids maintained a closer position to *Alligator* than to the basal neosuchian longirostrine forms.

The result of this analysis shows that the removed characters were essential in establishing a link between *Mariliasuchus* and *Comahuesuchus*. This link is not supported otherwise, but the result provides no answer to which factor could determine this relationship. It could be either the lack of the excluded information *per se* or the construction of characters and definition of states. This problem was addressed in the last step of the analysis. The exclusion of these characters did not change the results in Neosuchia, or the effect of ordering and successive weighting. Ordering is again an important element to improve resolution within Neosuchia, but successive weighting introduces more resolution.

THIRD STEP OF THE SECOND ANALYSIS – In this step the information previously excluded is reintroduced with the addition of seven characters. Unordered analysis (225 MPTs, 621 steps) shows six polytomic groups (Fig.19), only two of them in Notosuchia. In the notosuchian lineage, the *Mariliasuchus+Notosuchus* clade is also present, but *Comahuesuchus* occupies an even more basal position than in the previous step. *Simosuchus* shows a shifting behavior and induces a polytomy with the closest taxa. The reintroduction of the information did not affect the relationships inside Neosuchia. Bootstrap shows a reasonable support (>50%) for approximately 50% of the mesoeucrocodylians, but only eight clades (approximately 30%) show a good support index (≥75%). Ordering (45 MPTs, 635 steps) only improves the position of *Gavialis* and *Eutretauranosuchus*. Successive weighting affects the longirostrine forms, as in the previous steps, but also *Comahuesuchus* and *Simosuchus*, from the notosuchian branch.

In all cases, *Sphagesaurus* figures as sister-group to *Chimaerasuchus*, representing a lineage associated to *Baurusuchus* and similar forms.

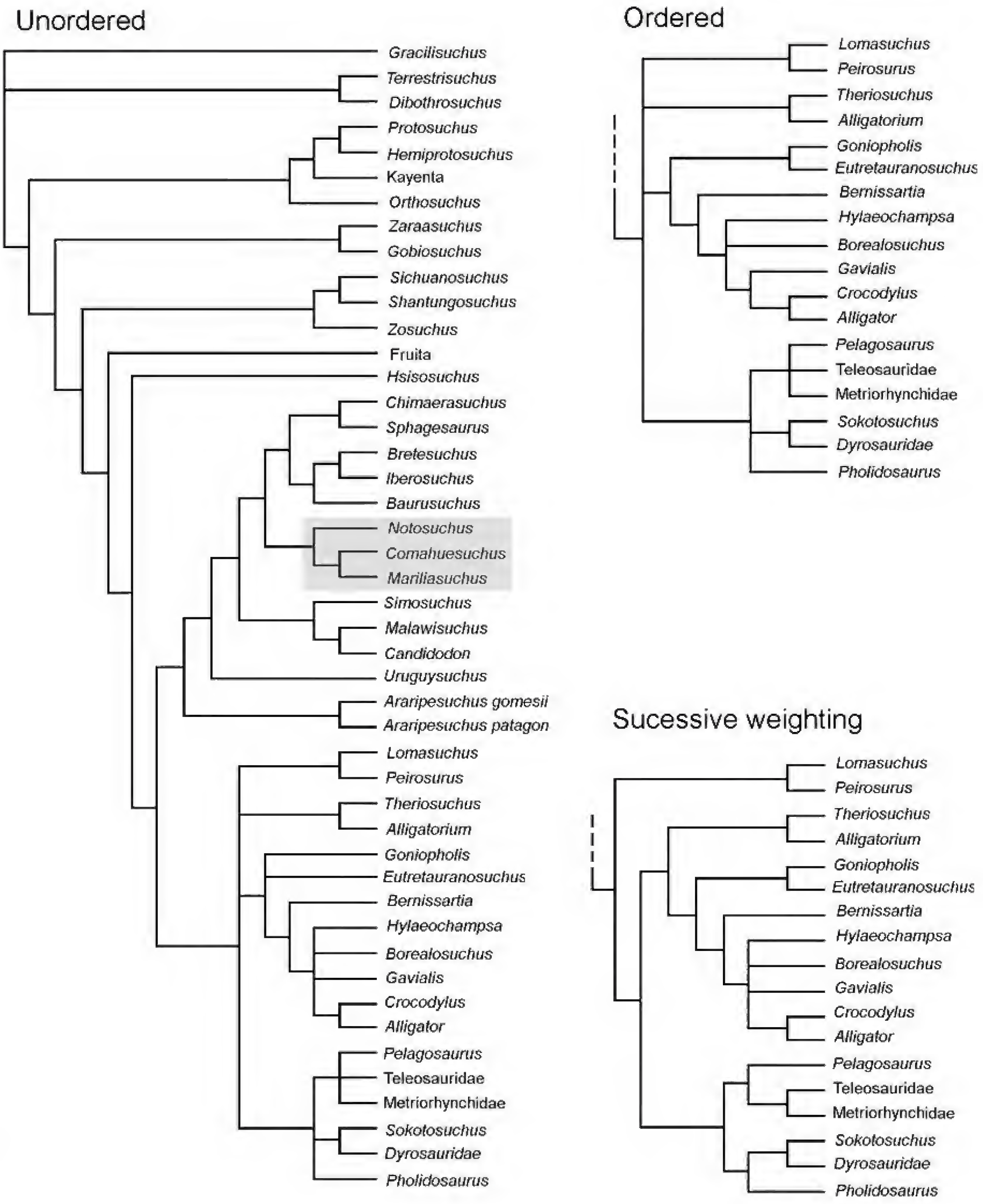

Fig.17- First step in the revaluation of the original dataset by Zaher *et al.* (2006), with corrected data from the matrix. Unordered analysis led to a strict consensus of 95 MPTs (615 steps, CI = 0.43). Ordered analysis (22 MPTs, 629 steps) and successive weighting (right) introduced changes only to the neosuchian branch. Wagner parsimony applied for 18 characters. Note the stable position of *Notosuchus* relative to *Comahuesuchus* and *Mariliasuchus*, indicated by the shaded area, and the distant relationship with *Candidodon* and *Malawisuchus*.

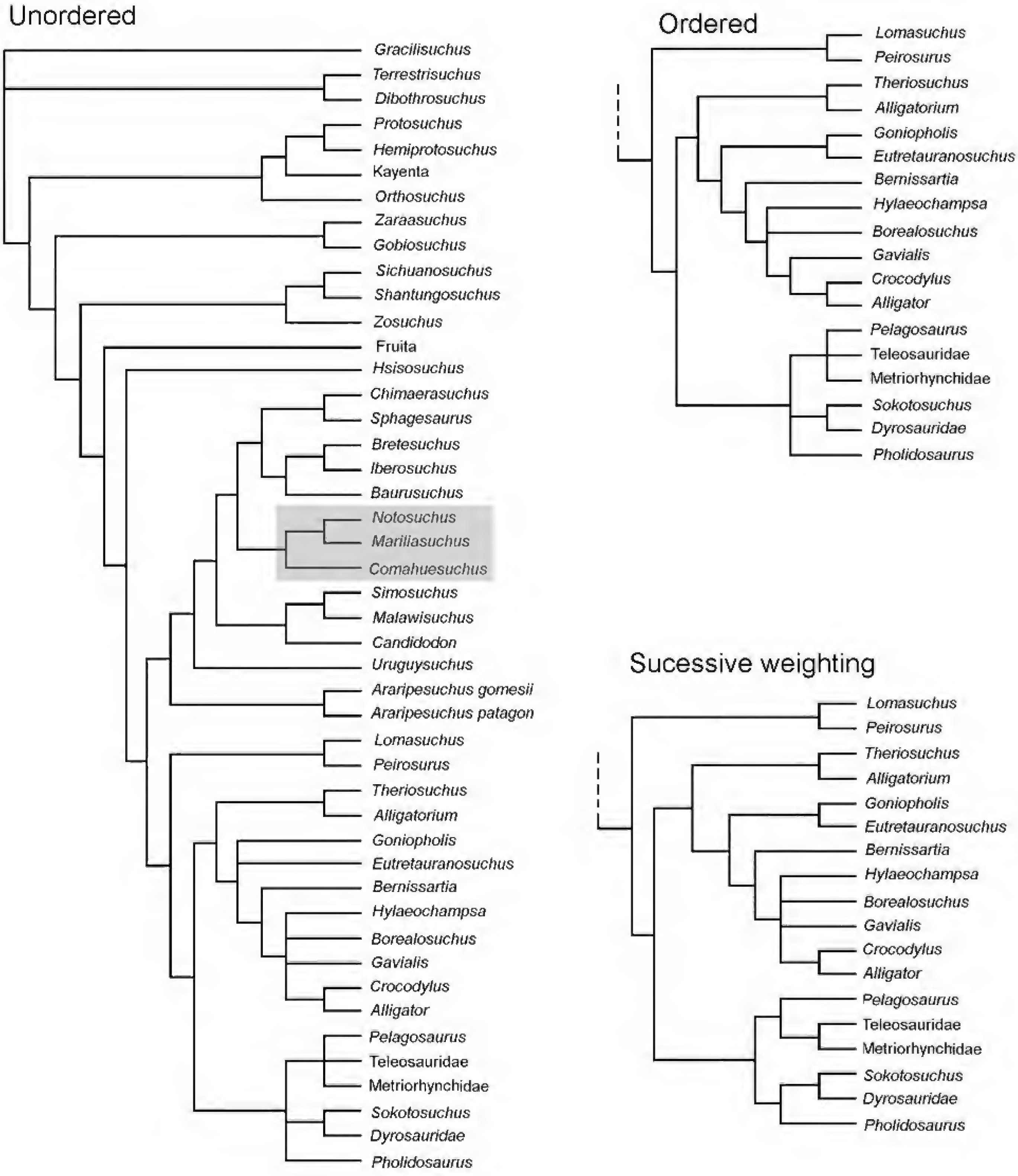

Fig.18- Second step in the revaluation of the original dataset by Zaher *et al.* (2006), with the exclusion of problematic characters (5, 105, 107, 120, 192, 193, 194). The unordered analysis led to a strict consensus of 76 MPTs (615 steps, CI = 0.43). Ordered analysis (25 MPTs, 597 steps) and successive weighting (right) only affected the neosuchian branch. Wagner parsimony applied for 18 characters. Note the shift in the position of *Comahuesuchus* and *Mariliasuchus* relative to *Notosuchus* (shaded area), showing the effect produced by the exclusion of characters.

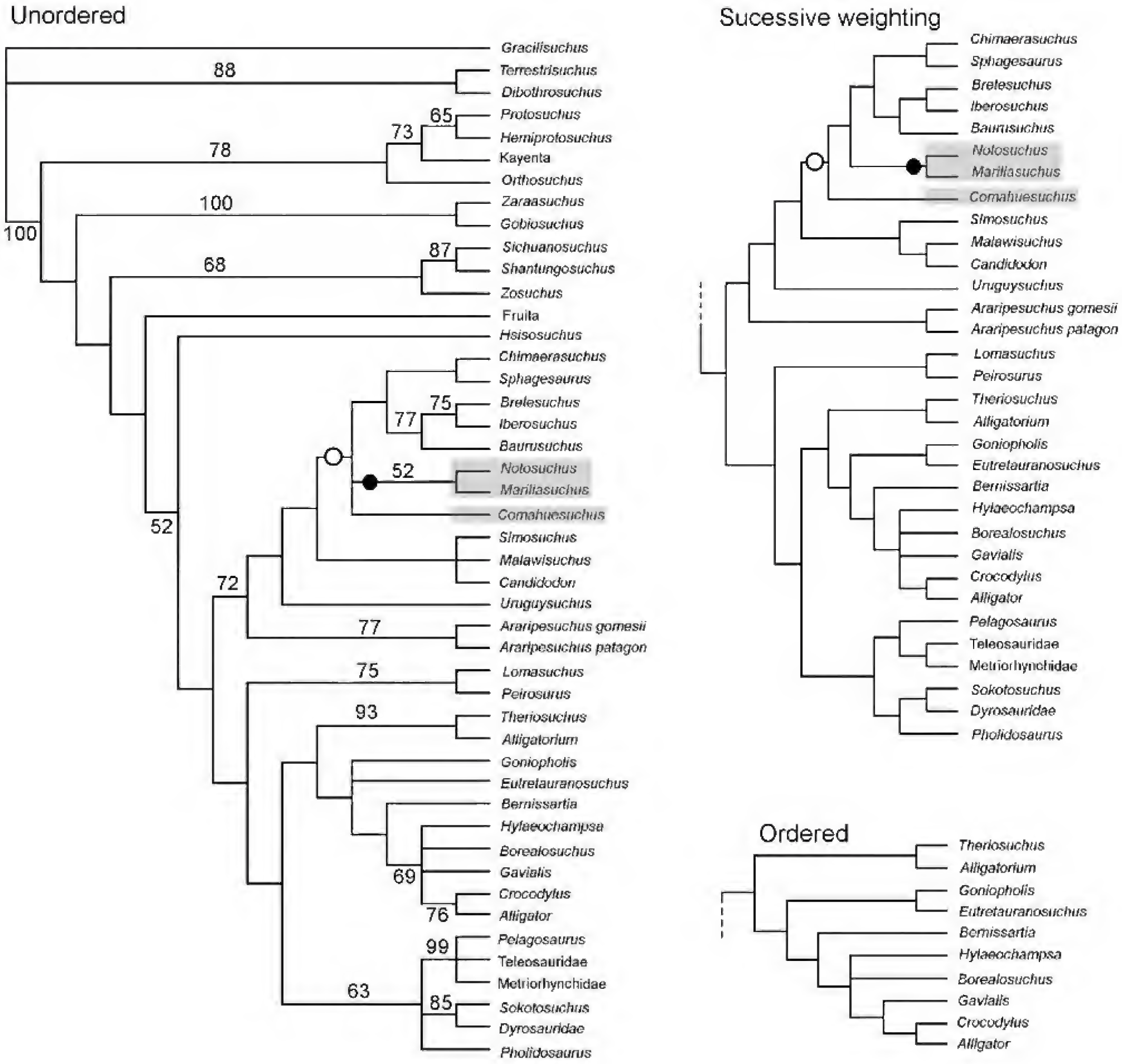

Fig.19- Third step in the revaluation of the original dataset by Zaher *et al.* (2006), with the reintroduction of the information excluded in the previous step, using reorganized characters. The positions of *Notosuchus*, *Mariliasuchus* and *Comahuesuchus* are indicated by a shaded area. The unordered analysis (left) led to a strict consensus of 225 MPTs (621 steps, CI = 0.43, RI = 0.68, RC = 0.29), where *Comahuesuchus* shows a shifting behavior, either figuring as sister-clade to Notosuchidae (black circle) or to all other derived notosuchians (white circle). Ordered analysis (bottom right) (45 MPTs, 635 steps) only affected the neosuchian branch, but the use of successive weighting (top right) affects Notosuchia and determines an even more basal position for *Comahuesuchus*. Numbers on each node refer to bootstrap. Ordered option applied for 19 characters. Note the position and reasonable support for *Mariliasuchus* and *Notosuchus*, but the overall poor support for most relations within Mesoeucrocodylia.

Candidodon, *Malawisuchus* and *Simosuchus* appear as a single lineage of notosuchians. *Uruguaysuchus* appears as a separated, more basal lineage within Notosuchia. *Araripesuchus* figures as the basalmost group of Notosuchia (*sensu* SERENO *et al.*, 2001). Also in all cases, the position of *Hylaeochampsa* remains unresolved relative to *Borealosuchus* and the extant eusuchians, and atoposaurids mantained a closer position to *Alligator* than to the longirostrine forms.

The reintroduction of these characters did not change the results in Neosuchia, as the use of ordering and successive weighting. Nevertheless, the reintroduction of information clearly affects the position of *Comahuesuchus* and improves the influence of successive weighting over *Comahuesuchus* and *Simosuchus*. In the unordered and ordered topologies, *Comahuesuchus* has collapsed into a position as basal as the lineage that leads to *Sphagesaurus* and the highly predaceous notosuchians (*e.g.*, Baurusuchidae). When successive weighting was applied to improve resolution, *Comahuesuchus* assumes an even more basal position (with a similar effect to the position of *Simosuchus*). Once more, successive weighting also introduces more resolution than ordering, for this particular dataset.

OVERALL RESULTS OF THE SECOND ANALYSIS – The second analysis was introduced to corroborate results from the preliminary analysis with an independent dataset. Furthermore, it allows understanding the effect that characters, information and options had over the final topology. The results from the second analysis show that: (i) corrected information was determinant to define the position of *Notosuchus*; (ii) the exclusion of the selected characters clearly has an effect on the position of *Comahuesuchus*; (iii) the reintroduction of the information does not support a closest relationship between *Comahuesuchus* and *Mariliasuchus*; (iv) in no single result, *Candidodon* shows a close relationship with *Mariliasuchus*; (v) successive weighting and ordering produce essentially concordant results, but successive weighting introduces more resolution in this particular dataset. In overview, the implementation of the third step shows that the construction of a small group of characters may be determinant to the position of certain terminals within an analysis. In this special case, *Comahuesuchus* is particularly affected (but not *Notosuchus*). It was the particular way the selected characters are constructed that led to changes to the position of *Comahuesuchus*. On the other hand, correction of the morphologic information in step one was determinant to improve the position of *Notosuchus*.

The combined results from the preliminary and the second analysis show that: (i) *Mariliasuchus* and *Notosuchus* are closely related forms; (ii) the position of *Comahuesuchus* is poorly defined, but it may be closely related to *Notosuchus*+*Mariliasuchus* than to any other notosuchian; (iii) a closer exclusive relationship between *Candidodon* and *Mariliasuchus* is extensively rejected; (iv) *Mariliasuchus, Notosuchus, Comahuesuchus, Sphagesaurus, Chimaerasuchus* and highly predaceous notosuchians seems to be closely related to each other than to any other notosuchian; (vi) *Candidodon, Malawisuchus* and *Simosuchus* possibly constitute a different notosuchian lineage, which may include *Uruguaysuchus*; (v) there is an overall poor support for most clades within Notosuchia and Neosuchia, especially for basal branches within these groups.

DISCUSSION

The comparison between *Notosuchus, Mariliasuchus, Comahuesuchus* and *Candidodon* allowed the identification of morpho-anatomical similarities and discrepancies between these taxa. Neither the jugal foramen, nor the absence of contact between lachrymal and jugal are exclusive characteristics of *Mariliasuchus* and *Comahuesuchus*. There are further similarities regarding the dentition that are often ignored because of a lack of agreement on the morphology, either for *Notosuchus* and *Mariliasuchus*. The intermediate position occupied by the first postcaniniform is problematic, as it is difficult to recognize which element (the premaxilla or the maxilla) is actually related to the tooth. On the other hand, the fact that both the premaxilla and the maxilla take part on the first postcaniniform alveolus represents an important observation. Other aspects include the development of fenestrae. Though *Mariliasuchus* and *Comahuesuchus* do not have an antorbital fenestra, unlike *Notosuchus*, this condition is also present in other closely related forms (*Sphagesaurus huenei, Chimaerasuchus*?, baurusuchids). On the other hand, *Mariliasuchus* and *Notosuchus* are the only notosuchians that have maxillo-palatine fenestra, which show exactly the same morphology. The morpho-anatomical study shows that there is a lack of important information on *Comahuesuchus* and *Candidodon*, due to the incompleteness of the specimens, although critical information on *Candidodon* only awaits description. The morpho-anatomical study also confirmed the autapomorphic features of *Notosuchus*, *Mariliasuchus* and *Comahuesuchus* previously described by several authors (Woodward, 1896; Gasparini, 1971; Bonaparte, 1991; Carvalho & Bertini, 1999; Martinelli, 2003; Andrade, 2005; Zaher *et al.*, 2006).

Intra-specific variability still does not play an important role in phylogenetic analysis, because there is lack of data for most species. Even for *Notosuchus* and *Mariliasuchus*, there is only a limited amount of information that can be used. Both species show intra-specific variability regarding the parietal morphology, which may be linked to sexual dimorphism, but this depends on the proper study of larger numbers of specimens. At least for *Notosuchus*, the different types of parietal seem to occur in a bimodal distribution within the sample. However, it is currently impossible to evaluate the occurrence of sexual variability in other notosuchian taxa due to the small samples currently available. Ontogenetic variability may be more clearly identified in *Mariliasuchus*, but several important aspects need evaluation (*e.g.*, rotation of teeth, rostrum differentiation, development of ornamentation). As for the sexual dimorphism, the sample does not allow identification of ontogenetic variability in most other Mesoeucrocodylia.

Notosuchus and *Mariliasuchus* show a great degree of resemblance that led to the reevaluation of their phylogenetic relationships, confirming their proximity, as originally proposed by Carvalho & Bertini (1999). Therefore, *Mariliasuchus* should be understood as a Notosuchidae, rather than a Candidodontidae or a Comahuesuchidae. The comparative study and the phylogenetic analysis do not disprove Zaher *et al.* (2006), but in fact supports the recognition of similarities of *Comahuesuchus* and Notosuchidae. Most of all, results presented here show that the position of *Comahuesuchus* lacks stability, rather than the position of *Notosuchus*.

In overview, much still needs to be done to improve the understanding of crocodylomorph evolution. Several taxa still present a reasonable amount of missing data. As in the character list presented here (Appendix 2), the main part of data from most analysis focus on cranial characters (82.5%, in the case of the preliminary analysis). Even considering the current information on postcranial material, the amount of missing data is extensive. The relevance of postcranial remains for phylogenetic analysis has already been pointed out by Pol (1999, 2005). Even though postcranial remains are reported for several taxa, the material is still unpublished (*e.g.*, *Mariliasuchus, Baurusuchus, Uberabasuchus*). The extensive use of characters related to acquisition of food (rostrum, mandible, dentition) may be one of the factor introducing misleading information and leading to incongruent homoplastic datasets. The detailed revision of the character-states and recognition of specific conditions may help to reduce the number of homoplastic conditions throughout the analysis, increasing support and stability.

As a result of the highly homoplastic datasets and poor support and stability, the current bibliography provides a number of alternative hypothesis for the evolution of mesoeucrocodylians (*e.g.*, Benton & Clark, 1988; Clark, 1994; Wu & Sues, 1996; Gomani, 1997; Buckley *et al.*, 2000; Ortega *et al.*, 2000; Sereno *et al.*, 2001, 2003; Martinelli, 2003; Pol, 2003; Pol & Norell, 2004a, 2004b; Pol & Apesteguia, 2005; Andrade, 2005; Fiorelli, 2005; Turner & Calvo, 2005; Turner, 2006; Zaher *et al.*, 2006; Larsson & Sues, 2007; Laupraset *et al.*, 2007). Nevertheless, in a general overview, most aspects from the preliminary analysis presented here still reach some measure of agreement with other analysis. In particular, comparison was made to another dataset to falsify the results in respect to the phylogenetic position of *Mariliasuchus*.

Both analysis indicate that *Notosuchus* is closely related to *Mariliasuchus*. When potentially misleading data (due to character construction and coding) was excluded from the second analysis, no evidence of an exclusive relationship between *Mariliasuchus* and *Comahuesuchus* remained. When data on dentition and jugal were treated on the same manner in both analysis, results pointed to an exclusive monophyletic clade joining *Mariliasuchus* and *Notosuchus*, with a rather more basal position to *Comahuesuchus*. In similar conditions, both datasets performed in the same manner, indicating that interpretation of the morphology and construction of characters are the true determining agents on the position of these taxa. On the other hand, the inclusion of new cranial data from Nobre & Carvalho (2002) and changes to the character list did not influence the position of *Candidodon*. In fact, all analysis show that *Candidodon* seems to be associated with *Malawisuchus* (as originally proposed by Nobre & Carvalho, 2002), rather than to *Mariliasuchus*.

In overview, apart from the limited shifting behavior shown by some of the taxa, the structure is the same. *Notosuchus* and *Mariliasuchus* are closely related, and this group is related to highly predaceous notosuchians (*Baurusuchus*, *Bretesuchus*, *Iberosuchus*), as to the clade *Sphagesaurus*+ *Chimaerasuchus*. Other notosuchians, such as *Candidodon, Malawisuchus* and *Uruguaysuchus*, seem to be in a reasonably stable position, much more basal.

The preliminary analysis also rejected the sister-group relationship between *Anatosuchus* and *Comahuesuchus*, originally proposed by SERENO *et al.* (2003) and followed by TURNER & CALVO (2005) and TURNER (2006). Such relationship has been repeatedly repelled by other works (MARTINELLI, 2003; ANDRADE, 2005; ANDRADE *et al.*, 2006; ZAHER *et al.*, 2006), but the problem still deserves further clarification. Nevertheless, they seem to represent different patterns of skull construction and eventual rostral similarities are more likely to be convergences, rather than secondary homologies. These convergences can be explained by common aspects of their paleoecology (*e.g.*, composition of diet, foraging mode). The genus *Araripesuchus*, due to its shifting position in different analysis, may either be considered as a basal Neosuchia (according to the definitions by SERENO *et al.*, 2001), as previous analysis already suggested (*e.g.*, BUCKLEY *et al.*, 2000; ORTEGA *et al.*, 2000; POL, 2003; POL & APESTEGUIA, 2005; TURNER & CALVO, 2005; TURNER, 2006; LAUPRASERT *et al.*, 2007) or a basal Notosuchia (FIORELLI, 2005; FIORELLI & CALVO, 2005; ZAHER *et al.*, 2006). The future recognition of undisputable characters uniting *Araripesuchus* and notosuchians may contribute to the debate. A better approach could be the recognition of the genus as an independent lineage, which may either be related to Neosuchia (*sensu* BENTON & CLARK, 1988) or to Notosuchia (*sensu* GASPARINI, 1971). Here, the use of linnean nomenclature becomes more adequate than the "phylogenetic" definition, since in the last there is no clear content of these clades. Currently, the traditional linnean definition of Notosuchia may appear as paraphyletic due to inclusion of *Araripesuchus* and exclusion of *Baurusuchus* and related forms. The exclusion of taxa with unstable behavior (*Araripesuchus, Anatosuchus*) and inclusion of baurusuchids (and relater forms) will allow a wider and more straightforward use of the linnean definition of Notosuchia. On the other hand, this redefinition does mean that the *Araripesuchus* and the notosuchian lineages are not related, but only that *Araripesuchus* is not a Notosuchia. This definition would be in agreement with most published phylogenetic works (*e.g.*, BENTON & CLARK, 1988; CLARK, 1994; BUCKLEY *et al.*, 2000; ORTEGA *et al.*, 2000; POL, 2003; POL & APESTEGUIA, 2005; TURNER & CALVO, 2005; TURNER, 2006; ZAHER *et al.*, 2006; LAUPRASERT *et al.*, 2007).

Further problems remain to be solved also in the notosuchian branch. *Comahuesuchus* and *Simosuchus* seem to show a particularly important unstable behavior. Their shifts in the apical and the basal sections of the topologies may account for the low branch decay and bootstrap indexes present in the notosuchian branch of the preliminary analysis. Despite what has been done to describe these species, there is still much to be understood about them. *Comahuesuchus* would benefit from a greater number of more complete specimens, as well as information on teeth. On the other hand, fossil crocodylians long described (*Uruguaysuchus, Candidodon*) need an extensive reevaluation, which would certainly bring further details into the analysis, help to stabilize the position of the shifting taxa and eventually correct misled interpretations.

CONCLUSIONS

Notosuchus and *Mariliasuchus* are closely related notosuchians, sharing several similar characteristics (*e.g.*, teeth, premaxilla, maxillo-palatine fenestrae, choanae, quadrate fenestrae, retroarticular process). Similarities between dentition may indicate similar foraging behaviour, and variability in the parietal morphology may indicate sexual dimorphism in both taxa. *Notosuchus* and *Mariliasuchus* come from the Upper Cretaceous of South America, from units interpreted as semi-arid environments and areas not very distant from each other. The idea that either *Notosuchus* or *Mariliasuchus* may be related to the Lower Cretaceous *Candidodon* is unlikely, given the phylogenetic results obtained. Nevertheless, data presented and discussed here support that both *Notosuchus* and *Mariliasuchus* may show a close relationship with *Comahuesuchus*, which is also from the Upper Cretaceous of South America. In a broader view, *Comahuesuchus*, *Mariliasuchus* and *Notosuchus* certainly show to be more closely related to each other than to *Malawisuchus*, *Candidodon*, *Uruguaysuchus* or even with *Anatosuchus* and *Araripesuchus*. *Araripesuchus* and *Anatosuchus* may be better defined as independent lineages, although the position of *Anatosuchus* still needs further clarification.

They may either be related to Neosuchia (*sensu* Benton & Clark, 1988) or to Notosuchia (*sensu* Gasparini, 1971), but there is no need to consider them as part of these groups in a linnean definition.

In a broad view, there are still several disagreement points in the current phylogenetic hypothesis for evolutionary relationships of Mesoeucrocodylia. Most frameworks do not agree in many aspects, presenting an overall poor support. A few of these works may be affected by a biased sample of taxa and even by problems on the construction of characters. The overall structure of the group, as the internal structure of Notosuchia (*sensu* Sereno *et al.*, 2001) is yet to be refined. A more comprehensive idea on the evolution of notosuchians and mesoeucrocodylians will only be achieved with detailed comparative description of specimens, reduction of missing data currently in the analysis, evaluation of intraspecific variability in range and further discussion on character construction and recognition of independent states.

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APPENDIX 1

Specimens of *Notosuchus*, *Mariliasuchus* and other Notosuchia (*sensu* Gasparini, 1971) examined. Type specimens in bold. The number in parentheses is the original designation for MLP specimens of *Notosuchus*, given by A. Smith Woodward. *Notosuchus* lectotype elected by Gasparini (1971), from the original assemblage of specimens used in the original description (Woodward, 1896).

Araripesuchus patagonicus – MUCPv-267, MUCPv-268, MUCPv-268b, **MUCPv-269**, MUCPv-270.

Candidodon itapecuruense – UFRJ-DG-113-R, UFRJ-DG-114-R.

Comahuesuchus brachybuccalis – MACN-Pv-N-31, MOZ-P-6131, **MUCPv-202**.

Mariliasuchus amarali – MN 6298-V, MN 6756-V, **UFRJ-DG-50-R**, UFRJ-DG-105-R, UFRJ-DG-106-R, URC R•67, URC R•68, URC R•69, URC R•74 and URC R•75.

Notosuchus terrestris – MACN–Pv–N–22, MACN–Pv–N–23, MACN–Pv–N–24, MACN–Pv–N–43, MACN–Pv–N–107, MACN–Pv–RN–1015, MACN–Pv–RN–1037, MACN–Pv–RN–1038, MACN–Pv–RN–1039, MACN–Pv–RN–1040, MACN–Pv–RN–1041, MACN–Pv–RN–1043, MACN–Pv–RN–1044, MACN–Pv–RN–1045, MACN–Pv–RN–1046, MACN–Pv–RN–1047, MACN–Pv–RN–1048, MACN–Pv–RN–1118, MACN–Pv–RN–1119, MLP–64–IV–16–1, **MLP–64–IV–16–5(253)**, MLP–64–IV–16–6(203), MLP–64–IV–16–7(219), MLP–64–IV–16–8(209), MLP–64–IV–16–10(221), MLP–64–IV–16–11, MLP–64–IV–16–12, MLP–64–IV–16–13, MLP–64–IV–16–14, MLP–64–IV–16–15, MLP–64–IV–16–16, MLP–64–IV–16–17, MLP–64–IV–16–18, MLP–64–IV–16–20, MLP–64–IV–16–21, MLP–64–IV–16–22, MLP–64–IV–16–23, MLP–64–IV–16–24, MLP–64–IV–16–25, MLP–64–IV–16–28, MLP–64–IV–16–30, MLP–64–IV–16–31(206), MPCA–Pv–528; MPCA–Pv–789/1; MPCA–Pv–791.

Sphagesaurus huenei – **DGM-332-R**, DGM-333-R, DGM-1411-R, RCL-100.

APPENDIX 2

List of characters used in the phylogenetic analysis. Total number of characters 183, distributed as follows: 120 cranial (65.57%); 28 dental (15.3%); 32 postcranial (17.5%). Main anatomical element indicated in bolt, in the description of the character. Characters either new or obtained from previous works, designated by code and original number, presented in chronological order inside brackets. 'm' indicates characters modified from the original. Codes for bibliographic origin of characters as follows: A = Andrade, 2005; Buckley *et al.*, 2000; C = Clark, 1994; G = Gomani, 1997; M = Martinelli, 2003; O = Ortega *et al.*, 2000; Pa = Pol, 1999; Pb = Pol, 2003; S = Sereno *et al.*, 2003; W = Wu & Sues, 1996.

General (3 characters; 1.64% of total)

1.***Skull surface*** *[O01]*: **(0)** smooth or ornamented with an irregular pattern of ridges rugosities and anastomosing grooves; **(1)** ornamented with circular to polygonal pits, with eventual sulcation (not anastomosed).

2.***Skull height****, in posterior view [C03m; S06m; P03m; A02]*: **(0)** skull higher than wider or subequal; **(1)** skull larger than higher.

3.*Orientation of the* ***orbits*** *[A3]*: **(0)** lateral; **(1)** laterodorsal.

Rostrum (28 characters; 15.3% of total)

4.*Proportional length of the* ***rostrum*** *in lateral view [W4m]*: **(0)** short, orbits at the skull midlength; **(1)** long, orbits at the posterior half of the skull.

5.***Rostrum*** *height, anterior view [C03]*: **(0)** rostrum higher than wider; **(1)** rostrum subquadrate; **(2)** rostrum wider than higher.

6.***Rostrum****, in dorsal view [C02]*: **(0)** is narrow, abruptly widening to adjust the skull outline; **(1)** gradually fits the skull outline, with a general triangular shape.

7.*External* ***nares*** *[C06; S02m+07m; Pb06m]*: **(0)** terminal, opening anteriorly; **(1)** lateral or semi–lateral; **(2)** anterodorsal or dorsal.

8.***Internarial bar*** *[S7]*: **(0)** absent; **(1)** gracile, narrow; **(2)** present as a wide bar.

9.***Anterorbital region*** *[C68m; W16m; S03m]*: **(0)** smooth and flat; **(1)** vestigial or small antorbital fenestra; **(2)** well developed antorbital fenestra.

10.*Anteriormost portion of the* ***premaxilla****, at the region at the front and below the narial opening [C5; S9]*:

(0) narrower than the lateral part of the premaxilla; **(1)** high, subequal to the height of the lateral part of the premaxilla.

11.***Premaxilla–maxilla foramen*** *[Pa149; O13; Pb135]*: **(0)** absent; **(1)** present.

12.***Premaxilla–maxilla suture****, lateral view [A13m]*: **(0)** straight, vertical; **(1)** curved or composed by two planes (lower vertical, upper diagonal), with a posterodorsal process, flanking the nasals; **(2)** straight, diagonal.

13.*Inferior border of the* ***premaxilla–maxilla suture****, in lateral view [C09m]*: **(0)** without constriction or notch, region between premaxilla and maxilla flat, composing a straight border; **(1)** evident constriction, forming a notch.

14.***Premaxilla–maxilla suture****, in dorsal view [C09m; O14m; S10m; Pb09m]*: **(0)** without constriction, with flat surface; **(1)** evident constriction.

15.***Maxilla*** *[A16; Z192m]*: **(0)** does not contribute to the orbit; **(1)** contributes to the orbit.

16.***Maxilla****, proportional number of neurovascular foramina relative to the number of teeth [A17m]*: **(0)** small number of foramina, usually 1–2 for each tooth; **(1)** greater number of foramina, widely surpassing the number of teeth.

17.***Maxilla****, distance between neurovascular foramina and teeth [A17m]*: **(0)** small distance, foramina positioned close to teeth; **(1)** foramina clearly apart from teeth.

18.*Inferior margin of the* ***maxilla*** *[W29; M24]*: **(0)** not different than the remaining surface from maxilla; **(1)** smooth surface, mesially inclined.

19.*Inferior margin of the* ***maxilla****, in lateral view [C79m]*: **(0)** concave at the anteriormost region and convex at the posteriormost region; **(1)** straight; **(2)** convex at the anteriormost region and convex and straight at the posteriormost region; **(3)** concave at the anteriormost region, convex at the midlength and concave at the posteriormost region, “festooned”.

20.*Anterior border of the* ***nasals*** *[C13m]*: **(0)** short, at best with a small stiliform projection over the naris (eventually not in contact to the external naris due to isolation by the premaxillae); **(1)** moderately developed, projecting over the naris as a narrow lamina, without covering the naris; **(2)** well developed, completely covering the naris.

21.***Nasals****, general shape [A21]*: **(0)** triangular, posterior region wider than anterior region; **(1)** rectangular; **(2)** triangular, with the anteriormost region wider than the posterior region.

22.***Lachrymal*** *[C11; M05]*: **(0)** does not contact nasal, prevented by large contact among prefrontal–maxilla; **(1)** with small contact to nasal; **(2)** with large contact with nasal, preventing any contact among prefrontal–maxilla.

23.***Lachrymal*** *size [A23]*: **(0)** small; **(1)** well developed.

24.*Relative position of the anteriormost margin of the* ***prefrontal*** *[A25]*: **(0)** with anteriormost margin at the same relative position as the anteriormost margin of frontal; **(1)** anteriormost margin surpasses the anteriormost margin of frontal.

25.*Posterior margin of* ***prefrontal*** *[A26]*: **(0)** short, limited to anterodorsal border of the orbit; **(1)** elongated, composing the dorsal border of the orbit.

26.***Prefrontal pillars****, construction [C15m; S34m; Pb15m]*: **(0)** incomplete, without contact between the descending ramus of the prefrontal and palatine; **(1)** complete, with contact between the descending ramus of the prefrontal and palatine.

27.***Prefrontal pillars****, structure [C15m]*: **(0)** small contact area; **(1)** wide contact area.

28.***Frontal****, shape of anterior border [A28]*: **(0)** straight; **(1)** triangular to stiliform, projecting forward between nasals.

29.***Frontal*** *anterior border, suture [A29]*: **(0)** straight or with minor interdigitation; **(1)** strongly interdigitated.

30.***Interfrontal longitudinal ridge*** *[C22; A30]*: **(0)** absent; **(1)** present.

31.***Rostral transversal crest*** *[A31]*: **(0)** absent; **(1)** present.

32.***Frontal****, position of anterior border [A32]*: **(0)** between orbits; **(1)** at the same position that the anteriormost orbital border, in dorsal aspect; **(2)** positioned ahead of the orbits, in dorsal aspect.

Skull table (8 characters; 4.37% of total)

33.***Frontal*** *posterior border [C23; S20; M08]*: **(0)** short, with limited contact with the postorbital; **(1)** well developed, fairly contacting the postorbital and contributing to the supratemporal fenestra.

34.***Parietal*** *surface [C22m; M09m; S26m]*: **(0)** flat and wide; **(1)** flat, but narrow due to the development of the supratemporal fenestra; **(2)** sagittal crest.

35.*Anterolateral process of* ***postorbital*** *[C28; S24]*: **(0)** absent; **(1)** present.

36.***Supratemporal fenestra****, shape [A36m]*: **(0)** circular to subcircular; **(1)** elliptical, main axis clearly identifiable.

37.*External border of the* ***supratemporal fenestra****, orientation of the main axis in dorsal view [A37m]*: **(0)** diagonal, projection of the main axes converge posteriorly; **(1)** parallel, projection of the axes do not meet; **(2)** diagonal, projection of the main axes converge anteriorly.

38.*Proportional size of the* ***supratemporal fenestra*** *(main axis of the internal border) [C68m; S04m]*: **(0)** smaller than the diameter of the orbit; **(1)** subequal or bigger than the diameter of the orbit.

39.*Relation among the internal and external borders of the* ***supratemporal fenestra*** *[A39]:* **(0)** without significant difference; **(1)** external border slightly larger; **(2)** external border much larger.

40.*Area posterior to the* ***supratemporal fenestra****, where lies the parietal–squamosal suture [A40]*: **(0)** ample and flat horizontal surface; **(1)** surface extremely narrow and high, forming a crest transversal to the skull.

41.*Ventrolateral ramus of* ***squamosal****, in dorsal view [A41]*: **(0)** only slightly developed, suture with the quadrate covered by the superior lateral (temporal) ramus of the squamosal in dorsal view; **(1)** well developed, suture with the quadrate exposed in dorsal view.

TEMPORAL REGION (26 CHARACTERS; 14.2% OF TOTAL)

42.***Jugal*** *anterior ramus, shape in lateral view [S16m; M07m]*: **(0)** narrow throughout, widening directly at the contact with the maxilla; **(1)** gradually widening anteriorly; **(2)** sudden widening from the base of the ramus, “leaf–shaped”.

43.***Jugal*** *anterior ramus, external surface [A43; Z193]*: **(0)** well developed single neurovascular foramen, directed anteriorly to anterolateraly; **(1)** even surface, either flat or ornamented, without any kind or number of foramina; **(2)** two or more foramina, all small, facing ventrally.

44.***Jugal*** *anterior ramus, length [Pa134; Pb122; M29]*: **(0)** short, anteriormost margin does not reach the anterior margin of the orbit in lateral view; **(1)** long, either reaching or surpassing the anterior margin of the orbit in lateral view.

45.***Jugal*** *anterior ramus, relative position in lateral view [A45]*: **(0)** horizontal; **(1)** inclined diagonally, anterior border ventral to the base of the ramus.

46.*Jugal anterior ramus, occurrence of an external lateral crest [Pa133m; O145m; Pb121m]*: **(0)** absent; **(1)** present.

47.***Jugal*** *anterior ramus, cross–section [C18m]*: **(0)** circular to subcircular; **(1)** elliptical, with evident lateral compression.

48.***Jugal*** *posterior ramus [new]:* **(0)** straight; **(1)** dorsally arched.

49.***Postorbital bar****, relation to dermis [C25m]*: **(0)** subdermic, distinct, originating mesially from the jugal ramus; **(1)** dermic, gradually narrowing.

50.***Postorbital bar*** *[new]*: **(0)** straight; **(1)** posteroventrally bended at midlength.

51.***Postorbital bar****, constitution from ectopterygoid [C26m; S22]*: **(0)** does not receive contribution from ectopterygoid; **(1)** receive contribution from ectopterygoid.

52.***Postorbital bar****, ectopterygoid–postorbital contact [C26m; Pa158; O36; Pb144]*: **(0)** absent; **(1)** present.

53.***Postorbital bar****, general structure [C25m]*: **(0)** gracile; **(1)** robust.

54.***Postorbital bar****, inclination in lateral view [A54]*: **(0)** vertical; **(1)** diagonally inclined, distal end fairly anterior to the proximal end.

55.***Postorbital bar****, dorsal end next to the postorbital body [C30; S25]*: **(0)** bar gradually expanding towards the main body of the postorbital, without a well defined limit; **(1)** constriction delimiting the distinction between the postorbital bar and the postorbital body.

56.***Postorbital bar****, occurrence of vascular foramen on the lateral edge of the postorbital margin [C27; S23; T27]*: **(0)** absent; **(1)** present.

57.***Postorbital bar****, cross–section [C26; S21]*: **(0)** subcircular; **(1)** elliptical, with lateral compression.

58.***Postorbital bar****, implantation of the proximal end to the postorbital body [A58]*: **(0)** postorbital bar next to the laterodorsal border of the postorbital body; **(1)** postorbital bar next to the ventral portion of the postorbital body.

59.***Laterotemporal fenestrae*** *[O46]*: **(0)** facing laterally; **(1)** facing laterodorsally.

60.***Quadratojugal*** *mesial border, ornamentation of the posterodorsal margin of the laterotemporal fenestra) [S18m]*: **(0)** absent; **(1)** present, either ornamented with a discrete crest or a well defined spine (*Spina quadratojugalis*).

61.***Quadratojugal*** *anterodorsal ramus, development [C19m; S19m]*: **(0)** narrow and gracile; **(1)** wide and robust.

62.***Quadratojugal*** *anterodorsal ramus, contribution to postorbital bar [C19m; S19m]*: **(0)** does not contribute to postorbital bar; **(1)** contribute to postorbital bar.

63.***Quadratojugal*** *anterodorsal ramus, contact with postorbital bone [C19m; S19m]*: **(0)** contact posterior region of postorbital body; **(1)** contact anterior region of postorbital body.

64.***Quadratojugal****, contact with jugal [O39]*: **(0)** suture between jugal and quadratojugal lies next to the posterior vertex of the laterotemporal fenestra; **(1)** suture between jugal and quadratojugal lies below the laterotemporal fenestra, due to the development of a small process from the quadratojugal.

65.***Quadrate fenestrae*** *[C45m; S35m]*: **(0)** with no more than one fenestra; **(1)** with at least two well defined fenestrae.

66.***Quadrate****, surface [O154]*: **(0)** surface flat and even; **(1)** presenting one depression with triangular shape.

67.*Relative position of the* ***quadrate condyle****, in lateral/posterior views [W24m; S46m; Pb104]*: **(0)** at the same height than the occipital condyle, clearly above the teeth row; **(1)** below the occipital condyle, approximately at the same height of the teeth row; **(2)** clearly below the teeth row and the occipital condyle.

68.***Quadrate****, medial articulation facet of the condyle [O53]*: **(0)** small, with the same dimensions than the lateral articular facet; **(1)** large, bigger than the lateral articular facet, projecting ventrally.

Basicranium (10 characters; 5.47% of total)

69.***Basisphenoid****, at the ventral portion of the skull [C56; S36; T56m]*: **(0)** exposed ventrally; **(1)** almost completely covered by the pterygoids and basioccipital.

70.***Basioccipital–quadrate contact*** *[new]*: **(0)** small or absent; **(1)** well developed, excluding the basisphenoid from the exoccipital and this last element from the ventral surface of the quadrate.

71.***Basioccipital*** *and* ***occipital condyle*** *[G32m; O176m; Pb112m]*: **(0)** facing posteriorly; **(1)** facing posteroventrally.

72.*Contact between* ***quadrate, squamosal*** *and* ***exoccipitals*** *[C49m; T49m; M14m]*: **(0)** without significant contact; **(1)** with well developed contact, lateral to cranioquadrate passage.

73.***Occipital surface****, in dorsal view [new]*: **(0)** overall flat; **(1)** “U–shaped”, concave but flat in the area posterior to the skull table; **(2)** “V–shaped”, exoccipitals posteromedially oriented from near the medial line.

74.***Exoccipital*** *surface, above the occipital crest [new]*: **(0)** faces posteriorly; **(1)** faces posterodorsally.

75.*Insertion area for the m. depressor mandibulae, at the surface of* ***occipital*** *[A72]*: **(0)** slightly developed surface, narrow and low, smaller than the muscle attachment area of the exoccipitals; **(1)** well developed surface, with muscle attachment area similar to the surface of the exoccipitals.

76.*Lateral* ***occipital*** *surface of the squamosal [A73]*: **(0)** flat or slightly bended posteriorly; **(1)** strongly bended posteriorly, so the border is positioned posteriorly to the occipital condyle.

77.*External surface of the occipital portion of the* ***squamosal****, inclination [A74]*: **(0)** faces posteriorly; **(1)** faces posterodorsally.

78.*Occipital surface of* ***supraoccipital****, inclination [A75]*: **(0)** faces posteriorly; **(1)** faces posterodorsally.

79.*Occipital surface of* ***supraoccipital****, in dorsal view [A76]*: **(0)** surface either flat and even or concave; **(1)** in “V”, projecting posteriorly forming a vertically oriented medial ridge, or even a crest.

Palate and perichoanal elements (23 characters; 12.57% of total)

80.***Naso–oral fenestra*** *(=incisive foramen) [C07; O11–12m; S29; Pb07]*: **(0)** absent; **(1)** present, limited by the premaxilla; **(2)** present, limited by both the maxilla and premaxilla.

81.*Development of the palatine rami of the* ***maxilla*** *[C10m; S33m; Pb10m]*: **(0)** rami slightly developed; **(1)** rami well developed.

82.*Contact between palatine rami of the* ***maxilla*** *[C10m; S33m; Pb10m]*: **(0)** rami do not contact each other at the palate surface; **(1)** rami contact each other at the palate surface, eventually separated by vomer–palatine or vomer–pterygoids, but always forming a bony palate, separating nasal and oral cavities.

83.***Palatines*** *[C37; T37]*: **(0)** do not contact each other and do not contribute to a secondary palate; **(1)** contact each other, as part of the secondary palate.

84.*Bony surface of the* ***secondary palate*** *[O175; M47]*: **(0)** flat and even, or slightly convex; **(1)** concave.

85.***Maxillo–palatine fenestrae*** *[A82]*: **(0)** absent; **(1)** present.

86.***Suborbital fenestrae****, shape of anterior border [new]*: **(0)** rounded, smooth; **(1)** in sharp angle, forming a notch, fenestrae with the shape of a wide fissure.

87.***Suborbital fenestrae***, *composition of lateral border [O61m]*: **(0)** jugal takes part of the lateral border; **(1)** both ectopterygoid and maxilla compose the lateral border, excluding the jugal.
88.***Suborbital fenestrae***, *composition of anteromedial border [new]*: **(0)** composed exclusively by the palatines; **(1)** palatine ramus of the maxilla contributes to the anteromedial border, by means of a narrow and elongated process, directed posteriorly.
89.***Suborbital fenestrae***, *composition of posterior border [M35]*: **(0)** pterygoid takes part of the posterior border; **(1)** posterior border composed exclusively by the palatine and ectopterygoid, with pterygoid excluded by palatine–ectopterygoid contact.
90.***Palatine*** *anterior border [Z129]*: **(0)** do not exceed the anterior borders of the suborbital fenestrae; **(1)** clearly exceed the anterior border of the suborbital fenestra, directed anteriorly.
91.***Internal nares***, *shape, in palatal view [A87; Z195m]*: **(0)** anterior border usually straight or slightly arched, posterior border bended, with the overall shape of a reversed triangle; **(1)** slightly elongated, from rectangular or elliptical/ subcircular; **(2)** anterior border "V–shaped" due to the presence of posterolateral palatine processes (=palatine bar), posterior border straight or slightly bended, with the overall shape of a triangle.
92.***Internal nares***, *perichoanal crest delimiting at least the posterior border of the choanae [A88]*: **(0)** absent, borders smooth; **(1)** present.
93.***Internal naris*** *in adult specimens, orientation [A89m]*: **(0)** facing ventrally; **(1)** facing posteroventrally.
94.***Pterygoid*** *ventral rami, size [A90]*: **(0)** small; **(1)** well developed.
95.***Pterygoid*** *ventral rami, inclination [A91]*: **(0)** slightly inclined, posteroventrally oriented; **(1)** well inclined, ventrally oriented.
96.***Pterygoid*** *ventral rami, structure [A91]*: **(0)** gracile, with a laminar profile; **(1)** robust, thick.
97.*Fusion of the caudal portion of* ***pterygoids*** *[C41; O58; M12]*: **(0)** absent; **(1)** present.
98.***Ectopterygoid*** *medial process of the posterior ramus [A93; Z196m]*: **(0)** absent or incipient, ectopterygoid excluded from the internal naris by pterygoid–palatine contact; **(1)** present and well developed, contributing to the anterolateral border of the internal naris.
99.***Internal naris*** *anterior border [C44m; W59; S30m]*: **(0)** formed by either maxilla or palatines, in an anteriormost position, anterior to the suborbital fenestrae; **(1)** formed by palatines, text to the posterior margins of the suborbital fenestrae; **(2)** formed by pterygoids, positioned far posteriorly to the suborbital fenestra.
100.***Internal naris*** *posterior border [C44m; W59m; S30m]*: **(0)** maxillae or palatines; **(1)** pterygoids.
101.***Internal naris***, *length (compared to the length of suborbital fenestrae) [C42m; S31m]*: **(0)** clearly smaller than the suborbital fenestrae; **(1)** subequal in length.
102.***Interchoanal septum*** *[C69m; S32m; Pb69m]*: **(0)** absent; **(1)** present, laminar; **(2)** present, robust.
103.***Parachoanal fossae*** *[new]*: **(0)** absent; **(1)** present.

MANDIBLE (16 CHARACTERS; 8.75% OF TOTAL)

104.***Mandibular symphysis***, *length [O151m]*: **(0)** short, limited to the anteriormost portion of the rostrum, do not extend posteriorly further than the maxilla–premaxilla suture; **(1)** long, extending posteriorly beyond the maxilla–premaxilla suture, to a position below the 2nd–4th maxillary teeth.
105.***Mandibular symphysis***, *structure [W17; S44]*: **(0)** shallow, spatulated anteriorly; **(1)** deep.
106.***Mandibulary symphysis***, *contribution of splenials [C77; Pb77]*: **(0)** do not take part of the symphysis or at least do not take part with ventral exposure; **(1)** clearly take part of the symphysis, with ventral exposure.
107.*Disposition of* ***mandibulary rami***, *ant the anterior and middle sections [Pb155m]*: **(0)** mandibulary rami very close to each other, parallel; **(1)** mandibulary rami confluent, with a "V" or "Y" shape; **(2)** mandibulary rami parallel, but distant to each other, with the shape of a "U", forming an arch.
108.***Dentary***, *lateral aspect [A107]*: **(0)** anterior potion as deep as the posterior one; **(1)** dentary ramus gradually expand posteriorly, the posterior region been deeper than the anterior region; **(2)** dentary ramus suddenly expand posteriorly, the posterior region been deeper than the anterior region.
109.*Lateral surface of* ***dentary***, *at midsection [O81; M42]*: **(0)** flat, with lateral compression, with high lateral margin; **(1)** without lateral compression, lateroventral surface convex.
110.***Dentary*** *alveolar margin [W29m; M24m]*: **(0)** undifferentiated from the remaining dentary surface; **(1)** region flat and smooth, inclined mesially.
111.*Shape of the* ***dentary*** *alveolar margin, in lateral view [O84; S38]*: **(0)** straight or with a single elevation (if bearing an hypertrophied caniniform); **(1)** sinusoidal, undulated, with at least two concave regions and two tooth bearing elevations alternating to each other.
112.*Shape of anteromedial margin of* ***surangular*** *[C74; S41; Pb74]*: **(0)** straight, coronoid process absent;

(1) dorsally arched (coronoid process).

113.***Surangular*** *anterior border [new]:* **(0)** single or lightly furcated, directed to the lateral surface of the mandible; **(1)** clearly furcated and divergent, the medial ramus directed toward the splenial and the lateral ramus directed toward the dentary.

114.***Angular****, height of anterior ramus, in lateral view [C70; W18]*: **(0)** narrow; **(1)** high, excluding completely the posteroventral ramus of the dentary from the internal border of the maxillary fenestra.

115.***Angular****, length of the anterior ramus [A114]*: **(0)** short, not surpassing the anterior border of the mandibular fenestra; **(1)** moderately elongated, slightly surpassing the mandibular fenestra; **(2)** very long, reaching far beyond the fenestra.

116.***Prearticular*** *[C72; S39]*: **(0)** absent; **(1)** present.

117.*General proportions of* ***glenoid fossa*** *[W23m; M22m; S45; Pb103]*: **(0)** wider than longer or subequal; **(1)** longer than wider.

118.*Posterior border of the* ***glenoid fossa*** *[W23m]:* **(0)** posterior border even with the glenoid surface or, at best, incipient; **(1)** with a well developed posterior border, limiting anteroposterior movements from the mandible.

119.***Retroarticular process*** *[S47m]*: **(0)** posterodorsally oriented; **(1)** slightly developed or directed posteriorly; **(2)** posteroventrally oriented.

120.***Angular****, extension of the insertion area for m. pterigoideus posterior at the medial surface [C76; S42; P76]*: **(0)** absent; **(1)** present.

Dentition (28 characters; 15.3% of total)

121.***Teeth apex****, shape [A142]*: **(0)** apex usually rhomboid; **(1)** apex usually acute.

122.***Teeth apex****, inclination [A143]*: **(0)** without inclination or lingually inclined; **(1)** inclined posteriorly or posterolingually.

123.*Maxillary/dentary* ***posterior teeth****, surface [A126m]*: **(0)** smooth; **(1)** well striated by a great number of almost microscopic anastomosed ridges, with a general pattern from base to apex (but not exclusively); **(2)** macroscopic striation (base–apex), composed by gracile narrow ridges; **(3)** small number of robust ridges (base–apex), large and wide, similar to carinae, usually over the entire surface of the each crown.

124.*Total number of* ***premaxillary teeth*** *[W27m; O133m; Pb105m]*: **(0)** one; **(1)** two; **(2)** three; **(3)** at least four.

125.***Hypertrophied caniniform*** *at the premaxilla [A119]:* **(0)** present, without anterior teeth; **(1)** present, preceded by one tooth; **(2)** present, preceded by two teeth; **(3)** present, preceded by 3 teeth; **(4)** absent.

126.***Premaxillary* tooth** *posterior to the premaxillary hypertrophied caniniform [A120]:* **(0)** absent; **(1)** present.

127.*Distribution of* ***premaxillary teeth*** *[S74m]*: **(0)** over the whole alveolar surface of premaxilla; **(1)** edentulous region between premaxillary teeth, composing a medial diastema at the anteriormost region of the jaws.

128.*Premaxillary posteroventral extensions embracing partially or completely the base of the crown of the* ***first maxillary tooth*** *[new]:* **(0)** absent; **(1)** present.

129.*Total number of* ***maxillary teeth*** *[W30m; O164m; S51m; Pb107m]*: **(0)** no more than seven teeth; **(1)** no less than 10 teeth.

130.***Anterior maxillary dentition*** *[A124]:* **(0)** all maxillary teeth caniniform (subisometric and isomorphic); **(1)** hypertrophied caniniform preceded by 3–4 smaller teeth and followed by smaller caniniform teeth; **(2)** hypertrophied caniniform preceded by 1–2 smaller caniniform teeth and followed by smaller caniniform teeth; **(3)** hypertrophied caniniform, preceded by 1–2 smaller caniniform teeth and followed by smaller molariform teeth; **(4)** slightly enlarged molariform, preceded by 1–2 molariform–caniniform teeth and followed by molariforms; **(5)** all maxillary teeth molariform (subisometric and isomorphic).

131.*Area occupied by the* ***maxillary teeth****, in palatal view [A125]*: **(0)** proportionally small teeth, occupying only a marginal portion of the ventral surface of the maxilla; **(1)** proportionally well developed teeth, occupying large area the maxillary ventral surface (at least one third of the surface available).

132.*Mesial and distal surfaces of* ***maxillary teeth*** *[B104m; S53m]:* **(0)** heterogeneous carina, composed by anisomorphic tubercle–like denticles, developed preferentially at the posterior border; **(1)** either a smooth surface or a homogenous carina (crenulations may appear s a result of superficial ornamentation), extending over most of the anterior and posterior tooth surfaces; **(2)** homogenous carina, serrated with true denticulation (ziphodont dentition), extending over most of the anterior and posterior tooth surfaces.

133.*Implantation of* ***maxillary teeth*** *[P137]*: **(0)** not oblique; **(1)** oblique.

134.*Dental implantation at the* ***maxilla*** *(anterior and middle teeth) [O19m; M38m]*: **(0)** teeth set disposed in a groove, the roots originally isolated from each other only by soft tissue; **(1)** teeth set in isolated alveoli.

135.*Transverse section of posterior* ***maxillary teeth*** *[B116m; O104m; S52m; Pb140m]*: **(0)** strong lateral compression; **(1)** transverse section circular to subcircular, without significant lateral compression; **(2)**

transverse section 'teardrop–like' (=triangular), with asymmetric lateral compression occurring on the distal margin.

136.*Relative position of the* ***last maxillary tooth*** *[O18m; M37]*: **(0)** last tooth in anterior to the anteriormost border of the suborbital fenestra; **(1)** last tooth positioned posteriorly to the anteriormost border of the suborbital fenestra.

137.*Implantation of* ***posterior teeth at maxilla and dentary*** *[O18m; M38–39m]*: **(0)** teeth set disposed in a groove, the roots originally isolated from each other only by soft tissue; **(1)** teeth set in isolated alveoli.

138.*Occurrence of abrasion surfaces in* ***dentary and maxillary teeth*** *[A132]:* **(0)** teeth without abrasion surfaces due to masticatory action; **(1)** anteroposterior wear surface, indicating capacity for proal/propalinal movements of the mandible; **(2)** diagonal wear surface, indicating capacity for lateral movements of the mandible.

139.*Number of* ***dentary teeth*** *[A133]:* **(0)** no more than 10; **(1)** at least 11.

140.*Orientation of the* ***anterior dentary teeth*** *[A134]:* **(0)** vertical or subvertical; **(1)** mildly procumbent, anteriorly inclined; **(2)** strongly procumbent, anteriorly inclined, the first pair of teeth almost horizontal.

141.***Dentary symphyseal teeth battery*** *[new]:* **(0)** absent; **(1)** present, teeth from each pair closer to each other than to other teeth in the same hemimandible.

142.*Length of the* ***dentary teeth*** *occluding at the maxillary/premaxillary contact [C80; S54]*: **(0)** small to medium sized, subequal to other surrounding teeth; **(1)** hypertrophied, at least twice longer than surrounding teeth.

143.***Middle and posterior dentary teeth*** *(posterior to the maxillary/premaxillary suture) [C81m; O20m; S55m; Pb81m]*: **(0)** gradually bigger and than smaller, the same trait occurring with the occluding teeth at maxilla; **(1)** diminishing posteriorly; **(2)** gradually bigger and than smaller, the opposite occurring with the occluding teeth at maxilla.

144.*Implantation of the* ***middle and posterior dentary teeth*** *[new]*: **(0)** not oblique or slightly altered; **(1)** oblique (more than 30 degrees).

145.*Implantation of* ***middle dentary teeth*** *[O18m; M39m]*: **(0)** teeth set disposed in a groove, the roots originally isolated from each other only by soft tissue; **(1)** teeth set in isolated alveoli.

146.*Transverse section of* ***middle and posterior dentary teeth*** *[B116m; O104m; S52m; Pb140m]*: **(0)** strong lateral compression; **(1)** transverse section circular to subcircular, without significant lateral compression; **(2)** transverse section 'teardrop–like' (=triangular) to lozenge shaped, with asymmetric lateral compression occurring mostly on the anterior margin.

147.*Constriction at the crown–root transition, in* ***posterior maxillary and middle/posterior dentary teeth*** *[B117; S50; Pb157m]*: **(0)** absent; **(1)** present.

148.*Number of cusps of* ***posterior teeth*** *[G46m; B113m; Pb162m]:* **(0)** single apical cusp; **(1)** multicusped teeth, with two or more cusps.

149.*Lingual cingulus at the base of the crown of the* ***middle and posterior teeth*** *[A145]:* **(0)** absent; **(1)** present, with accessory cusps and styli.

Axial elements (16 characters; 8.75% of total)

150.***Cervical vertebrae*** *[C92; S57; P92]*: **(0)** amphiplatyc or amphicoelic; **(1)** procoelic.

151.***Axis*** *centrum, length [A147]:* **(0)** centrum short, as long as high; **(1)** centrum clearly longer than higher.

152.***Axis****, neural spine laminae [Pb152m]*: **(0)** slightly developed, limited to the posterior half of the neural arch; **(1)** well developed over the whole extension of the neural arch due to the presence of prespinal and postspinal laminae, extending both anteriorly and posteriorly to the neural channel.

153.***Anterior cervical vertebrae****, neural spine laminae [C90m; Pb90m]*: **(0)** prespinal and postspinal laminae present; **(1)** laminae absent, neural spine rod–shaped.

154.***Anterior cervical vertebrae****, structure of neural spine [A151]*: **(0)** base narrow, gracile; **(1)** base short, wide, robust.

155.***Third cervical vertebrae*** *(CIII), development of prezygapophysis [A152]:* **(0)** slightly developed, projecting slightly anterior to the centrum; **(1)** well developed, clearly projecting anterior to the centrum.

156.***Posterior cervical vertebrae****, neural spine laminae [C90m; Pb90m]*: **(0)** prespinal and postspinal laminae present; **(1)** laminae absent, neural spine rod–shaped.

157.***Posterior cervical vertebrae****, structure of the neural spine [A153]*: **(0)** base narrow, gracile; **(1)** base short, wide, robust.

158.***Posterior cervical vertebrae****, development of the hypapophysis [Pb91m; W37m]*: **(0)** absent or slightly developed, no more than a sagittal ridge in the anterior portion of the centrum ventral surface; **(1)** present, well developed, laminar shaft projecting ventrally from the centrum anteroventral surface.

159.***Dorsal vertebrae**, development of the hypapophysis [A155]*: **(0)** absent or slightly developed, no more than a sagittal ridge in the anterior portion of the centrum ventral surface; **(1)** present, well developed, laminar shaft projecting ventrally from the centrum anteroventral surface.
160.***Dorsal vertebrae** [C93; S58; Pb93]*: **(0)** amphiplatyc or amphicoelic; **(1)** procoelic.
161.***Caudal vertebrae** [C94m; Pb94m]*: **(0)** amphiplatyc or amphicoelic; **(1)** procoelic, the first vertebra eventually biconvex.
162.*Paramedian dorsal **osteoderms** (trunk) [C95; S61; Pb95]*: **(0)** wider than longer, rectangular; **(1)** as long as wide, with variable shape (square to subcircular); **(2)** longer than wider, elliptical.
163.*Anterolateral process developed at the anterior border of dorsal **osteoderms** [C96; S62; Pb96]*: **(0)** absent; **(1)** present.
164.*Number of **osteoderm** dorsal rows (trunk) [C97; S63; Pb97m]*: **(0)** two paramedial rows; **(1)** four rows, two paramedial and two accessory.
165.*Accessory **osteoderms** (trunk) [Pb97m]*: **(0)** absent; **(1)** present.
166.*Ventral **osteoderms** (trunk) [C100; S66; Pb100]*: **(0)** absent; **(1)** present.

APPENDICULAR ELEMENTS (16 CHARACTERS; 8.75% OF TOTAL)
167.*Anterior surface of **scapula** [C82; O120m; Pb82]*: **(0)** curved; **(1)** straight.
168.*Coracoid length, proportional to the **scapula** [C83m; S59m; Pb83]*: **(0)** much smaller, no more than half the length of the **scapula**; **(1)** smaller, approximately 60–75% of the length of the scapula; **(2)** subequal.
169.*Glenoid surface of **coracoid** extended on an oblique plane and the glenoid tip facing outwards and posteroventrally [O122m]*: **(0)** absent; **(1)** present.
170.*Styliform process of **coracoid** [O118]*: **(0)** absent; **(1)** present.
171.*Proximal head of **humerus** [O123]*: **(0)** facing backwards, posterodorsally; **(1)** facing dorsally, with a lateromedial major axis.
172.*Internal tuberosity at the proximal articulation of the **humerus** [O124]*: **(0)** slightly developed, with the articular surface dorsally oriented; **(1)** well developed, with articular facet ventral or oblique.
173.*Ligamentary depression at the surface of **humerus** [O125]*: **(0)** lateral to the internal tuberosity and below the proximal articulation of the humerus; **(1)** located laterally to the articulation of the proximal end of humerus.
174.***Humerus**, lateral aspect of the deltapectoral crest [O126]*: **(0)** convex; **(1)** concave.
175.***Ulna**, lateral compression [O168]*: **(0)** absent; **(1)** present at least at the distal end.
176.***Radial** [O127]*: **(0)** longer than wider; **(1)** length subequal to width.
177.***Radiale**, proximal end [Pb117]*: **(0)** symmetric, similar to distal articulation; **(1)** asymmetric, mesial exposure more representative than lateral.
178.***Ilium**, proportional length between the preacetabular and postacetabular processes [C84; S60; Pb84]*: **(0)** subequal; **(1)** postacetabular process clearly longer (approximately four times longer).
179.***Ilium**, orientation of the postacetabular process [W41; Pb110]*: **(0)** posteriorly or posteroventrally directed; **(1)** posterodorsally directed, positioned well above the preacetabular process.
180.***Ilium**, presence of the supracetabular crest [Pb116]*: **(0)** absent; **(1)** present.
181.***Femur** torsion [O149]*: **(0)** femur with light torsion, the difference in the orientation between the proximal and distal articulation facets approximately equals to 30 degrees; **(1)** femur with evident torsion, the difference in the orientation between the proximal and distal articulation facets approximately equals to 60 degrees.
182.***Femur**, position of the 4th trochanter [A178]*: **(0)** anteromedial; **(1)** posteromedial.
183.***Tibia**, proximal end [O87]*: **(0)** single concavity; **(1)** medial crest separating two concavities.

APPENDIX 3

Matrix used in the analysis. 20 terminals included, presented in alphabetical order, after the outgroups. 183 characters for each taxon. Characters grouped, with periods (‘.’) indicating clusters of 10; each line with 50 characters; periods not originally included in the matrix. Coding varies between 0–5; ‘?’ = missing entries; ‘–‘ = inapplicable characters; ‘{ }’ indicating variable condition of a character within the terminal.

Outgroup 1 – Sphenosuchia
0001101220.0101010020.021110?100.0212010101.0011000010.
0000001000.0000111000.1021111100.000??0000-.?0000?0000.
?00?100100.00?001011?.11?24?0012.1101011010.0010100000.
1100100000.?210000001.0100001000.001

Outgroup 2 – Protosuchia
0000101220.1?100??001.{01}{12}1110?000.01{01}201{01}001.0010000010.
0010001000.1?{01}0111000.1021110002.000100000-.?000010000.
?00?100100.00?0010110.????4??010.11010{01}1010.0110100000.
??00?00000.?010010001.0100001000.001

Alligatoridae
1111212{01}01.0210010030.1211111{01}{01}0.12000??010.1221101101.
1101110011.0011000010.0100000001.1110001101.0101101021.
0100101110.1000200101.10{12}3310011.0101110011.01?011{01}001.
1100111111.11011{01}1210.1011110110.110

Anatosuchus
0101210020.01000??002.0111110000.0000010010.0111101?0?.
0001????1?.001?001000.1?00?1001?.111000?001.10000?1011.
1100012100.00?110011?.10?34?1012.0101?110?0.00?01??00?.
??????????.??????????.??????????.???

Araripesuchus gomesii
1100111120.1101010031.1211111010.0210110010.0111101000.
1?01100110.0011001000.1100?1000?.1110001001.1000001011.
1101111110.00?1201011.11024?0012.010111?010.00?0110000.
?1????100.0010000200.01?01??1??.10?

Araripesuchus patagonicus
1100211120.1?01010021.12101??110.0210110010.0111101000.
??01100110.0011001000.1100100001.1110001001.1000001011.
0101?11110.00?1101011.11034?0012.010111?010.00?0110000.
?????????0.?0100?0??0.01001????1.1??

Baurusuchidae
0001002101.1?1101002?.?1111?1101.0101112111.0111{01}1100?.
0011100110.1101002100.1121111102.1110001?10.2011111111.
1111011001.01?1101121.1103210002.0201101000.0120110000.
?????????0.01?00??2?0.????11????.???

Bernissartia
1111212001.0211?10030.1??1111??0.0?0000?010.12?1101?0?.
11011100?1.0011???10.0100????1.1110001??1.??01101?21.
0100111110.10??00100.0013310011.0101?1?01?.0?201?0000.
??00?11110.1001110?10.1011???1??.11?

Candidodon
0000110010.1010001112.?00?????0.0010010010.011?00100?.
??0110?110.??0?00??0?.1?11?1??10.111?0110??.10000?1011.
1101??1???.0?????????.000321?003.0101011???.??????101?.
?????????0.?1????????.????1?????.???

Chimaerasuchus
0??0100010.0111001101.0011??????.??????????.?????1????.
??????????.??????????.?????????2.01?1??????.??????????.
???100??0?.???1?010{12}1.1101100005.11011?110?.??1011?100.
0011?1110?.??0????10?.??????1101.???

Comahuesuchus
0010210000.0110?01122.01010??100.00?1?1?021.0100111?1?.
0001??????.??????2?00.112111110?.1110001110.201??1?011.
1??1112101.01?1??????.010?4??002.01?100?011.001?0??00?.
??????????.??????????.??????????.???

Crocodylidae
1111212{01}01.0211010030.?211111100.020000?010.1221101{01}01.
1101110011.0010000010.0100000001.1110001101.0101101021.
0100101110.1000200101.10{12}3310011.0101110011.0120110001.
1100111111.1101101210.1011110110.110

Malawisuchus
0000110110.0110101112.?210110000.02?0110010.00101000?0.
??0110?110.00010?2?00.101111?0??.111101100?.10000?1011.
0001011101.00?1001021.1{01}03210003.01010011?0.??10101110.
??11?11100.020??10???.????1?????.00?

Mariliasuchus
0100110000.0200101122.0?01010101.0111100021.0100101110.
0001101110.0001102100.111111101?.1110101010.2010011011.
1201011201.01110?1021.01122{01}0104.0010210102.001002100?.
00110110??.??????????.????1?????.???

Notosuchus
0100100020.1100?01122.0211010101.0111111011.0111100100.
0001101110.1?01102100.1111111011.1110101010.2010011111.
1201011201.01?11?1021.01?3300104.0?10210101.0010020000.
0011011000.00000?0100.01001111?1.001

Sebecus
0001012101.0111010021.1210111100.0101002010.0211101010.
1110101010.0011001000.11101?00?1.1111001101.10011?1011.
11010111?0.0000200101.11034?0011.0201001011.002010000?.
??????????.??????????.??????????.???

Simosuchus
0000211221.1200001112.2211110000.111110?021.021100?000.
0001101110.1110002100.1011111101.1101001001.?0?0?110??.
??00012001.01?1200121.00034?0015.0101001010.0010101100.
??11?11100.?2?101????.??????????.???

Sphagesaurus huenei
0000110000.1?00001112.?????10???.0??????0??.?001010000.
0001101110.0001????01.112??????2.1110001?0.201???1?11.
12?10?????.0?????????.0131011104.101121?2?1.1001?2100?.
?0????????.??????????.??????????.???

Thalattosuchia
0001112121.0200010010.021110?100.0112012100.0011000010.
0010001000.000000{12}000.0010101101.11100000??.10000?1011.
1001110110.00??10111.11?14?0010.0101111011.0010110000.
?100?00000.001001?2??.??????????.???

Uruguaysuchus
1000110020.1210110?22.00011??100.0110010010.?01000?000.
??01101110.??1?002000.1?11111101.111?00?001.1000011011.
11010111?1.00????0101.10032100?3.0?0?00?010.?0?0?0110?.
????????00.010?????00.101?1?0101.001

APPENDIX 4

Characters used by Zaher *et al.* (2006), and particularly referred in this analysis. Characters with a "+" were treated as ordered by Zaher *et al.* (2006). Characters labeled '**M**' are multistate, where order cannot be established between all or part of the states. Characters labeled '**X**' were excluded from the third step and substituted by a revised version in the fourth (final) step of the analysis, represented by a following number, also in bold.

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). **M**

Character 3 (modified from Clark, 1994; character 3). + Rostrum proportions: narrow oreinirostral (0) or broad oreinirostral (1) or nearly tubular (2) or platyrostral (3). **M**

Character 65 (modified from Clark, 1994; character 65). + One small palpebral present in orbit (0) or one large palpebral (1) or two large palpebrals (2). **M**

Character 67 (Clark, 1994; character 67). + Antorbital fenestra: as large as orbit (0) or about half the diameter of the orbit (1) or much smaller than the orbit (2) or absent (3). **M**

Character 105 (modified from Wu & Sues, 1996, and Ortega *et al.*, 2000; character 27 and character 133, respectively). + Premaxillary teeth: five (0), four (1), three (2), or two (3). **M/X-200, 202**

Character 107 (modified from Wu & Sues, 1996; character 30). + Maxilla: with eight or more teeth (0) or seven (1) or six (2) or five (3) or four (4) teeth. **M/X-201, 202**

Character 120 (Ortega *et al.*, 1996, 2000; characters 11 and 100, respectively). Tooth margins: with denticulate carinae (0) or without carinae or with smooth or crenulated carinae (1). **X-204**

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

Character 192 (original from Zaher *et al.*, 2006). Ventral half of lacrimal: extending posteroventrally, widely contacting the jugal (0) or tapers posteroventrally, not contacting or contacting slightly the jugal (1). **X-203**

Character 193 (original from Zaher *et al.*, 2006). Large foramen on lateral surface of anterior jugal: absent (0) or present (1). **X-199**

Character 194 (original from Zaher *et al.*, 2006). Procumbent premaxilary and anterior dentary alveoli: absent (0) or present (1). **X-205**

APPENDIX 5

Characters included in the modified matrix from Zaher *et al.* (2006), translated and adapted from Andrade (2005).

Character 199 [Andrade, 2005 (43); mod. Zaher *et al.*, 2006 (193)]. Ventrolateral surface of anterior ramus, near its contact with the maxilla: smooth or ornamented surface, without the development of neurovascular foramina (0) or single well-developed neurovascular foramen, anteriorly directed (1) or two or more neurovascular foramina, ventrally oriented (2).

Character 200 [mod. Wu & Sues, 1996 (*27*); mod. Ortega *et al.*, 2000 (*133*); mod. Zaher *et al.*, 2006 (*105*)]. Teeth supported exclusively by the premaxilla: five (0), four (1), three (2), or two or one (3).

Character 201 [mod. Wu & Sues, 1996 (*27*); mod. Zaher *et al.*, 2006 (*107*)]. Number of teeth supported entirely by the maxilla: eight or more teeth (0) or seven (1) or six (2) or five (3) or four (4) teeth.

Character 202 [mod. Andrade, 2005 (*122*)]. Intermediate tooth at the upper series, partially supported by the maxilla posteriorly and by posterior extensions of the premaxilla, anteriorly: absent (0) present (1).

Character 203 [mod. Andrade, 2005 (*16*); mod. Zaher *et al.*, 2006 (*192*)]. Maxilla: is excluded from the orbit by lachrymal-jugal contact (0) or reaches the anteroventral border of the orbit, preventing lachrymal-jugal contact (1).

Character 204 [mod. Ortega *et al.*, 1996 (*11*), 2000 (*100*); mod. Andrade, 2005 (*126*); mod. Zaher *et al.*, 2006 (*120*)]. Teeth margins: at least anterior and medial teeth with a homogeneous denticulate carinae, composed of true blade-like ziphodont denticles (0), or all teeth smooth or with a homogeneous crenulated false-ziphodont carinae (1) or anterior dentition smooth and medial/posterior teeth with heterogeneous denticulated carinae composed of tuberous and romboid denticles (2).

Character 205 [mod. Zaher *et al.*, 2006 (*194*)]. Premaxilary and anterior dentary alveoli: procumbent, with well-developed curved caniniform teeth (0), mostly vertical, with curved caniniform teeth (1) or procumbent, with small to medium incisiform teeth (2).

APPENDIX 6

Character entries for revised taxa, used in the modified matrix of Zaher *et al.* (2006). States in bold represent changes in the original matrix (1-198) or characters added in this analysis (199-205). Characters grouped, with periods ('.') indicating clusters of 10; each line with 50 characters; periods not originally included in the matrix.

*Notosuchus*NEW
101?001101.0**0**00111000.1111110011.0001022110.1100211120.
11?1000010.?110211111.2?01011100.01{01}111?1?2.00001000??.
0122011???.1100101**0**11.01**1**0100**1**10.**1**0001**0**1111.1**0**11?00011.
1100100001.01**?**1011000.0111011000.0000000000.00001111**01.21022**

*Comahuesuchus*NEW
103??0?101.??00?????0.112???????.?0010?2???.?1?011?1??.
??????????.?????131??.???**1**0?1010.1?????????.??????????.
????{01}13???.1??????0?1.0**1**1**1**1201**1**0.1?????011?.?0?1????11.
???11?0010.0?1?0??000.???100??0?.000??0????.011110?1**1?.30112**

*Mariliasuchus*NEW
101?00**0**101.0000111000.1(01)**1**1110001.1001022110.100**0**21?120.
11?1000010.?1?0213111.210**1**0?1100.0????????**2.00**????????.
??22111???.11?????0**1**1.0**1**101001**1**?.1100{01}0**(01)**111.10110?0011.
1100110001.00110**1**1000.01?1010000.0000000???.011110?1**12.31122**

*Candidodon*NEW
?**01**??**0**??**01**.??**00**??**11**??.???**11**?????.??????**2**???.??**00**??????.
??????**0**???.????**(12)1**?**1**??.???????**11**?.??????????.??????????.
???**(12)**?**11**???.?????????1.??????????.??????0??**1**.??**1**???????.
???**0**?1?**0**??.2??????**0**??.????????**00**.??**000**?????.**0000**????**0?**.**10011**

*Sphagesaurus*NEW
101?000101.??00??100?.????110???.??????2110.1?00?????0.
11?1000???.?????13?2?.???????100.**0**???????1?.??????????.
????312???.?0???????1.1111101111.11111**0**1111.10**1**1110111.
1?0**0**11?0??.011?0**1**10??.01??000000.?00???????.00**1**0**11**1**113.3?022**

*Uruguaysuchus*NEW
201?001101.??00??10??.1??1????1?.??01022?10.1?0011????.
1?????0??0.???01111(12)?.??00011010.0??1?1????.??0000?0??.
01?2100210.0?00?000?{01}.???01?1?00.????1?0111.?11?????11.
?????1?000.1????????0.???10?????.00????????.0**1**????1?**?1.00111**

*Malawisuchus*NEW
101?00?111.0000?(01)1000.1(01){01}1100?11.0001?22110.100011??20.
???1000?10.?1?02?111(01).2?01011100.01????1??2.10000010??.
01(12)2111???.01?0???011.00101?1100.0???110110.101?0?0001.
???0?100??.21110?1000.0111000000.0000000???.0**1**?00?10**?1.10111**

*Aragomesii*NEW
2010001101.0000111000.1011111011.(01)001022110.1000111120.
11?10000?0.?110201121.210001101{01}.{01}1{01}11111?1.{234}000100010.

0111100210.010010101**1**.0100100100.0000100110.0021000011.
0?0011{01}000.0111101000.011100?000.0000000000.0?000?10**01**.**00011**

*Arapatagonicus*NEW
201000?101.0000?1{01}000.101111?011.1001022?10.100011?12?.
11?1000??0.?1?02?1121.2?0?011{01}1?.?1?1??????.????1000??.
0111100???.01???0?01**1**.01101?0100.00??100110.102?0??01?.
???0??{01}100.0111?01000.01110?0000.0000000000.0?000?10**01**.**00011**

APPENDIX 7

Additional matrix entries for added characters (199-205), used in the phylogenetic analysis based on a modified version of matrix by Zaher *et al.* (2006). Periods ('.') indicate the 200th character, but not originally included in the matrix.

Gracilisuchus	?2.00?01	*Lomasuchus*	0?.00?0?
Terrestrisuchus	??.00?0?	*Peirosaurus*	?0.00?01
Dibothrosuchus	00.00?01	*Theriosuchus*	?0.00?1?
Protosuchus	01.00001	*Alligatorium*	??.?????
Hemiprotosuchus	??.00001	*Goniopholis*	00.00?1?
Orthosuchus	?1.40011	*Eutretauranosuchus*	00.00?1?
Kayenta	?1.20?1?	*Pelagosaurus*	??.00?1?
Zaraasuchus	??.?????	Teleosauridae	?1.00?1?
Gobiosuchus	02.00?11	Metriorhynchidae	?2.00010
Sichuanosuchus	01.00011	*Sokotosuchus*	??.???1?
Shantungosuchus	??.???11	Dyrosauridae	??.??010
Zosuchus	02.30?11	*Pholidosaurus*	??.??01?
Fruita	??.00?1?	*Bernissartia*	?0.0001?
Hsisosuchus	0?.00001	*Hylaeochampsa*	??.???1?
Chimaeresuchus	03.40012	*Borealosuchus*	?0.00?1?
Simosuchus	00.00011	*Gavialis*	20.00010
Bretesuchus	?1.0000?	*Crocodylus*	20.00010
Baurusuchus	?1.30001	*Alligator*	20.00010
Iberosuchus	0?.???01		

APPENDIX 8

Command lines for PAUP used in the phylogenetic analysis, shown under brackets.

Sets the use of simplest optimization between ACCTRAN and DELTRAN:
[pset opt=minf;]

Exclude character 5, due to redundance in the matrix, as in Pol (2003) (steps 1-3):
[exclude 5;]

[Exclude revised characters (step 1):
[exclude 199 200 201 202 203 204 205;]

Exclude selected characters (steps 2-3):
[exclude 105 107 120 192 193 194;]

Excludes from the analysis taxa as coded in this study (step 1):
[delete *Notosuchus*NEW *Comahuesuchus*NEW *Mariliasuchus*NEW *Candidodon*NEW *Sphagesaurus*NEW *Uruguaysuchus*NEW *Malawisuchus*NEW *Aragomesii*NEW *Arapatagonicus*NEW;]

Excludes from the analysis taxa as originally coded (steps 2-3):

[delete *Notosuchus Comahuesuchus Mariliasuchus Candidodon Sphagesaurus Uruguaysuchus Malawisuchus Aragomesii Arapatagonicus*;]

Order characters as originally used by Zaher *et al.* (2006):
[ctype ord: 1 3 6 23 37 45 49 65 67 69 73 77 79 90 91 96 97 103 104 105 107 126 143 149 165;]

Order characters - reduced list (steps 1-2):
[ctype ord: 6 23 37 45 49 69 73 77 79 90 91 96 97 103 104 126 149 165;]

Order characters according to reduced criteria, including new characters (step 3):
[ctype ord: 6 23 37 45 49 69 73 77 79 90 91 96 97 103 104 126 149 165 204 205;]

NOTE ADDED IN PRESS:

After the conclusion of this manuscript, Nobre *et al.* (2007; see references) described a new species, *Mariliasuchus robustus*, which is not mentioned in this paper. However, the holotype of the new species (UFRJ-DG-56-R) is cited and included in the range of the specimens of *M. amarali*. The existance of two or more species of *Mariliasuchus* does not preclude the classification of this genus in Notosuchidae or hinders the intergeneric comparisons presented here. However, the matter is relevant to the intraspecific variability of *M. amarali*. We understand that: (i) the poor preservation of the holotype (as discussed in this paper) does not allow a secure diferentiation of the specimen UFRJ-DG-56-R from *M. amarali*; (ii) robustness itself cannot support the recognition of a different species; (iii) the diagnosis presented by Nobre *et al.* (2007) lacked convincing autapomorphies to support *M. robustus*, and no distinctive characteristic was provided to support the distinction of *M. amarali* from *M. robustus*. Until new evidence arrises and further work is produced to understand the variability of *Mariliasuchus*, a conservative approach is preferred. Therefore, UFRJ-DG-56-R is here considered as part of *M. amarali*.

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MORPHOLOGY OF THE DENTAL CARINAE IN *MARILIASUCHUS AMARALI* (CROCODYLOMORPHA, NOTOSUCHIA) AND THE PATTERN OF TOOTH SERRATION AMONG BASAL MESOEUCROCODYLIA [1]

(With 7 figures)

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ABSTRACT. Carinated teeth are common in Mesoeucrocodylia, and the occurrence of denticles over the carinae is related to high predacious species, often referred as ziphodont. This characteristic is broadly recognized as homoplastic. Carinae morphology is cryptic, difficult to be studied under common techniques, and Scanning Electronic Microscopy (SEM) allows the access to detailed information, offering a higher degree of confidence. Previous SEM study allowed the recognition of true/false ziphodont patterns, according to the morphology of the denticles, but such studies on gondwanan mesoeucrocodyles are uncommon. *Mariliasuchus amarali* is an Upper Cretaceous notosuchian mesoeucrocodyle from South America (Bauru Group, Brazil), with carinated teeth and specialized dentition. Its geological and biochronological distribution are reappraised. SEM study of two teeth shows carinae composed of isolated tuberous anisomorphic true denticles, supporting previous study. Enamel ornamentation does not develop over the carinae, and fabric becomes anastomosed in middle and posterior teeth. Carinae only occur in posterior molariform teeth, related to food processing. Morphological variability of *Mariliasuchus* is commented, focusing on dentition. Overall characteristics, molariform morphology and wear planes support a non-predacious habit for *Mariliasuchus*. *Mariliasuchus* pattern could not be related to true/false ziphodont patterns, either by morphology or function, and is defined as ziphomorph. Ziphomorph pattern is evaluated within the range of mesoeucrocodyles. The detailed study of homoplastic characteristics, such as dental carinae, may provide useful apomorphic information for cladistic analysis.

Key words: Tooth morphology. Crocodylomorpha. Notosuchia. Cretaceous. Ziphomorphy.

RESUMO. Morfologia das carenas dentárias em *Mariliasuchus amarali* (Crocodylomorpha, Notosuchia) e a variação no padrão de carena em dentes de Mesoeucrocodylia basais.

Dentes carenados são comuns em Mesoeucrocodylia, e a ocorrência de dentículos sobre a carena está relacionada a espécies altamente predatórias, frequentemente referidas como zifodontes. Esta característica é amplamente reconhecida como homoplástica. A morfologia da carena é críptica, difícil de ser estudada através de técnicas comuns, e Microscopia Eletrônica de Varredura (MEV) permite acesso a informações detalhadas, oferecendo um grau maior de confiança. Estudos anteriores em MEV permitiram o reconhecimento de padrões zifodontes verdadeiro/falso, de acordo com a morfologia dos dentículos, porém este tipo de estudo em mesoeucrocodilos gondwânicos é incomum. *Mariliasuchus amarali* é um mesoeucrocodilo gondwânico do Cretáceo Superior da América do Sul (Grupo Bauru, Brasil), com dentes carenados e dentição especializada. Suas distribuições geológica e biocronológica são reavaliadas. Estudos em MEV de dois dentes mostraram que carenas são compostas por dentículos verdadeiros, tuberosos e anisomorfos, suportando estudo anterior. Ornamentação não se desenvolve sobre a carena, e o padrão se torna anastomosado em dentes médios e posteriores. Carenas ocorrem apenas em dentes molariformes, relacionados ao processamento do alimento. A variabilidade morfológica de *Mariliasuchus* é comentada, com foco em dentição. Características gerais, morfologia dos molariformes e a presença de planos de desgaste suportam um hábito não predatório para *Mariliasuchus*. O padrão de carenas de *Mariliasuchus*

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não pôde ser relacionado aos padrões zifodontes verdadeiro/falso, tanto por morfologia quanto por função, sendo aqui definido como zifomorfo. O padrão zifomorfo é avaliado dentro do espectro dos Mesoeucrocodylia. O estudo detalhado de características homoplásticas, como o carenamento de dentes, pode fornecer informações apomórficas úteis para análises cladísticas.

Palavras-chaves: Morfologia dentária. Crocodylomorpha. Notosuchia. Cretáceo. Zifomorfia.

INTRODUCTION

Features regarding dentition are widely used in evolutionary studies, including crocodylomorphs (*e.g.*, WOODWARD, 1896; RUSCONI, 1933; COLBERT, 1946; PRICE, 1950; BERG, 1966; KUHN, 1968; EDMUND, 1969; LANGSTON, 1956, 1975; GASPARINI, 1971, 1972; BUFFETAUT, 1976, 1979, 1982; BENTON & CLARK, 1988; CARVALHO & CAMPOS, 1988; CLARK *et al.*, 1989; BONAPARTE, 1991; BUFFETAUT & MARSHALL, 1991; ORTEGA *et al.*, 1993, 2000; CARVALHO, 1994; CLARK, 1994; WU & SUES, 1996; WU *et al.*, 1995; GOMANI, 1997; CARVALHO & BERTINI, 1999; BUCKLEY *et al.*, 2000; RIFF & KELLNER, 2001; PRASAD & BROIN, 2002; CLEMENS *et al.*, 2003; POL, 2003; SERENO *et al.*, 2003; TURNER & CALVO, 2005; TURNER, 2006; ZAHER *et al.*, 2006). From general aspects (*e.g.*, arrangement between dental series) to very specific morphological features (*e.g.*, morphology of the carinae), information proved to be both useful and controversial to phylogenetic and paleoecologic aspects. Crocodylomorph teeth have a wide range of morphological variation, including number and arrangement of cusps, inclination and orientation of the apex, overall shape in lateral view, compression of the crown, compression of the root and presence of cingulus, base-to-apex ornamentation, among others (PRICE, 1950; CARVALHO, 1994; WU *et al.*, 1995; WU & SUES, 1996; GOMANI, 1997; BUCKLEY *et al.*, 2000; RIFF & KELLNER, 2001; NOBRE & CARVALHO, 2002; VASCONCELLOS & CARVALHO, 2005; ELIAS, 2006; TURNER, 2006; ZAHER *et al.*, 2006). The variations include convergences with mammalian dentition (CARVALHO & CAMPOS, 1988; CLARK *et al.*, 1989; BONAPARTE, 1991; CARVALHO, 1994; WU & SUES, 1996; WU *et al.*, 1995; GOMANI, 1997), with a similar nomenclature (incisiforms, caniniforms, and molariforms) referring to specialized teeth.

The term "ziphodont" have long been applied to Mesoeucrocodylia, including several genera from a broad range of families. Characters related to the ziphodont dentition are included (explicitly or not) as part of several works in phylogenetics (*e.g.*, BENTON & CLARK, 1988; CLARK *et al.*, 1989; CLARK, 1994; WU & SUES, 1996; WU *et al.*, 1995; GOMANI, 1997; BUCKLEY *et al.*, 2000; ORTEGA *et al.*, 2000; CLEMENS *et al.*, 2003; POL, 2003; SERENO *et al.*, 2003; TURNER & CALVO, 2005; TURNER, 2006; ZAHER *et al.*, 2006). The morphology of the carinae, present in several species, is of particular interest. ORTEGA *et al.* (2000) defined the Ziphosuchia as a group of Mesoeucrocodylia comprised by *Notosuchus*, *Libycosuchus*, and Sebecosuchia, which should have the ziphodont dentition, defined by the carinae morphology. Nevertheless, there is not much agreement on this characterization. As TURNER (2006) pointed out, for long time the use of ziphodont dentition is considered to be of limited value as phylogenetic information (LANGSTON, 1956; BERG, 1966; HECHT & ARCHER, 1977; TURNER & CALVO, 2005; ZAHER *et al.*, 2006).

Although used in previous studies (LANGSTON, 1956; BERG, 1966), the classical ziphodont dentition (LANGSTON, 1975) is defined as crocodylomorph teeth with morphology similar to equivalents observed in carnivorous dinosaurs. The concept is based on characteristics such as general tooth shape, apex morphology and presence of carinae. Ziphodont carinae are typically serrated and formed by isolated denticles. This idea was posteriorly modified by PRASAD & BROIN (2002), restricting the definition to the composition of the dental carinae, which allowed: a) some morphological variability in dental series and specimens; b) the recognition of other crocodylomorphs as ziphodont species (Fig.1). Examples of ziphodont crocodylomorphs, by this definition, include *Iberosuchus*, *Sebecus*, *Pristichampsus*, *Hamadasuchus*, and cf. *Araripesuchus wegeneri*.

PRASAD & BROIN (2002) also described another pattern, defined as false-ziphodont dentition, which is attributed to mesoeucrocodylians, such as *Asiatosuchus*, *Trematochampsa*, *Sarcosuchus*, and *Sphagesaurus*. False-ziphodont teeth are characterized by the presence of crenulations, composed by the extension of the enamel ridges over the carina. These ridges are often irregular, creating an anastomosing fabric over the labial and lingual teeth surface. When this fabric reaches out up to the mesial and distal borders, it modifies the morphology of the carinae, which usually have a continuous and uniform structure.

The resulting surface becomes crenulated, giving the false impression, under observation by simple optical resources, that the carina is composed by several isolated denticles (Prasad & Broin, 2002). This pattern seems to be analogous to the true ziphodont morphology, but as Prasad & Broin (2002) point out, its structure is completely different (Fig.2). Prasad & Broin (2002) stress that the identification of patterns is especially difficult without sufficiently magnified views, and the use of Scanning Electronic Microscopy (SEM) can prove to be a valuable tool.

The morphological description of the carina as to two basic types, ziphodont and false-ziphodont, seems to be limited when the wide range of morphology types is taken into consideration. In fact, the nature of the denticles and their distribution over the crown, seems to be much wider. Also, several basal Mesoeucrocodylia were heterodont, and morphologic variation can be expected along the series. Thus, teeth morphological variation in crocodylomophs should not be represented solely by "theropod-like" and "false-theropod-like" morphologies.

Furthermore, there seems to be a sample bias regarding information from Scanning Electronic Microscopy (SEM). Several scientific contributions include detailed descriptions and images from dinosaur teeth, but most of them are almost totally dedicated to Laurasian theropods (Farlow, 1987; Currie *et al.*, 1990; Farlow *et al.*, 1991; Fiorillo & Currie, 1994; Rauhut & Werner, 1995; Buscalioni *et al.*, 1996; Franco-Rosas, 2000). In the other hand, there are few publications dedicated to the dental morphology in crocodylomorphs, with the help of SEM (*e.g.*, Carvalho, 1994; Legasa *et al.*, 1994; Prasad & Broin, 2002; Andrade, 2005; Elias, 2006), and information about Gondwanan taxa is very limited. While this kind of information may be significant for evolutionary studies to crocodylomorphs, there is still a huge lack of knowledge regarding the descriptions of teeth from South-American taxa.

Among the South-American mesoeucrocodyles, the Brazilian *Mariliasuchus amarali* Carvalho & Bertini, 1999, from the Campanian of the Bauru Group (Araçatuba/Adamantina formations) is well known from several specimens (Carvalho & Bertini, 1999; Andrade, 2005; Vasconcellos & Carvalho, 2005, 2006; Zaher *et al.*, 2006). Tooth morphology was studied by Zaher *et al.* (2006), under common optical techniques, describing the serrations as "*composed of a series of round tubercles, instead of sharp denticles present in ziphodont crocodiliforms*".

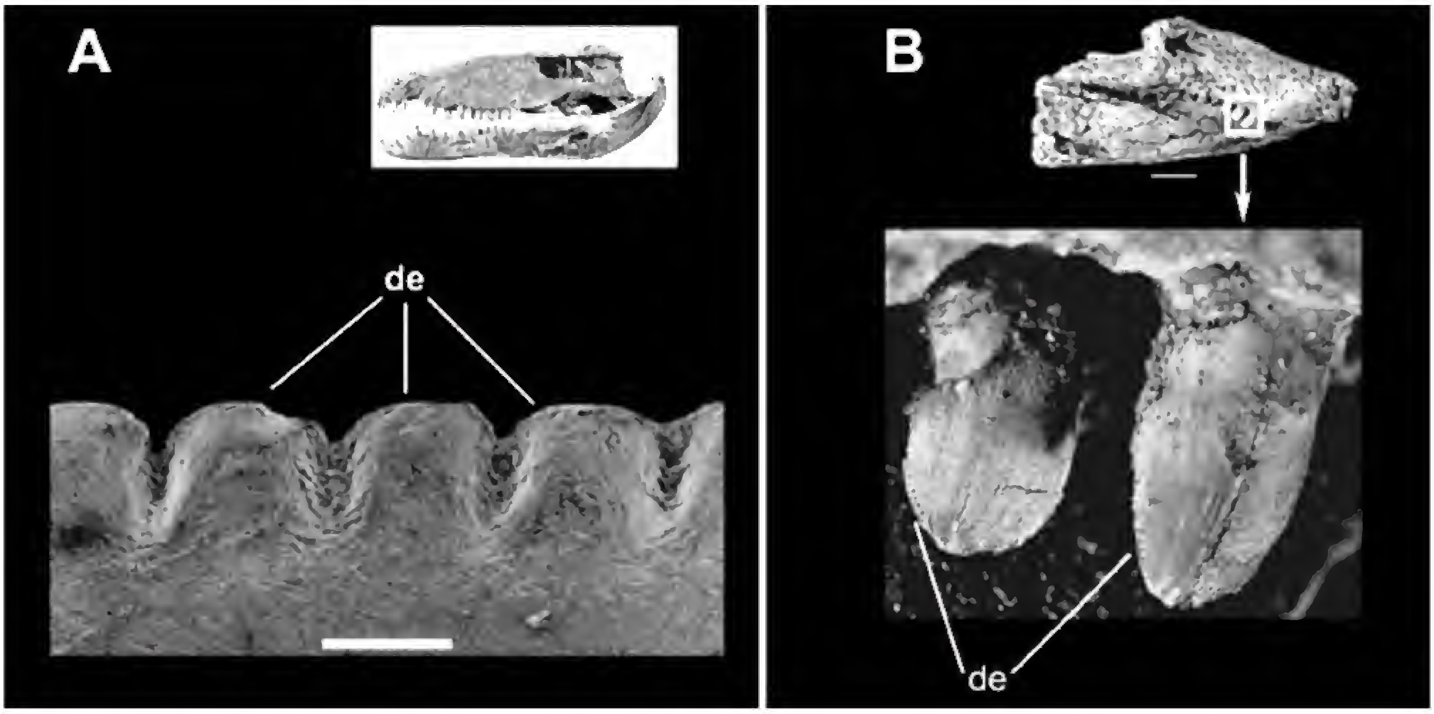

Fig.1- Ziphodont crocodylomorphs, showing major features of the true ziphodont pattern: A) *Sebecus icaeorhinus* skull (above), with detail of the carina from MNHN (P) VIV-69, *Sebecus* sp. (below); B) cf. *Araripesuchus wegeneri*, GDF 700, holotype (above), with detail of its maxillary teeth bearing carinae, composed of true denticles (below). Scale bars = 0.1mm (A); 10mm (B). (A - adapted from Colbert, 1946 and Prasad & Broin, 2002; B - adapted from Ortega *et al.*, 2000 and Turner, 2006).

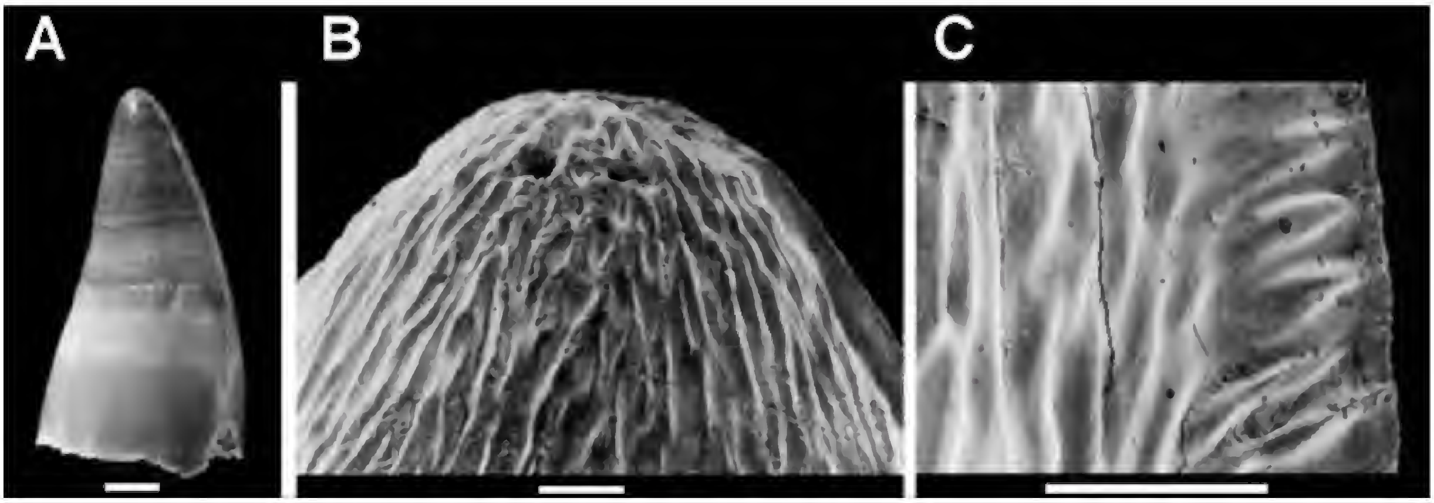

Fig.2- False-ziphodonty in *Asiatosuchus*: A) general aspect of MNHN (P) AG-20, caniniform tooth; B) apex of the tooth MNHN (P) BR-15230, showing superficial ornamentation; C) detail of the carina of the tooth MNHN (P) BR-15230, showing ornamentation composed by enamel ridges that develop over the carina, resembling denticles of ziphosuchian Mesoeucrocodylia. Note that such condition is very difficult to identify without Scanning Electronic Microscopy. Scale bars = 10mm (A); 0.5mm (B-C). (Adapted from Prasad & Broin, 2002).

Here we study teeth from *Mariliasuchus amarali* under Scanning Electronic Microscopy, review the information provided by Zaher *et al.* (2006) and compare this particular morphology to the typical ziphodont dentition. Functional aspects of *Mariliasuchus* are explored, to further demonstrate that this morphology is truly diverse from the ziphodont pattern.

MATERIAL AND METHODS

Abbreviations

Institutional. DES, Department of Earth Sciences, University of Bristol, Bristol, United Kingdom; GDF, MNHN (P) AG, MNHN (P) BR, MNHN (P) VIV, Muséum National d'Histoire Naturelle, Paris, France; IGCE-UNESP, Departamento de Geociências e Ciências Exatas, Universidade Estadual Paulista, Rio Claro, Brazil; MEF, Museo Paleontologico Egidio Feruglio, Trelew, Argentina; MN, Museu Nacional, UFRJ, Rio de Janeiro, Brazil; MUZUSP, MZSP-PV, Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil; UFRJ, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; URC, Museu de Paleontologia e Estratigrafia "Prof. Dr. Paulo Milton Barbosa Landim", Universidade Estadual Paulista, Rio Claro, Brazil.

Anatomical. c, hypertrophied caniniform tooth; cr, tooth crown; de, carina denticle; Den, dentary; er, enamel ridge; FMP, maxillo-palatinae fenestra; FSO, suborbital fenestra; laf, labial face; lif, lingual face; ma, maxillary tooth; Mx, maxilla; Pal, palatine; Pmx, premaxilla; ro, tooth root; Sp, splenial.

Material

Mariliasuchus amarali is a Notosuchia (*sensu* Gasparini, 1971) and most probably a Notosuchidae (Carvalho & Bertini, 1999; Andrade, 2005; Fiorelli & Calvo, 2005; *contra* Carvalho *et al.*, 2004; Zaher *et al.*, 2006), as *Notosuchus terrestris* Woodward, 1896. Remains come from several outcrops, at the vicinities of the Marília City (Nava, 2004), and are currently housed by several institutions, including MUZUSP, MN, UFRJ, and URC (Andrade, 2005; Vasconcellos & Carvalho, 2005, 2006; Zaher *et al.*, 2006). It is agreed that *Mariliasuchus* comes from the Late Cretaceous of Bauru Group, in the vicinities of Marília City (Carvalho & Bertini, 1999, 2000; Andrade, 2005; Vasconcellos & Carvalho, 2005, 2006; Zaher *et al.*, 2006).

We studied two well-preserved isolated teeth from *Mariliasuchus amarali* under Scanning Electronic Microscopy. They were both found in close association to well-preserved and partially articulated *M. amarali* cranial and post-cranial remains (URC R•67, URC R•68, URC R•69). It is not certain if the teeth come from either one of those specimens or from a fourth individual. Furthermore, they could not have come from URC R•67, as this specimen has a complete dental series preserved. The isolated teeth were respectively identified as URC R•74 (caniniform) and URC R•75 (molariform) by comparison with URC R•67 and URC R•68. All these specimens, including the teeth, came from the type-locality of the Rio do Peixe outcrop. The specimens of MN 6298-V and MN 6756-V were also studied for further comparison. MN 6298-V is composed of a partial skull, without the mandible, while MN 6756-V is composed of a well-preserved set of skull and mandible. This last specimen shows lateral compression (Zaher *et al.*, 2006). In Zaher *et al.* (2006; p.7, 2nd column, lines 8-15), the identification of these specimens is changed, as MN 6298-V is identified as MN 6756-V and vice versa.

Geological Settings

A bibliographic review of *Mariliasuchus* shows some differences of interpretation on the origin of the specimens. Carvalho & Bertini (2000), Vasconcellos & Carvalho (2005), Candeiro & Martinelli (2006), and Zaher *et al.* (2006) considered that the remains came from the Adamantina Formation. Andrade (2005) and Vasconcellos & Carvalho (2006) described them as originated from the Araçatuba/Adamantina formations. Divergences may be partially explained because of the different definitions of the Araçatuba sedimentary unit.

These sediments have been usually considered as the base of the Adamantina Formation (as in Kellner & Campos, 1999; Dias Brito *et al.*, 2001; Candeiro & Martinelli, 2006). Barcelos (1984) referred this geological unit as Member Araçatuba. Its original definition as Araçatuba Formation (Zaine *et al.*, 1980) was most recently modified (Batezelli, 1998, 2003; Batezelli *et al.*, 1999, 2003; Fernandes *et al.*, 2003), extending the area of occurrence and lithologic column. Although Carvalho & Bertini (1999, 2000) and Vasconcellos & Carvalho (2005) use the traditional definition (Araçatuba as a lithofacies of the Adamantina Formation), it should be noticed that specimens are always preserved in close association with pelitic sediments (Carvalho & Bertini, 1999, 2000). Vasconcellos & Carvalho (2006) considered difficulties in the determination of the units and limits, assuming Araçatuba/Adamantina Formation for the UFRJ specimens. Nobre & Carvalho (2006) directly address the problem and state that Adamantina sediments on the margins of the Peixe River, at the base of the Rio do Peixe outcrop, are the same as the Araçatuba Formation, as defined by Batezelli *et al.* (1999) and Fernandes *et al.* (2003). Zaher *et al.* (2006), describing the geologic settings of *Mariliasuchus*, refers to a single locality for all specimens, at the left margin of the *"(...) Agua Formosa creek (coordinates 22°20'28"S and 49°56'46"W), 10 km south from the urban area of Marília (...)"* (Zaher *et al.*, 2006; p.2, 1st column, 2nd §). In the same paper, the authors provided locality and horizon as *"(...) a road cut at the left margin of the Peixe River, 18 km from the city of Marilia, (...) from the upper part of the Adamantina Formation, Bauru Group"* (Zaher *et al.*, 2006). Differences of distance are clearly due to the way they were obtained, as 10km is the distance in a straight line, taken from maps, and 18km can be understood as the distance taken using main roads necessary to access the outcrop. The locality itself is well known as Rio do Peixe outcrop from previous works (Carvalho & Bertini, 1999, 2000; Andrade, 2005) and there is no question as to which river is related the outcrop. The Peixe River spring is located northeastern to the GPS location provided by Zaher *et al.* (2006), closer to Garça City. From its spring, the Peixe River flows to the western, passing through the *Mariliasuchus* locality and continuing West-Northwestern to the Parana River, without changing its name (*e.g.*, Batezelli, 1998). Further disagreement comes from the collection of *Mariliasuchus*. Most papers refer to the same Rio do Peixe outcrop, but referring to one or few specimens (Carvalho & Bertini, 1999, 2000; Andrade, 2005; Vasconcellos & Carvalho, 2005, 2006). Zaher *et al.* (2006) declare that all specimens came from the same location, which is a broad definition, as 'location' could define 'outcrop', but also 'the vicinities of Marília City'. Nava (2004), on the other hand, clearly states that *Mariliasuchus* remains have been found in at least four sites in the same region, and many specimens have been recovered from these outcrops. It is possible that *Mariliasuchus* specimens were collected in other outcrops, but unfortunately, localities and specimens were not individually identified by Nava (2004), preventing further discussion. Nevertheless, holotype and URC specimens came from the type locality, vicinal road that gives access to Fazenda Doreto, Marília Municipality, 10km from the municipal headquarters, as described by Carvalho & Bertini (1999). No other locality has been officially identified.

Some divergences regard the provenance of the materials in the lithologic column. The Rio do Peixe outcrop includes only the Araçatuba and the Adamantina formations. The limits of these sedimentary units are not clearly defined, as the Araçatuba Formation broadly interbeds with the Adamantina Formation (*e.g.*, Batezelli, 1998, 2003).

At least the holotype, the UFRJ specimens, and the URC specimens were recovered from a horizon close to the bottom of the lithologycal column (CARVALHO & BERTINI, 1999, 2000; VASCONCELLOS & CARVALHO, 2006; NOBRE & CARVALHO, 2006), where there is a significative contribution of siltic matrix over sandstone (Araçatuba Formation *sensu* BATEZELLI, 1998; BATEZELLI *et al.*, 2003). As discussed previously, most studies agree that sediments at the base of the Rio do Peixe outcrop, where *Mariliasuchus* is originated, represents the contact between the Araçatuba and Adamantina formations, thus close to the bottom of the Adamantina Column (CARVALHO & BERTINI, 1999, 2000; ANDRADE, 2005; VASCONCELLOS & CARVALHO, 2005, 2006; NOBRE & CARVALHO, 2006). A different statement is provided by ZAHER *et al.* (2006), which consider the facies association as representative of the upper part of the Adamantina Formation, close to the contact of the Marília Formation (ZAHER *et al.*, 2006). The specimens are assigned in fact to four horizons (ZAHER *et al.*, 2006) in the columnar section of the referred outcrop, each one showing a different lithology. These are always rich in fine grained sediments, where brown/dark-brown shale interclasts are usually associated, and also a metric mudstone layer (ZAHER *et al.*, 2006). This description matches the upper section of the Araçatuba Formation (*sensu* BATEZELLI, 1998), and its intergrading contact with the Adamantina Formation.

Although disagreement is present in the bibliography, a conservative approach is here preferred. URC specimens came from the same locality and horizon provided for the holotype, and possibly for several other specimens, on the margins of the Peixe River, Rio do Peixe outcrop. The sediments associated with these specimens have been referred to as the Adamantina Formation (CARVALHO & BERTINI, 1999, 2000; VASCONCELLOS & CARVALHO, 2005), and several studies (BATEZELLI, 2003; BATEZELLI *et al.*, 1999, 2003; NOBRE & CARVALHO; 2006) recognized the same sediments as the gradational contact between the Araçatuba Formation *sensu* BATEZELLI, 1998. Type-horizon is therefore considered as the Araçatuba/Adamantina formations, rather than to the upper Adamantina column. As the Araçatuba and Adamantina formations are considered to be (at least) partially synchronic (BATEZELLI, 1998, 2003; BATEZELLI *et al.*, 1999, 2003; FERNANDES *et al.*, 2003), the occurrence of the same species in both sedimentary units is likely. In this context, we understand that there is no disagreement with most studies (CARVALHO & BERTINI, 1999, 2000; ANDRADE, 2005; VASCONCELLOS & CARVALHO, 2005, 2006; NOBRE & CARVALHO, 2006).

Further debate also exists on the age of the Upper Cretaceous deposits from the Bauru Group. DIAS-BRITO *et al.* (2001) argues for a Turonian-Maastrichtian age for the Bauru Group, with a Campanian depositional hiatus, indicating an early age for the Araçatuba Formation, possibly Turonian. The proposal by DIAS-BRITO *et al.* (2001) is widely adopted (VASCONCELLOS & CARVALHO, 2005, 2006; NOBRE & CARVALHO, 2006; ZAHER *et al.*, 2006). Nevertheless, the existence of several gradational contacts between the Adamantina and Marília formations (BATEZELLI, 1998, 2003; BATEZELLI *et al.*, 1999, 2003), recognized by ZAHER *et al.* (2006), implies that a Campanian depositional hiatus is unlikely to occur. ZAHER *et al.* (2006) considers a Campanian to Maastrichtian age for *Mariliasuchus*, although accepting a modified version of the model proposed by DIAS-BRITO *et al.* (2001), and considering the lithologic column from the type-locality as representative of the upper Adamantina section.

Correlations based on charophytes, ostracods, and vertebrates (GOBBO-RODRIGUES *et al.,* 2000a, 2000b, 2000c; GOBBO-RODRIGUES, 2001; SANTUCCI & BERTINI, 2001) indicate that the Araçatuba Formation was most probably Campanian (Fig.3), rather than Turonian. Although the age attributed for *Mariliasuchus* is similar for ZAHER *et al.* (2006) (Campanian-Maastrichtian), both models represent different interpretations of the data available.

RESULTS AND DISCUSSION

DESCRIPTION OF THE MATERIAL

URC R•74 shows a caniniform morphology (Fig.4), slightly curved, the apex not acute. URC R•75 is a typical molariform (Fig.5) although not particularly well-developed. In both elements, there is no constriction between crown and root, though differences of color and surface allowed the recognition of the actual boundaries.

URC R•74 is small and could have been positioned as an anterior premaxilary tooth, but not the hipertrophyed caniniform. It is comparable in size and general morphology to the regular premaxilary caniniforms of URC R•67. The crown is lightly curved, with a circular cross-section and no lateral compression. There was no evident difference between the lingual and labial surfaces. This tooth does not show any kind of serration, either in the

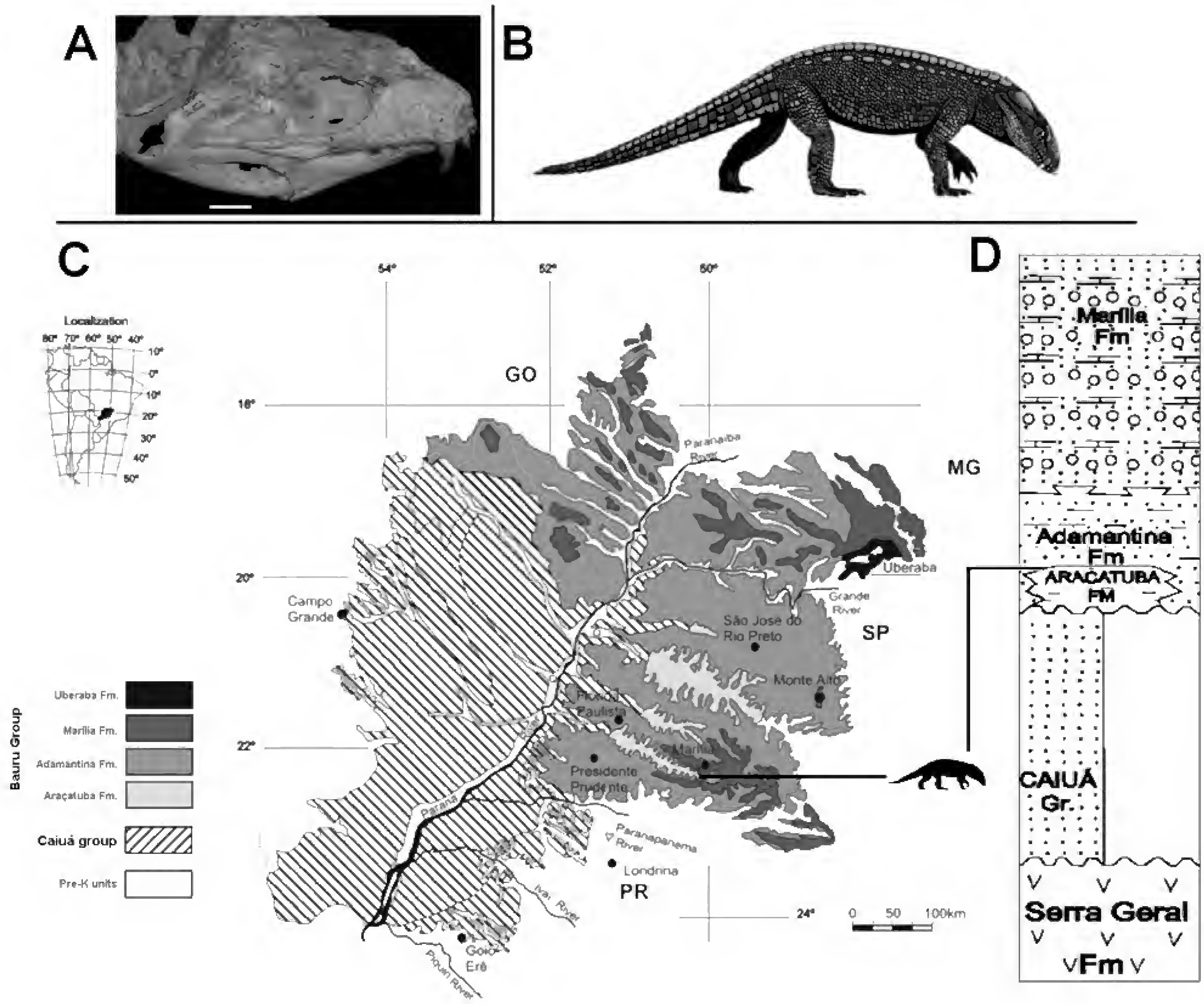

Fig.3- *Mariliasuchus amarali* and its geographical range: A) general aspect of the skull from URC R•67; B) artistic reconstruction of *Mariliasuchus*; C) map showing the geographical distribution of the sediments from the Bauru Group; D) lithologic column for the State of São Paulo, showing type-locality of holotype, UFRJ and URC specimens. Bar: 10mm (A). (B - illustration by Felipe A. Elias; C - modified from FERNANDES & COIMBRA, 1996; D - adapted from BATEZELLI *et al.*, 2003).

mesial or the distal surfaces. It rather had a smooth irregular surface, where base-to-apex ridges develop. The ridges are proportionally low and wide, are present through most of the crown length, and probably represent enamel ornamentation. The ridges do not progress to the apex, which seems to be a natural characteristic, as there is no indication that they were worn out or suffered physical erosion. The very apex is neither round, nor acute. It seems to have been worn out in a single, though irregular, plane.

URC R•75 is also small, and could have been either a maxillary tooth, or one of the posterior mandibular teeth. Based on the morphology and comparison to URC R•68, it is more likely that the specimen represents the fifth left mandibular tooth. The crown is lanceolated in lateral view, but short and with a blunt apex. The lingual and labial surfaces are different, with a "D-shaped" cross-section. The lingual surface is not as convex as the the labial surface. Considered this interpretation, serrations developed preferentially on the mesial surface, while the distal surface shown a smoother area and denticles were not so easily characterized.

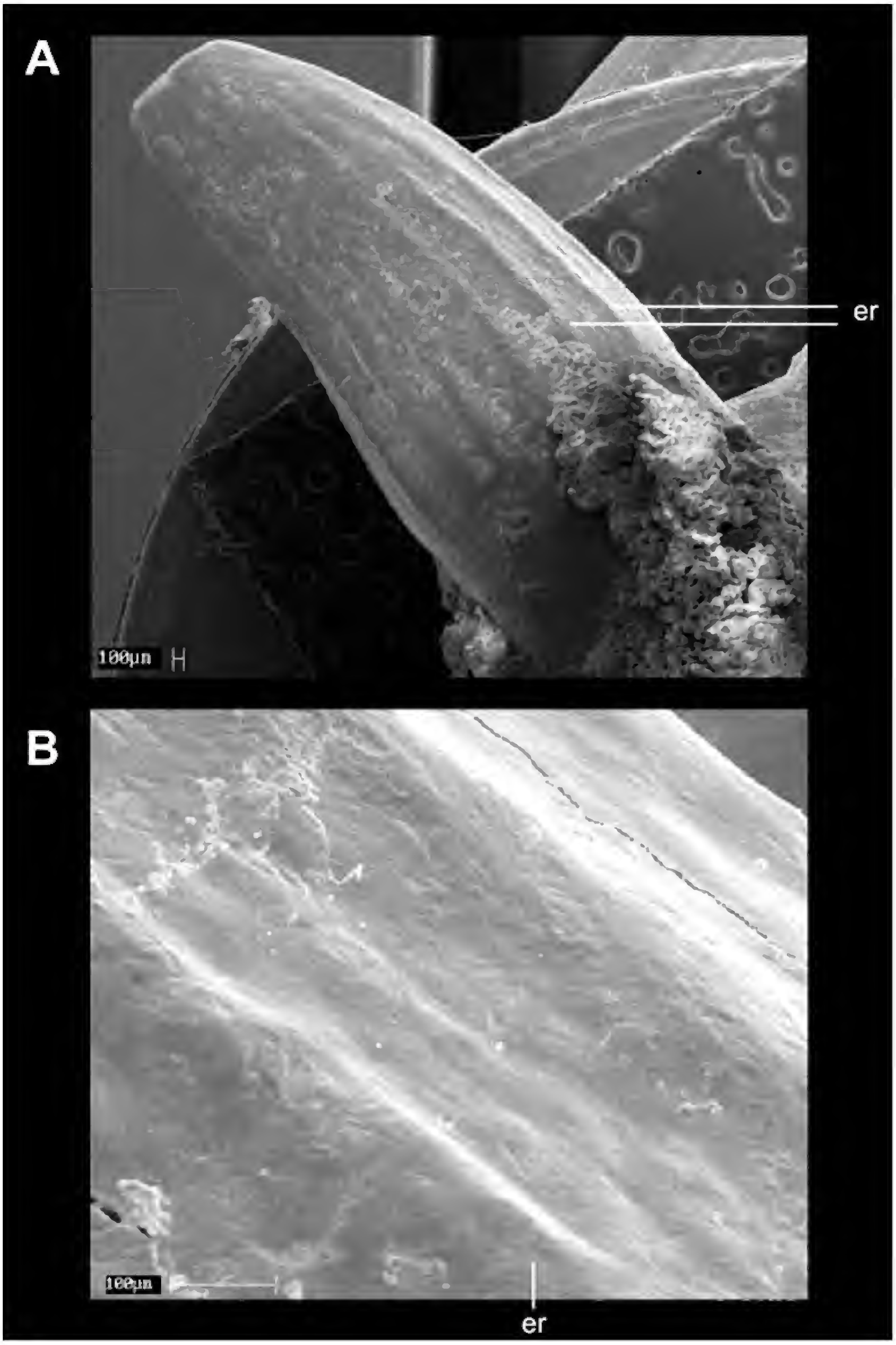

Fig.4- Labial view of the caniniform tooth URC R•74, from *Mariliasuchus amarali*, observed in scanning electronic microscopy: A) general aspect, showing the absence of carinae and the presence of ornamentation composed by base-to-apex enamel ridges; B) detail of the tooth surface, showing the ridges.

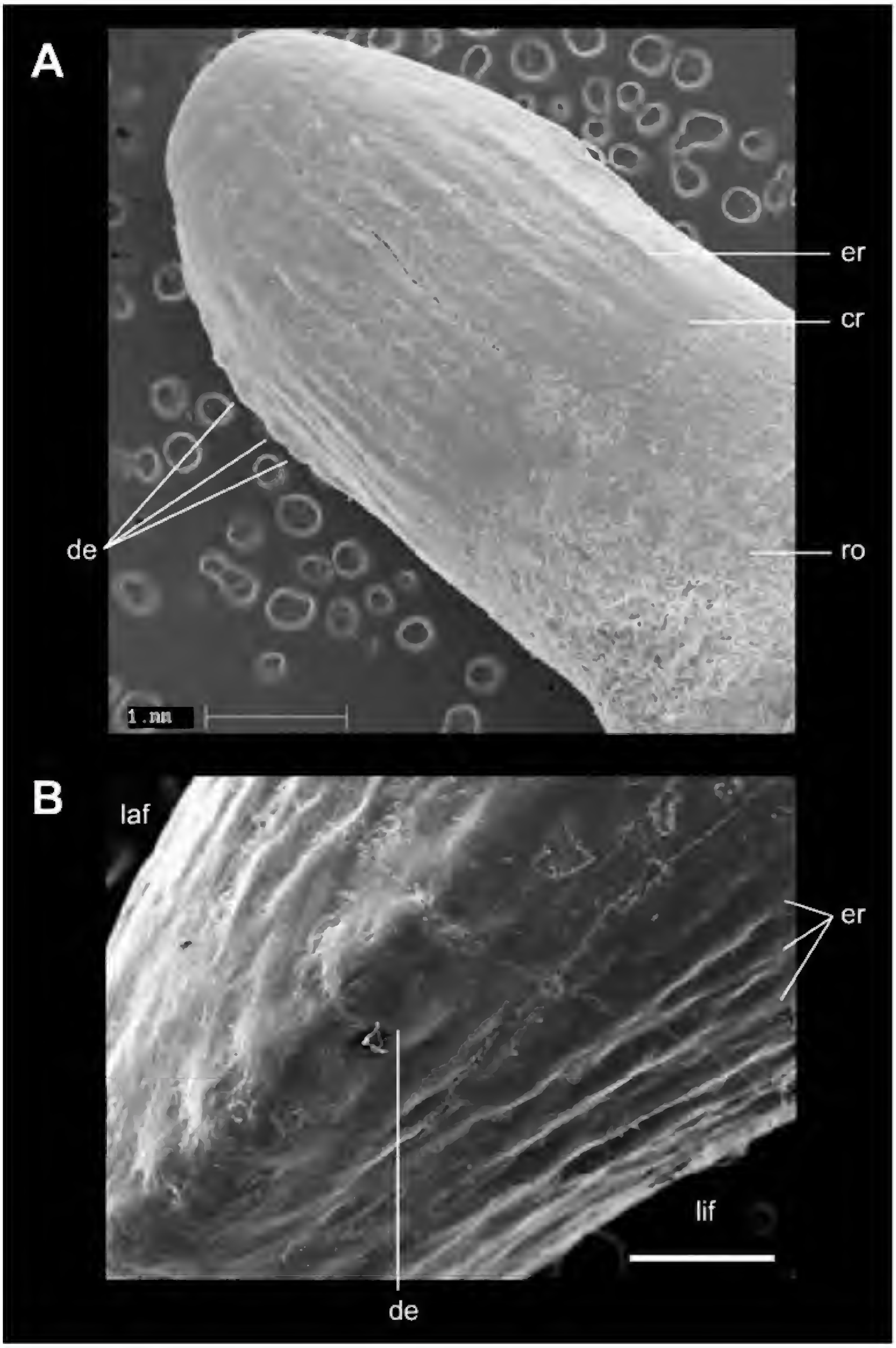

Fig.5- molariform tooth URC R•75, from *Mariliasuchus amarali*, observed in scanning electronic microscopy: A) general aspect from the molariform tooth in lingual view, showing the light ornamentation over the surface and the denticles at the border; B) detail of the denticles from the mesial border, with a very distinctive tuberous profile. Note the anastomosed pattern composed by the enamel ridges present over the labial and lingual faces of the crown. Scale bar = 0.25mm (B).

Each carina is formed by a collection of rhomboidal denticles, undefined in shape (anisomorphic), with subcircular cross-section. They are tuberous, with an irregular aspect. Furthermore, no additional structures could be observed over the denticles, or between them (Fig.5), as in *Sebecus* denticles (Fig.1).

URC R•75 also has an ornamentation pattern quite evident on its surface, with ridges developing from base to apex, but in an anastomosed pattern. This ornamentation does not extend over the carinae denticles, as would be expected for a false-ziphodont. These ridges are irregular and anastomosed. Observation of the dental series of URC R•67 and URC R•68 shows that this pattern progress from the anterior to the posterior teeth in a particular way. On the anteriormost teeth these crests or ridges are bigger and longer, occurring in smaller numbers, while in posterior teeth a greater number of ridges is present, and the anastomosis is more evident.

Although URC R•67 and URC R•68 could not be studied under SEM, observation under common optical resources can be included, especially regarding the carinae and wear surfaces. In URC R•68 the maxilla and the dentary are not bound together, and teeth can be examined in several positions, which is particularly important. The dental carinae are most likely situated on both mesial and distal surfaces, for most molariforms, but are present in all molariforms, without exception. Nevertheless, part of the dental series of URC R•68 had wear surfaces where the serrations should have developed, and it was impossible to positively identify the presence of denticles. Abrasion surfaces are plane, anteroposteriorly elongated and positioned over either the mesial or the distal border of the molariform teeth, but not on both surfaces of the same tooth. These planes can be especially seen on the sixth and seventh mandibular molariforms, and the opposing maxillary teeth. In mandibulary molariforms, the worn planes are present only on the mesial surface, inclined anteriorly and labially. In the opposing maxillary teeth, these surfaces are present on the distal surface, facing posteriorly and lingually (Fig.6). The upper and lower wear surfaces match each other, and the complete set (maxilla, premaxilla and mandible) were found in occlusion, in close association (Fig.7).

Worn areas have also been found in hypertrophied caniniforms of both URC R•67 and URC R•68. In URC R•67 there is an eroded plane on the left caniniform mesial crown surface. The worn plane is positioned on the tip of the crown, developing over the mesial surfaces of the teeth. In URC R•68 this worn plane is also preserved in the right hypertrophied caniniform, but it is more labial than mesial. This feature is not exclusive from URC specimens and is figured for MZSP-PV-50 (Zaher *et al.*, 2006). In fact, Vasconcellos & Carvalho (2005) also report wear surfaces in UFRJ DG-105-R e UFRJ DG-106-R. Furthermore, Zaher *et al.* (2006) describe extensive wear facets on the lingual surfaces of some second to fourth maxillary and sixth to eighth mandibulary teeth of MZSP-PV-50 and MZSP-PV-51. Extensive lingual worn surfaces can also be seen in three MN 6756-V maxillary molariforms, and at least in one of MN 6298-V. In MN 6756-V mandible, the sixth pair of molariforms show apical-labial wear surfaces.

Another aspect of *Mariliasuchus* deserving attention is that molariform teeth can show a certain degree of paramesial rotation, resulting into a slightly oblique implantation, as observed by several authors (Andrade, 2005; Vasconcellos & Carvalho, 2005, 2006; Zaher *et al.*, 2006). The distal carina is positioned coincident with the sagittal plane of the skull. This can be observed both in the maxilla and mandible. In URC R•68 this is more evident in three of the most developed right maxillary molariforms, and also from the sixth to the eighth right mandibular molariforms. As previously reported, this particular disposition can also be seen in MZSP PV-50 (Zaher *et al.*, 2006), on two maxillary pairs, and MN 6298-V and MZSP PV-51 (Zaher *et al.*, 2006), for three maxillary pairs. At least in the mandible from MZSP PV-50 (Zaher *et al.*, 2006), MZSP PV-51 (Zaher *et al.*, 2006) and MN 6298-V, there is a slight degree of rotation in the fifth to the eighth teeth. The pattern is more evident in URC R•68, and also in a variable degree and not in all the same mandibulary teeth for the other specimens, but it is present.

Carinae and Teeth from *Mariliasuchus amarali* and the Concept of Ziphomorph Dentition

The morphology observed in these isolated teeth of *Mariliasuchus amarali* shows clearly the presence of true denticles constituting a serrated border, on the molariform tooth observed. These structures are coherent with the description provided by Zaher *et al.* (2006) for teeth of other specimens, although in their descriptions they preferred to consider these structures as tubercles. Observations using SEM allowed to clearly state that the ornamentation does not participate in the composition of the carina and the denticles are real and individualized structures. This excludes completely the possibility of these teeth as to be characterized as false-ziphodont teeth.

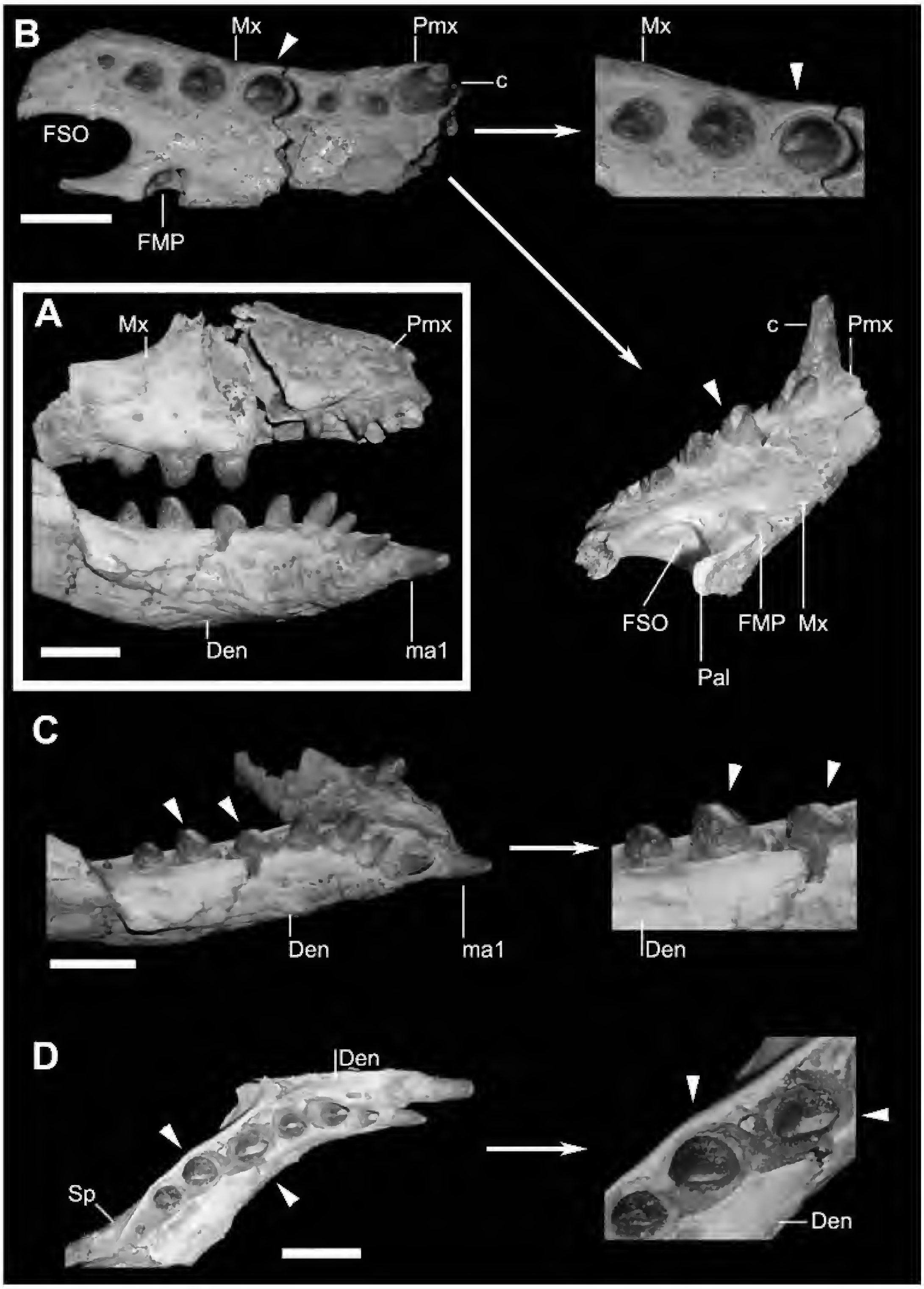

Fig.6- *Mariliasuchus amarali* URC R•68, observed in several views, showing the occurrence of elongated wear surfaces in maxillary and mandibulary teeth: A) general aspect in lateral view; B) the right premaxilla-maxilla, and detail of where abrasions can be observed in the distal border of a molariform, in palatal (above) and posteromedial (below) views; C) mandible set in latero-dorsal view, and detail showing abrasions on the mesial border of the sixth and seventh teeth; D) right mandible in dorsal view, and detail showing abrasions on the mesial border of the sixth and seventh teeth. Main wear surfaces indicated by white pointers. Note the inclination of the wear surfaces in maxillary (lingual) and mandibulary (labial) teeth; the complementary arrange of the mandibular and maxillary teeth; the presence of obliquely implanted teeth on the maxilla and the mandible, and a certain degree of variation on this condition along the dental series. Bar = 10mm.

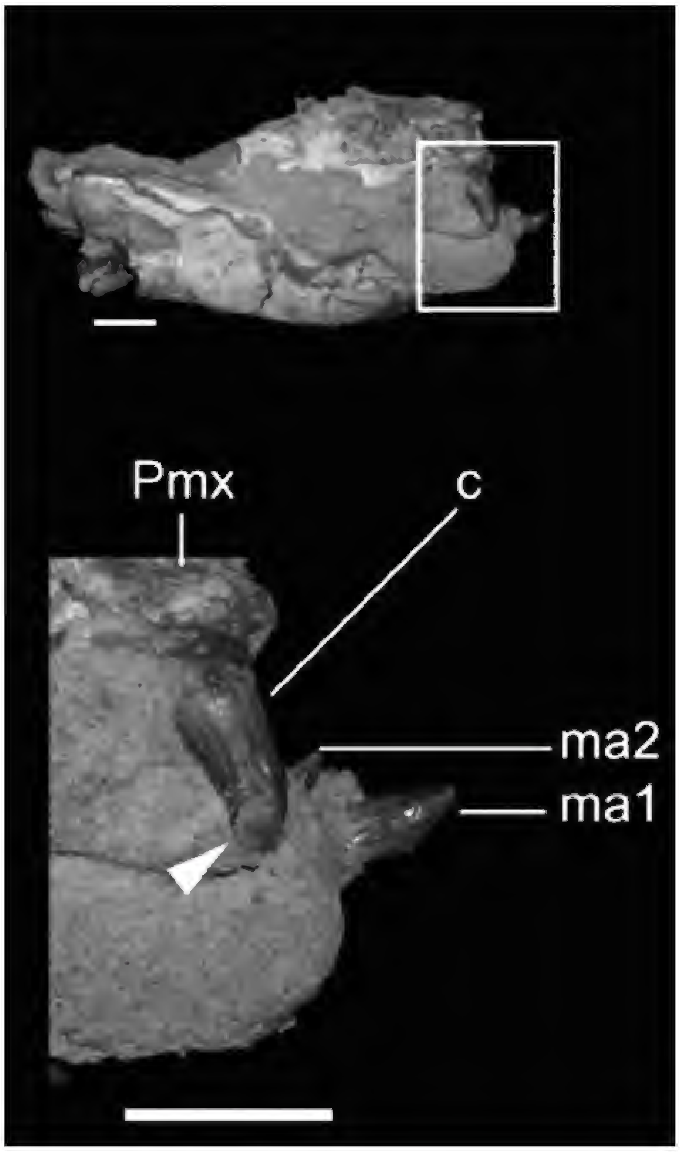

Fig.7- *Mariliasuchus amarali* URC R•68 in lateral view, during cleaning procedures. The set was found in close association (above). Detail (below) shows the right hypertrophied caniniform tooth, and the eroded surface exposed labially, indicated by the white marker. Scale bar = 10mm.

Study using SEM provide definitive identification that, in *Mariliasuchus*, denticles are far different in relation to typical ziphodont crocodylomorphs. *Mariliasuchus* shows clearly isolated and anisomorphic denticles, with tuberous shape. In ziphodont teeth, the carina is also formed by isolated denticles, but each denticle is more elongated, with a subrectangular to elliptical base. Ziphodont denticles are usually very close to each other and constitute a long series of repetitive isomorphic denticles. Each denticle may be keeled itself, as in *Sebecus*, although this is not the case for other ziphodont forms (*e.g.*, cf. *Araripesuchus wegeneri*). Furthermore, overall morphology of the teeth is very different from the carnivorous blade-like teeth, found either in *Sebecus* or in other ziphodont mesoeucrocodyles. Ziphodont crocodylomorphs develop carinae over highly compressed teeth, usually blade-like caniniforms. According either to the definitions figured in LANGSTON (1975) and PRASAD & BROIN (2002), *Mariliasuchus* cannot be characterized as a ziphodont form, as suggested by ZAHER *et al.* (2006), which was confirmed by observation under different techniques, as SEM and optical microscopy.

Since the definitions of true ziphodonty and false-ziphodonty do not apply to *Mariliasuchus amarali*, a more adequate terminology should be used. We define this pattern as the ziphomorph pattern, here characterized by teeth with anisomorphic, tuberous, and well-spaced true denticles composing a carina, with ornamented enamel surface (fabric) that does not developed onto the carina. This definition is important and especially useful as recognition of an independent evolutionary condition or an apomorphic character state.

As previously pointed out by many authors (LANGSTON, 1956; BERG, 1966; HECHT & ARCHER, 1977; TURNER & CALVO, 2005; TURNER, 2006; ZAHER *et al.*, 2006), ziphodont dentition is of little phylogenetic value. The original definition certainly constituted a homoplastic condition and this explains the limited value of this information. On the other hand, detailed studies on particular morphologies about carinae morphological variability can be potentially useful, providing apomorphic information. At the moment, the ziphomorph dentition constitutes a unique condition, therefore useful as diagnostic character for *Mariliasuchus* (as in ZAHER *et al.*, 2006). Similar tuberous denticles may be found in other genera, such as *Sphagesaurus*, *Notosuchus* and *Adamantinasuchus*. Detailed observation on the morphology of teeth and carinae, with additional comparison between specimens, is important and may provide reliable phylogenetic information regarding these taxa.

The use of modern techniques, such as SEM, should allow more precise definitions of the carinae in crocodyliforms and, eventually, the recognition of at least a few additional apomorphic patterns from the known ziphodont types. Such studies are important, as homoplastic generalizations may be converted in useful phylogenetic information, reducing “noise” in phylogenetic analysis.

MORPHOLOGICAL VARIATION OF TEETH AND DENTITION IN *MARILIASUCHUS AMARALI*

Previous works (CARVALHO & BERTINI, 1999; ANDRADE, 2005; VASCONCELLOS & CARVALHO, 2005, 2006; ZAHER *et al.*, 2006) provided a series of contributions on the knowledge of *Mariliasuchus*. Some morphological variation can be accounted for the material. The differences reported by VASCONCELLOS & CARVALHO (2006) for UFRJ specimens are mainly assumed as ontogenetic, though for UFRJ DG 56-R a taphonomic aspect should be considered, as this skull is not well-preserved. ZAHER *et al.* (2006), on the other hand, considered that MZSP-PV-51 could represent another species. Variation included the presence of: *foramen incisivum*, denser ornamentation, wider parietal width between the supratemporal fenestrae, and the presence of a frontal longitudinal ridge. At the moment, these variations were only identified for MZSP-PV-51 (ZAHER *et al.*, 2006) and URC specimens seem not to have such characters. Parietal width between the supratemporal fenestra is small for URC R•67, as in MN 6298-V, UFRJ DG-50, and MZSP-PV-50, but larger for MZSP-PV-51, UFRJ DG-106-R, and MN 6756-V. The description of ZAHER *et al.* (2006) presents the opposite condition to MN specimens, result of the mistaken reference of the identification codes. Variation on the skull table and parietal morphology is also known from *Notosuchus* (ANDRADE, 2005; FIORELLI, 2005), and might be related to sexual dimorphism, but proper data from a wider range specimens should be added before this hypothesis endure further consideration.

Although most of the carinae features described by ZAHER *et al.* (2006) could be verified, the additional tubercles on the base of the molariform crown labial surface are not present in any of the URC specimens. This is possibly due to the position of this molariform along the series, as URC R•75 was probably the fifth mandibular tooth. Ontogenetic differences constitute an alternative hypothesis, as the URC specimens are most likely subadults, thus younger than MZSP-PV-50.

The posteromedial orientation of the distal crest is common throughout the URC and MZSP specimens, especially related to molariform teeth that occlude with each other and are particularly developed, both on the maxilla and mandible (Fig.6). Nevertheless, this feature occurs in a clearly irregular manner along the range of individuals, and some of the teeth are not rotated, while others are clearly oblique. Differences could not be assigned to ontogenetic stages, and though the particular condition of UFRJ-DG material is unknown, VASCONCELLOS & CARVALHO (2005, 2006) report that a dietary ontogenetic variation is unlikely for *Mariliasuchus*. If *Mariliasuchus* maintained the same feeding pattern through its development, there is no basis for assuming that ontogenetic changes might be related to variations of tooth rotation. Variation could be due to preservation bias, but then the same variation would be expected to be present in the anterior dentition. To the moment, it can only be considered that *Mariliasuchus* by far does not show the regular arrangement of teeth for Mesoeucrocodylia, where the carinae are coincident to the dental series.

FUNCTIONAL INTERPRETATION OF THE ZIPHOMORPH PATTERN IN *MARILIASUCHUS AMARALI*

The differences observed between the three morphological patterns (ziphodont, false-ziphodont, and ziphomorph) are probably related to functional aspects of food processing and/or diet composition. The first two patterns are usually related to top-predator mesoeucrocodylians. Most typical zyphodont teeth has well developed carinae present in anterior, if not all teeth, as in *Baurusuchus*, *Pehuenchesuchus*, and *Sebecus* (RIFF & KELLNER, 2001; PRASAD & BROIN, 2002; TURNER & CALVO, 2005). These teeth are often compressed and strongly curved, exhibiting a typical morphology of a predator tooth. *Baurusuchus* seems to fit into this pattern for most characteristics, although teeth are more convex in the labial than in the lingual surface (RIFF & KELLNER, 2001), not as compressed as in the typical ziphodont forms. In cf. *Araripesuchus wegeneri* the morphology diverge broadly from the original definition (LANGSTON, 1975), as teeth do not show the same caniniform profile, although laterally compressed (PRASAD & BROIN, 2002; TURNER & CALVO, 2005; TURNER, 2006). While *Baurusuchus* is considered to present a ziphodont (theropodomorph) dentition (RIFF & KELLNER, 2001), the same can only be accepted for *Araripesuchus* by the broad ziphodont definition of PRASAD & BROIN (2002).

While the ziphodont theropod-like dentition is broadly used as a parameter to infer diet in crocodylomorphs, the same cannot be said for their contrapart, the ornitopods, sauropods, and prosauropods. It is true, though, that several herbivore dinosaurs had carinated teeth (GALTON, 1973, 1985, 1986; BARRETT, 2000). GALTON (1973, 1985, 1986) considers that differences on the carinae morphology (coarser denticles, less numerous, projecting at 45 degrees from the crown surface) should be indication of herbivore habit in prosauropods. At least partially, the ziphomorph pattern fits into *Mariliasuchus* description, except for the angle of denticle implantation. The projecting angle may not be relevant in this case, as denticles are round and tuberous, and it would be difficult to consider that a specific attack-angle could be of particular relevance. Futhermore, teeth specialization is not a prime requirement of herbivore diet, as other adaptations may allow food processing without leaving an evident fossil signal. This is exemplified by *Protorosaurus* (Late Permian, Germany), as mentioned by Barrett (2000). At least two specimens of this archosauromorph showed a gut content of *in situ* gastric mill and plant material from conifers and pterydosperms, even though possessing recurved and conical teeth (Munk & Sues, 1993).

Barrett (2000) points out that, regarding crocodylomorphs, dinosaurs, and lepidosauromorphs, the existence of certain features could indicate an herbivore diet, as extensive tooth wear associated with jaw antero-posterior motion, development of molariform teeth, loss/ modification of premaxilary teeth, and the presence of a dental battery. Most of these features also apply for *Mariliasuchus*. Nevertheless, Barrett's concept of herbivory does not exclude the carnivory, only indicating that the taxon is closer to the herbivorous end of the dietary spectrum (Barret, 2000). The same author also points out that dental correlates to omnivory have never been properly identified, meaning that it is only possible, to a certain extend, indicate the presence of vegetal or animal material in the diet, but not a definitive statement about feeding.

Nevertheless, *Mariliasuchus* certainly cannot be characterized as possessing a generalized dentition. In fact, as other notosuchians, there are clearly caniniform, incisiform and molariform teeth, which were functionally fitted for specific, and maybe complementary tasks. Its dentition showed carinae with denticles only in molariform teeth, as pointed out by Zaher *et al.* (2006), and this does not fit into a predator dentition for two main reasons: (1) serrations are not developing over anterior teeth, but over more posterior ones; (2) serrations are not developing over caniniforms, but over molariforms. Serrations are thus missing from all teeth that, for excellence, could be related to prey capture, especially the anterior hypertrophied caniniforms (Fig.6). Carinae are only present over the surface of teeth that could not participate of prey capture, particularly the sixth and seventh mandibulary teeth and the corresponding maxillary molariforms. This suggests that the carinae were important elements in food processing, not in capturing and killing prey. General aspects of the dentition and the distribution of the carinae on the dental series constitute evidence that *Mariliasuchus* was not a typical predator, such as *Sebecus* or *Baurusuchus*. Furthermore, the morphology of the denticles also support a non-predatorial habit for *Mariliasuchus*. As denticles are tuberous, they resemble a miniature molar tooth. Its value as a slashing tool should be no better than poor. Other general features support this hypothesis, as the long symphysis, high coronoid process and short rostrum (Figs.3,6). Dental features include proportionally short molariforms, mesiodistally and labiolingually expanded.

Three mandibulary pairs of teeth (sixth to eighth) and corresponding maxillary pairs are especially enlarged in all specimens (Zaher *et al.*, 2006, p.10, Fig.6), suggesting that they were able to cope with higher mechanical stress. Apart from this, Vasconcellos & Carvalho (2006) previously concluded that the ontogenetic development of some skull elements (*e.g.*, mandibular fenestra, laterotemporal fenestra) might indicate a gain of strength and resistance in the skull of *Mariliasuchus*, during its lifetime. Although there are other species clearly more adapted for a durophagic diet, such as *Sphagesaurus* (Pol, 2003; Andrade, 2005), the skull and teeth of *Mariliasuchus* (Fig.6) seems to be more fitted to forraging on harder and more abrasive items than to a diet of soft meat. The procumbent anterior dentition is clearly not what can be expected for a predator, although it may fit the idea of an insectivore species.

The occurrence of antero-posterior jaw movements in *Mariliasuchus* is possible, as the glenoid fossae are elongated (Andrade, 2005; Zaher *et al.*, 2006). This has been considered evidence of high-fiber ingestion in crocodylomorphs and other tetrapods (Maynard Smith & Savage, 1959; Wu *et al.*, 1995; Wu & Sues, 1996; Sues, 2000), but in a similar way the character could fit some very specific highly predatory forms (Clark *et al.*, 1989; Barrett, 2000). Herbivory was already proposed for *Notosuchus terrestris*, and related to the specialized dental morphology and jaw articulation (Bonaparte, 1987, 1991; Carvalho, 1994). These would allow a masticatory process resembling the ones observed in mammals, and inferred for therapsids and ornitischian dinosaurs (Bonaparte, 1991). The elongated mandibular articulation is concordant with worn surfaces of teeth in several *Mariliasuchus* specimens (Vasconcellos & Carvalho, 2005; Zaher *et al.*, 2006). The disposition of URC R•68 wear facets clearly supports this idea (Fig.6). The oblique implantation would allow apex to apex action. This contact becomes more extensive and lateral between the sixth to eighth mandibulary teeth and corresponding maxillary molariforms. The oblique disposition of these elements allowed at least some contact between the lingual surfaces of maxillary teeth and labial surfaces of mandibulary molariforms, resulting in inclined worn facets. Upon the existence of such an organized apparatus, food intake probably demanded elaborated processing of items, most likely undertaken by median maxillary and posterior mandibulary molariforms.

The presence of abrasion in the labial face of the hypertrophied caniniform is a special case, as it could not be produced by occlusion. These wear planes may constitute the effect of a preservation bias, as these teeth are highly exposed and could have been eroded. These facets could also develop as the result of a particular action over substrate (*e.g.*, bark, soil), and would fit in the specialized dentition of *Mariliasuchus*.

The rounded denticles of the carinae, the general skull structure, and the robust teeth from *Mariliasuchus amarali*, were not well suited for a typical predator. Molariform teeth are rather better tools for crushing or crumble fibrous, hard and/or abrasive food items (Bonaparte, 1991; Wu *et al.*, 1995; Wu & Sues, 1996; Sues, 2000). Abrasion is supported, in this case, by the occurrence of wear facets of *Mariliasuchus* molariform teeth. The existence of anterior-posterior abrasion planes is probably the result of fore-after movements of the mandible of *Mariliasuchus* (Zaher *et al.*, 2006).

While ziphodont crocodylomorphs are usually identified as carnivorous predators, *Mariliasuchus* had a ziphomorph dentition that was probably best suited for dealing with a variety of hard or fibrous items (*e.g.*, coarse leaves, seeds, pine-cones, but also arthropods), and inclusion of these in the diet is most likely, according to the information presented here and elsewhere (Vasconcellos & Carvalho, 2005, 2006; Zaher *et al.*, 2006). Evidence is composed by the morphology of the carinae and its denticles (ziphomorph pattern), in association with several other indicators, such as: absence of carinae and specialization of the anterior dentition; morphology of the jaw-joint articulation; elongation and inclination of wear planes; preferential occurrence of wear planes in posterior teeth; posterior dentition composed of non-shearing molariforms. All those features are indicative of ingestion of plants, while does not exclude the intake of animal material (*e.g.*, arthropods, worms, small vertebrates). The teeth morphology and interpretation are very different for *Mariliasuchus* and ziphodont crocodylomorphs, such as *Baurusuchus* and *Sebecus*. The inclusion of items other than meat is likely and, by morphological and functional aspects, its characterization as a ziphodont species seems highly inaccurate, or at least an unnecessary simplification.

CONCLUSIONS

The dentition of *Mariliasuchus* shows what we characterize as ziphomorph carinae. This pattern is defined as carinae composed by tuberous anisomorphic true denticles, without the development of enamel ornamentation over the denticles composing the carinae. In *Mariliasuchus*, the ziphomorph pattern is associated with molariform teeth, and its function is related to food processing rather than prey capturing and killing. At least in *Mariliasuchus*, the typical ziphodont and the new ziphomorph patterns are functionally different, the first one related to prey capture and killing (Langston, 1956, 1975), and the second one to food processing. Elaborated food intake and preference for hard and abrasive food items is supported by general skull features, elongated glenoid fossae and the dentition, development of molariforms, and the occurrence of wear facets (Maynard Smith & Savage, 1959; Wu *et al.*, 1995; Wu & Sues, 1996; Sues, 2000; Zaher *et al.*, 2006). *Adamantinasuchus*, *Sphagesaurus* and *Notosuchus* show similar dental features that suggest that the ziphomorph pattern is present in these taxa.

The ziphodont pattern does not provide reliable phylogenetic information because it represents a homoplastic feature, the result of overlooking cryptic information. The study of carinae morphology under SEM will provide further information for several taxa, as foreseen by Prasad & Broin (2002), and shall provide useful apomorphic characters for phylogenetic studies. Information on tooth morphology of several species of Mesoeucrocodylia is especially poor, but should contribute to the resolution of several systematic and taxonomic problems on the evolution of this particular group. The description here of the ziphomorph pattern also brings the idea of a wider range of diverse, unique morphologies and specializations, which were present during the Cretaceous.

Additionally, comparative investigations among dental material from Crocodylomorpha, Dinosauria, and other groups of the Archosauromorpha, may help the characterization of species and morphotypes, allowing the distinction of isolated teeth.

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NEW REMAINS OF *NOTOSUCHUS TERRESTRIS* WOODWARD, 1896 (CROCODYLIFORMES: MESOEUCROCODYLIA) FROM LATE CRETACEOUS OF NEUQUÉN, PATAGONIA, ARGENTINA [1]

(With 17 figures)

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ABSTRACT: New materials of *Notosuchus terrestris* are here described. They were found on Bajo de la Carpa Formation outcrops, near the Universidad Nacional del Comahue, Neuquén City. Descriptions were based on five specimens, one of them the only specimen of *Notosuchus* with postcranial remains articulated to the skull. As in *Sphagesaurus*, it presents triangular teeth in cross-section and oblique molariforms with worn facet surface. As in *Mariliasuchus*, it possesses procumbent mandibular incisiform teeth and, like in other notosuchians and basal crocodyliforms, it was able of proal mandibular movement. The centra of cervical vertebrae possess ventral keel as in *Chimaerasuchus*. Elongated cervical neural spines and suprapostzygapophyseal laminae in cervicodorsal vertebrae are observed. The scapular dorsal end is greatly enlarged, while the coracoid ventromedial process end is moderately developed. The dorsal surface of the ilium is lateromedially wide with a greatly expanded acetabular roof and a prominent anteromedial process in the femoral shaft. Based on diverse cranial and postcranial characters, we infer that *Notosuchus* possessed facial and perioral musculature well developed and an herbivore diet, confirming the suggestions of previous authors. *Notosuchus* represents, based on phylogenetic studies, the sister taxon of *Mariliasuchus* and the monophyly of Notosuchia is demonstrated. Paleobiogeographycally, the occurrence of *Chimaerasuchus* in China evidences the faunistic interchange between Gondwana and Central Asia during the Early Cretaceous.

Key words: Mesoeucrocodylia. *Notosuchus terrestris*. Cretaceous. Articulate remains. Functional anatomy.

RESUMO: Novos restos de *Notosuchus terrestris* Woodward, 1896 (Crocodyliformes: Mesoeucrocodylia) do Cretáceo Superior de Neuquén, Patagônia, Argentina.

Novos materiais de *Notosuchus terrestris* são aqui descritos. Eles provêm de afloramentos da Formação Bajo de la Carpa, localizados próximos à Universidad Nacional del Comahue, na cidade de Neuquén. As descrições foram baseadas em cinco exemplares, um deles o único espécime de *Notosuchus* com restos pós-cranianos articulados ao crânio. Como em *Sphagesaurus*, *N. terrestris* apresenta dentes triangulares em seção cruzada e molariformes oblíquos com superfície da faceta com desgaste. Como em *Mariliasuchus*, a espécie possui dentes mandibulares incisiformes procumbentes e, como em outros notossúquios e crocodiliformes basais, era possível realizar o movimento antero-posterior mandibular. Os centros das vértebras cervicais possuem uma quilha ventral como em *Chimaerasuchus*. Espinhos neurais cervicais alongados e lâminas suprapószigapofiseais em vértebras cérvico-dorsais são observados. A extremidade escapular dorsal é amplamente alargada, enquanto a extremidade do processo ventro-medial do coracóide é pouco desenvolvida. A superfície dorsal do ilium é larga látero-medialmente com um teto acetabular amplamente expandido e processo ântero-medial proeminente na diáfise femoral. Baseado em diversos caracteres cranianos e pós-cranianos, infere-se que *Notosuchus* apresentava grande desenvolvimento da musculatura facial e perioral e tinha uma dieta herbívora, confirmando o que foi sugerido anteriormente por outros autores. *Notosuchus* representa, baseado em estudos filogenéticos, o táxon irmão de *Mariliasuchus* e a monofilia de Notosuchia é demonstrada. Paleobiogeograficamente, a ocorrência de *Chimaerasuchus* na China evidencia o intercâmbio faunístico entre o Gondwana e a Ásia Central durante o Cretáceo Inferior.

Palavras-chave: Mesoeucrocodylia. *Notosuchus terrestris*. Cretáceo. Restos articulados. Anatomia funcional.

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INTRODUCTION

Notosuchia is a clade of small to medium basal brevirostrine Mesoeucrocodylia. Most of their taxa were registered and gathered in regions that were part of the old Gondwana during the Cretaceous. These taxa are represented by several species. *Notosuchus terrestris* Woodward, 1896 and *Comahuesuchus brachybuccalis* Bonaparte, 1991 come from the Upper Cretaceous of Argentina (Woodward, 1896; Gasparini, 1971; Bonaparte, 1991; Martinelli, 2003). *Candidodon itapecuruense* Carvalho & Campos, 1988 comes from the Early Cretaceous of Brazil (Carvalho, 1994; Nobre & Carvalho, 2002). *Sphagesaurus huenei* Price, 1950, *Adamantinasuchus navae* Nobre & Carvalho, 2006, and *Mariliasuchus amarali* Carvalho & Bertini, 1999 come from the Upper Cretaceous of Brazil (Price, 1950; Pol, 2003; Nobre & Carvalho, 2006; Carvalho & Bertini, 1999). Both species of *Uruguaysuchus*, *U. aznarezi* Rusconi, 1933 and *U. terrai* Rusconi, 1933, come from the Cretaceous of Uruguay (Rusconi, 1933) and were posteriorly included in the Notosuchia (Gasparini, 1971). From Africa, there are records of *Malawisuchus mwakasyungutiensis* Gomani, 1997, that comes from the Early Cretaceous of Malawi (Clark *et al.*, 1989; Gomani, 1997), *Anatosuchus minor* Sereno, Sidor, Larsson & Gado, 2003, from the Aptian-Albian of the Republic of Niger (Sereno *et al.*, 2003), and *Simosuchus clarki* Buckley, Brochu, Krause & Pol, 2000, from the Upper Cretaceous of Madagascar (Buckley *et al.*, 2000). Finally, *Chimaerasuchus paradoxus* Wu, Sues & Sun, 1995 comes from the Early Cretaceous of China (Wu *et al.*, 1995; Wu & Sues, 1996). In recent works, other notosuchians forms of different sites from South America have been notified (*e.g.*, Novas *et al.*, 2004; Andrade & Bertini, 2005a; Garcia *et al.*, 2005; Marconato, 2006); these forms are still under study but they may indicate a greater diversity of notosuchians in the continent. Phylogenetic relationships of Notosuchia have been discussed by many authors (Clark, 1994; Wu & Sues, 1996; Buckley *et al.*, 2000; Ortega *et al.*, 2000; Martinelli, 2003; Sereno *et al.*, 2003; Pol, 2003; Andrade, 2005; Pol & Apesteguia, 2005; Fiorelli, 2005; Zaher *et al.*, 2006). However, there is not a common agreement about them.

Notosuchus terrestris is a Crocodyliform with terrestrial and cursorials habits, with a short and relatively high skull, presenting plesiomophic and derived characteristics (Gasparini, 1971; Bonaparte, 1991; Pol, 2005; Fiorelli, 2005). For instance, in the rostral region of the muzzle, teeth and articular region, that present characteristics only developed in other notosuchians (Gasparini, 1971; Bonaparte, 1991; Wu & Sues, 1996; Gomani, 1997; Carvalho & Bertini, 1999; Pol, 2003; Fiorelli, 2005; Andrade, 2005; Nobre & Carvalho, 2006; Zaher *et al.*, 2006).

The first remains of *Notosuchus* were found in Neuquén Province at the end of the XIX century and Woodward (1896) was the one who carried out the first publication. Later, Gasparini (1971) and Bonaparte (1991), restudied the material described by Woodward together with new cranial materials, reaching important conclusions regarding their anatomy and phylogenetic relationships. Recently, new postcranial materials of *Notosuchus* were described in detail (POL, 2005). Due to the strong association with cranial remains, they were assigned to the taxon.

Since the first publication of Woodward, more than 50 skulls were recovered, some of them complete, collected in different paleosites of Bajo de la Carpa Formation. Few remains of postcranial materials were found associated, but not articulated to these skulls (Woodward, 1896; Pol, 1999, 2005), being a limiting factor to certify these studies. Here we describe new cranial materials associated and articulated to postcranial pieces of *Notosuchus terrestris*.

MATERIAL AND METHODS

Abbreviations: Institutional. MACN: Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MLP: Museo de Ciencias Naturales de La Plata, La Plata, Argentina; MUCP: Museo de Geología y Paleontología, Universidad Nacional del Comahue, Neuquén, Argentina.

MATERIAL

All the remains of *Notosuchus terrestris* described in the present work were collected in the south hill of the Neuquén River and in the current universitary campus of the Universidad Nacional del Comahue, located in North of Neuquén City (Fig.1). Outcrops belong to Bajo de la Carpa Formation, Río Colorado Subgroup, Neuquén Group (Digregorio, 1972; Cazau & Uliana, 1973; Ramos, 1981; Leanza *et al.*, 2004) (Fig.1).

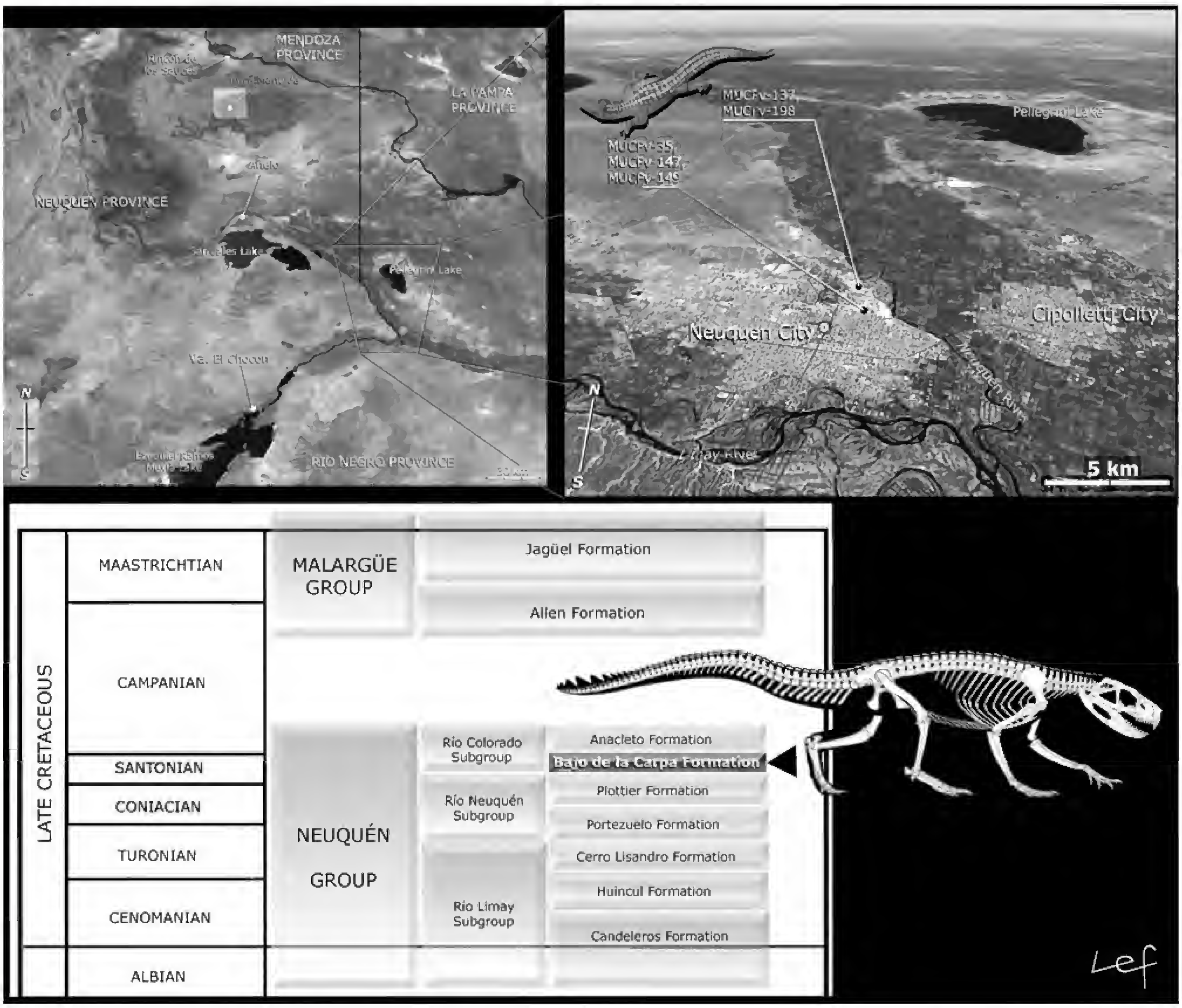

Fig.1- Up left: satellite map of Northern Patagonia region showing the location of the Neuquén Province and Comahue region. Up right: area of the Comahue and Neuquén City where were found and collected the materials of *Notosuchus terrestris* (MUCPV-35, 137, 147, 149 and 198). Below: stratigraphy of the Cretaceous of Neuquén Basin and stratigraphic column of the Neuquén Group (modified from LEANZA *et al.*, 2004).

GEOLOGICAL SETTINGS

Bajo de la Carpa Formation is one of the most homogeneous units in the Neuquén Group widely distributed with outcrops on the north, center and east of Neuquén Province, as well as towards the northwest of Río Negro Province. This Formation is composed of coarse-grained, light violet and pink sandstones of fluvial origin and it is Santonian in age (LEANZA *et al.*, 2004). This formation is registered in the paleontological site in the campus of the Universidad Nacional del Comahue. Besides *Notosuchus* remains, a wide variety of other crocodyliforms such as *Cynodontosuchus rothi* Woodward, 1896, *Comahuesuchus brachybuccalis*, *Neuquensuchus universitas* FIORELLI & CALVO, 2007, and considerable remains of a new peirosaurid crocodyliform (FIORELLI *et al.*, 2007); dinosaurs: *Alvarezsaurus calvoi* Bonaparte, 1991, *Velocisaurus* *unicus* Bonaparte, 1991, *Neuquenornis volans* Chiappe & Calvo, 1994, *Patagopteryx deferrariisi* Alvarenga & Bonaparte, 1992, cf. *Laplatasaurus* (Leanza *et al.*, 2004), Titanosauridae indet. (Chiappe & Calvo, 1994; pers. obs.), *Neuquensaurus* sp. (pers. obs.), *Antarctosaurus* Huene, 1929, and *Bonitasaura salgadoi* Apesteguía, 2004 (Bonaparte, 1991; Chiappe & Calvo, 1994; Alvarenga & Bonaparte, 1992; Bonaparte, 1992; Apesteguía, 2004); snakes: *Dinilysia patagonica* Woodward, 1901 (Woodward, 1901); a countless nests of birds containing small eggs with embryos (Schweitzer *et al.*, 2002), and dinosaur egg shells of *Megaloolithus patagonicus* Calvo, Englland, Heredia & Salgado, 1997 (Calvo *et al.*, 1997).

The remains of the peirosaurids *Lomasuchus palpebrosus* Gasparini, Chiappe & Fernandez, 1991 and *Peirosaurus tormini* Price, 1955 together with the remains of the turtle *Lomalatachelys* Broin & De La Fuente, 2001 coming from outcrops on the North Coast of Barreales Lake were assigned by Leanza *et al.* (2004) to the Bajo de la Carpa Formation. However, recent works show that the patagonian *L. palpebrosus* comes from the Portezuelo Formation (Upper Turonian – Lower Coniacian).

SYSTEMATIC PALEONTOLOGY

Crocodylomorpha Walker, 1970
Crocodyliformes Hay, 1930
(*sensu* Benton & Clark, 1988)
Mesoeucrocodylia Whetstone & Whybrow, 1983
Metasuchia Benton & Clark, 1988
Notosuchia Gasparini, 1971
Notosuchidae Dollo, 1914
Notosuchus Woodward, 1896

Type-species – *Notosuchus terrestris* Woodward, 1896.

Junior synonym *Notosuchus lepidus* Saez, 1957 (Gasparini, 1971)

Lectotype – MLP 64-IV-16-5, skull and jaw designated by Gasparini (1971).

Referred specimens – MUCPv-35: skull and anterior part of jaw (Fig.2); MUCPv-137: skull and incompletely articulated postcranial, together with associated postcranial remains (Fig.3); MUCPv-147: complete and articulated skull and jaw with associated postcranial remains (Fig.4); MUCPv-149: associated postcranial remains (Fig.5); MUCPv-198: cranial and disarticulated fragmentary postcranial associated materials (Fig.6).

Type-locality – The specimens MUCPv-35, MUCPv-147 and MUCPv-149 were found in the campus of the Universidad Nacional del Comahue, while MUCPv-137 and MUCPv-198 were found on the south hill of the Neuquén River, Neuquén Province, Argentina (Fig.1).

Type-horizon – Bajo de la Carpa Formation (Ramos, 1981), Río Colorado Subgroup, Neuquén Group (Santonian; Leanza *et al.*, 2004) (Fig.1).

Diagnosis (modified from Woodward, 1896 and Gasparini, 1971) – Extremely short and relatively high skull, with confluent and terminal external nares, vertical and anteriorly positioned, without nasal sept. Big orbit laterodorsally directed, covered partial and dorsally with anterior and posterior palpebrals. Rostrum lightly higher than wide. The premaxilla presents two (or three) incisiforms, a hipertrophied caniniform tooth, and a postcaniniform tooth (first molariform); each maxilla possesses 6 molariform teeth, depending on the specimen. The jaw exhibits a great lateral fenestra, anteroposteriorly lengthened. The occipital condyle is posteroventrally directed. Cervical vertebrae have slightly amphicoelous centra with a ventral kell and relatively high neural spines. Zygapophyses are width from the fourth to the eighth cervical vertebra and the cervical parapophyses are low. Presence of suprapostzygapophyseal lamina in cervicodorsal vertebrae. Presence of three sacral vertebrae fused between the second and third. Dorsal end of the scapula greatly enlarged. Distal end of the ventromedial process of the coracoid poor developed. Dorsal surface of the ilium lateromedially and acetabular roof both width. Femoral shaft with a well developed anteromedially directed process on the distal end.

RESULTS

Description of the material

We describe novel information about the cranial and postcranial anatomy of *Notosuchus*. Further data must be remitted to previous published references (Woodward, 1896; Gasparini, 1971; Bonaparte, 1991, 1996; Pol, 1999, 2005; Martinelli, 2003; Andrade, 2005; Andrade & Bertini, 2005a; Fiorelli, 2005).

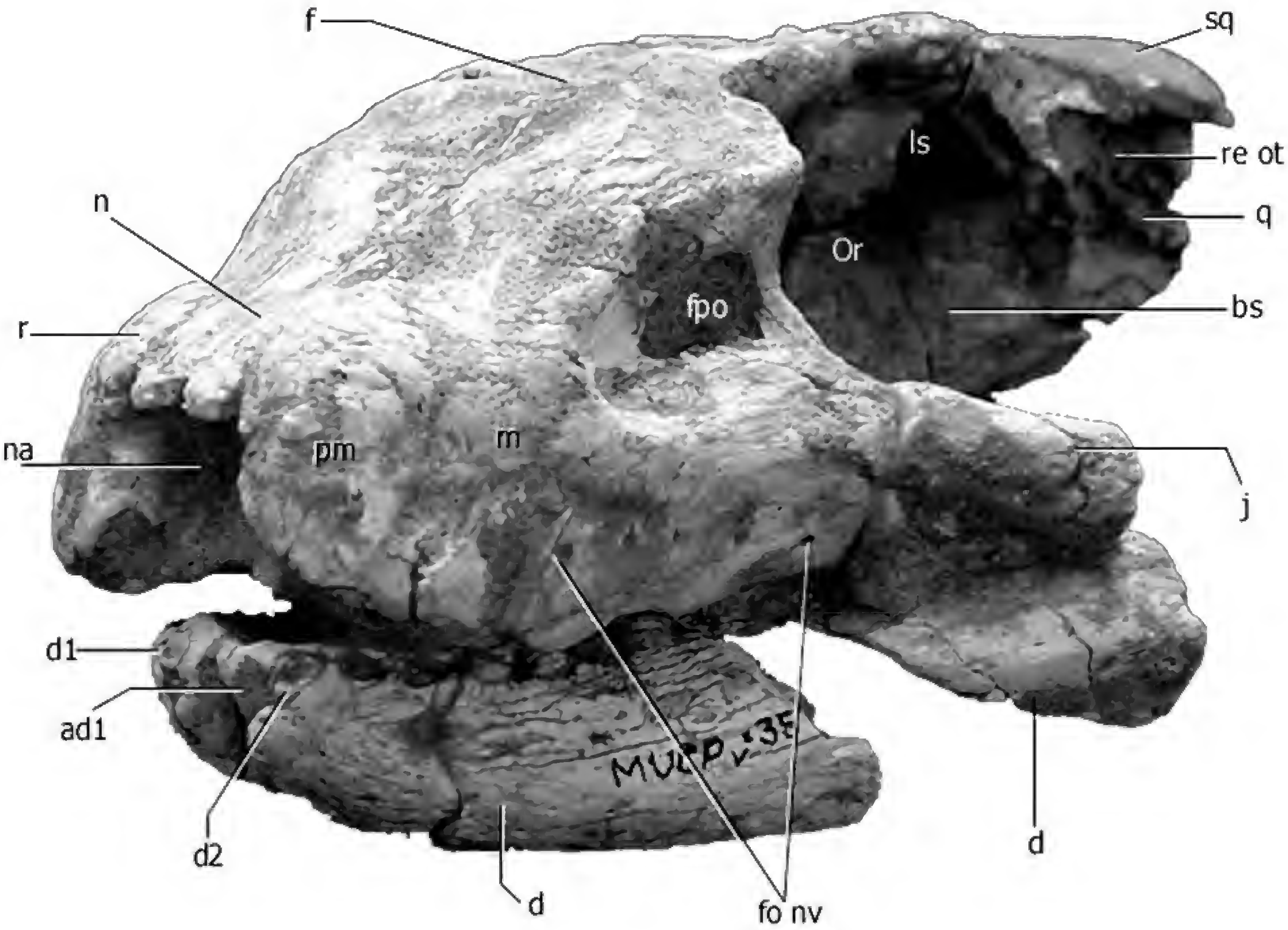

Fig.2- *Notosuchus terrestris*, MUCPv-35, referred materials. Skull and jaw in left anterolateral view. Abbreviations: (ad1) first dentary alveolus, (bs) basisphenoid, (d) dentary, (d1) first dentary tooth, (d2) second dentary tooth, (f) frontal, (fo nv.) neurovascular foramina, (fpo) anterorbital fenestra, (j) jugal, (ls) laterosphenoid, (m) maxilla, (n) nasal, (na) external nares, (Or) orbita, (pm) premaxilla, (q) quadrate, (r) protuberances and ruggedness, (re ot) otic region - otic groove, (sq) squamosal.

Skull – Cranial remains of specimens studied possess slight variations in sizes and longitude, due probably to ontogenetic and/or sexual differences (*e.g.*, the anteroposterior length – MUCPv-35: 142mm; MUCPv-137: 123mm; MUCPv-147: 137,9mm). The robustness as well as the ornamentations and ruggedness in the surface of the cranial bones varieties depend on the specimen. (MUCPv-35 is the most robust with much ruggedness and ornamentations).

Each premaxilla (Fig.7) is high, lateral and vertically exposed and unfused in ventral view with two incisiform teeth. However, it is probable that in between another smaller incisiform tooth is located between them, although in the specimen studied here these structures are not present. Contrary to notosuchians like *Sphagesaurus* (Pol, 2003) and *Chimaerasuchus* (Wu & Sues, 1996), *Notosuchus* and *Comahuesuchus* do not have a foramen incisivum in the premaxilla-maxilla suture (Bonaparte, 1991; Martinelli, 2003). Possibly, this suture would have been constituted by a delicate bony lamina, supporting the third incisiform (Figs.7C, 8A). The lack of bony nasal sept indicates the presence of cartilaginous conjunctive tissues corroborating therefore the observed and conjectured by other authors (Bonaparte, 1991; Andrade, 2005; Fiorelli, 2005; Fiorelli & Calvo, 2005).

The hiperatrophied caniniform implanted in the premaxilla is vertically directed with its root slightly curved posteriorly (Figs.7, 8). A premaxillary tooth near to this caniniform (Bonaparte, 1991) represents the first molariform tooth of the series (seen in MUCPv-35 and MUCPv-147) (Andrade *et al.*, 2006).

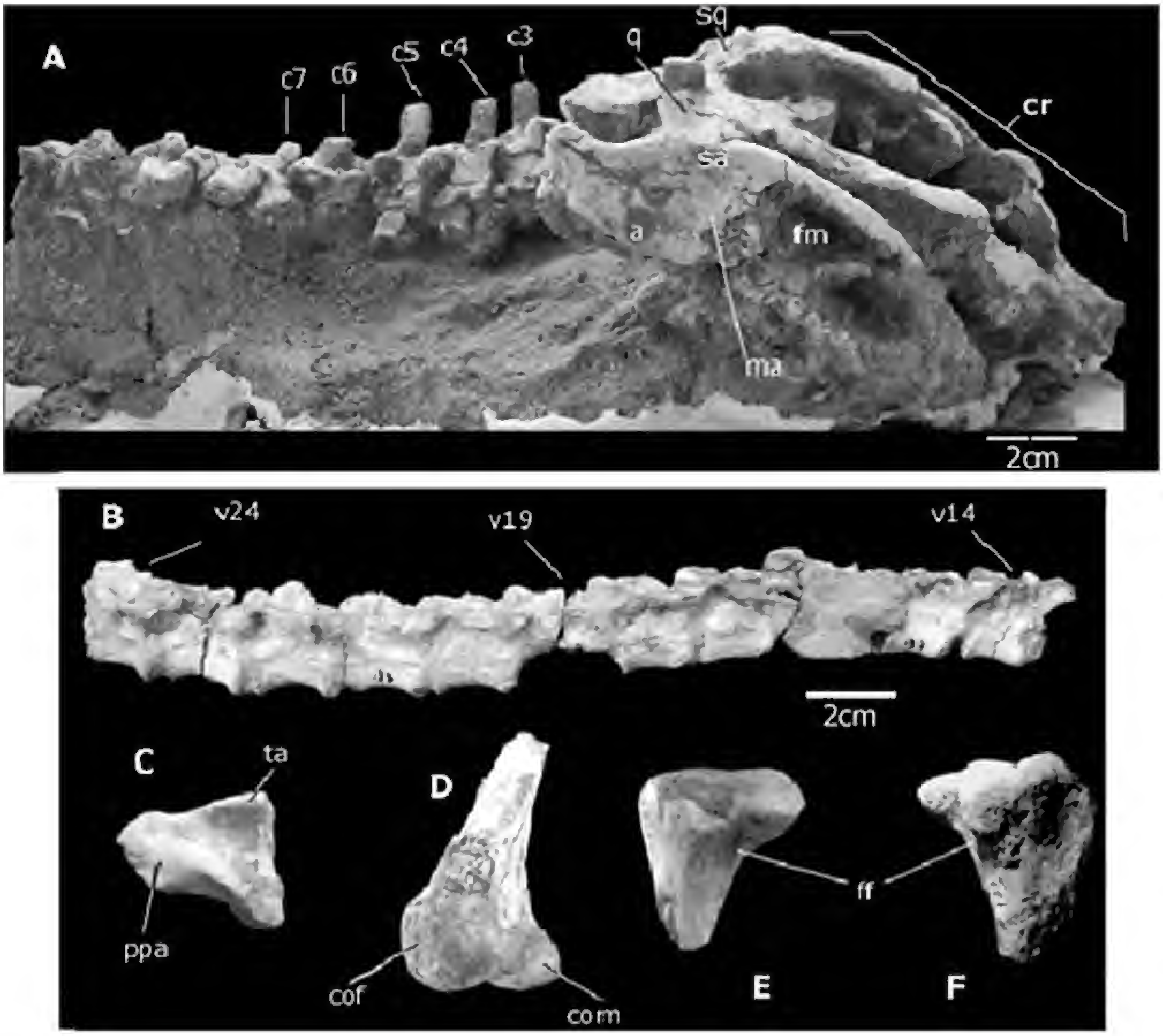

Fig.3- *Notosuchus terrestris*, MUCPv-137, referred materials. A, skull and articulated postcraneal in right lateral view. B, anterior and medial dorsal vertebrae in right lateral view. C, posterior fragment of the right ilium in lateral view. D, distal fragment of the left femur in lateral view. E and F, proximal fragments of both tibiae in posterolateral view (E, left tibia; F, right tibia). Abbreviations: (a) angular, (c) caniniform, (cof) fibular condyle, (com) medial condyle, (cr) cranium, (ff) fossa flexoria, (fm) mandibular fenestra, (ma) mandible, (ppa) postacetabular process, (q) quadrate, (sa) surangular, (sq) squamosal, (ta) acetabular roof, (v) vertebra.

Nasals are elongated and wide posteriorly. They form the dorsal end of the nares (Figs.7A, D). At the level of the antorbital fenestra, nasals are narrowed abruptly, forming a "V-shaped" contact surfaces with the lacrimals and prefrontals. On the nasals medial contact a longitudinal concavity with striations posteroanteriorly directed is developed (deeper in MUCPv-35 and MUCPv-147 but practically null in MUCPv-137).

A deep study of maxilla was done by BONAPARTE (1991); however, new data can be added. There is a longitudinal edge that defines the boundaries between the upper (rugged) and the lower (smooth) surfaces, due to the presence of strongly marked striations above the alveolar zone (Figs.7A, B). Below the alveolar zone and posteriorly, the maxilla possesses a relatively large foramen not seen in other specimens (MUCPv-35 and MUCPv-147).

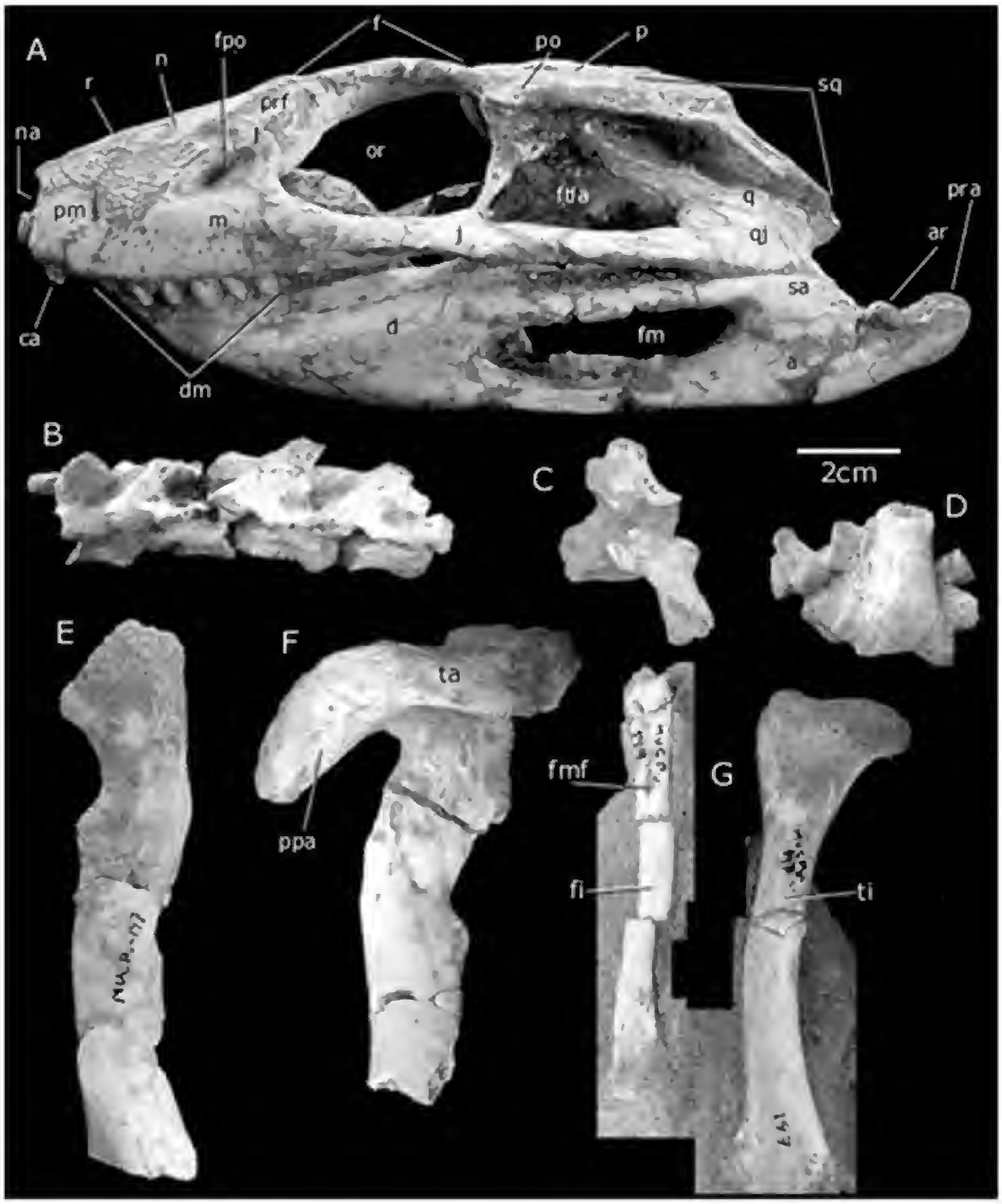

Fig.4- *Notosuchus terrestris*, MUCPv-147, referred materials. A, complete skull in left lateral view. B, posterior dorsal vertebrae in right lateral view. C, medial dorsal vertebra in right lateral view. D, distal end of the right tibia in anterior view. E, left femur in anterior view. F, right ilium in dorsal view and right fêmur in anterior view. G, left tibia and fibula in posterior view. Abbreviations: (a) angular, (ar) articular, (ca) caniniform, (d) dentary, (dm) maxillary teeth, (f) frontal, (fi) fibula, (fm) mandibular fenestra, (fmf) fossa medial fibular, (fpo) anterorbital fenestra, (ftla) infratemporal fenestra, (m) maxilla, (n) nasal, (na) external nares, (or) orbita, (p) parietal, (pm) premaxilla, (po) postorbital, (ppa) postacetabular process, (pra) retroarticular process, (prf) prefrontal, (q) quadrate, (qj) quadratojugal, (r) protuberances and ruggedness, (sa) surangular, (sq) squamosal, (ti) tibia.

The presence of dorsoventrally lineal striations associated to foramens indicates the presence of soft tissues to avoid food loss during the mastication (Bonaparte, 1991; 1996; Gomani, 1997; Fiorelli, 2005).

The features most remarkable in the maxilla are the teeth (Figs.7A, B, C, 8). Each maxilla possesses six molariform teeth. The first maxillary tooth is the second molariform in the series. Many authors proposed this kind of teeth as being of the ziphodont type, which would imply carnivore habits for *Notosuchus* and other notosuchians (Price, 1959; Gasparini, 1971; Benton & Clark, 1988; Clark *et al.*, 1989; Wu *et al.*, 1995; Wu & Sues, 1996; Buckley *et*

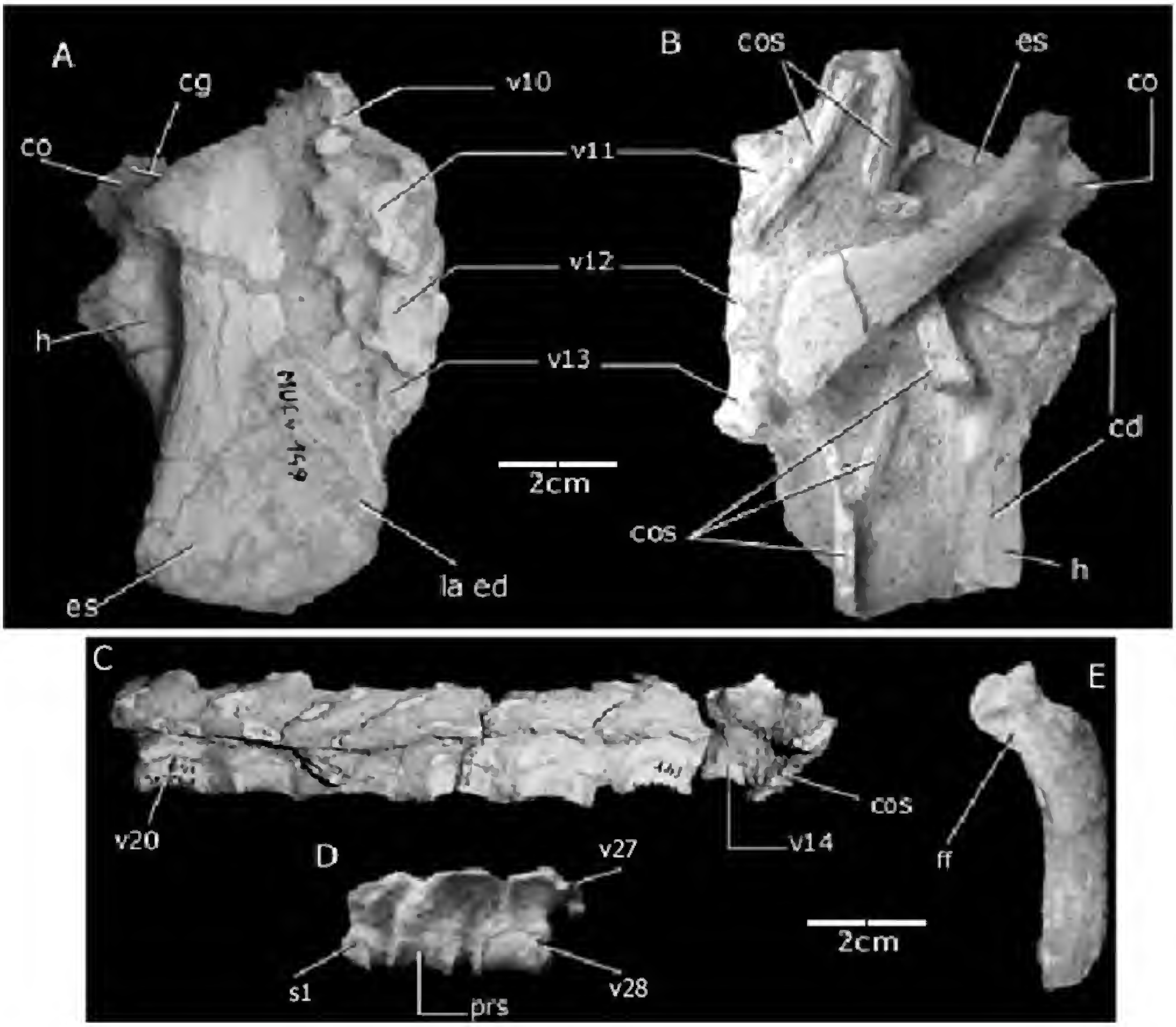

Fig.5- *Notosuchus terrestris*, MUCPv-149, referred materials. A and B, block containing the last cervical -10- and first dorsal vertebrae, left scapula, left coracoid, left humerus and ribs (A, in dorsal view and B, in ventral view). C, anterior and medial dorsal vertebrae in right lateral view. D, posterior dorsal vertebrae and fragment of the first sacral vertebra in right lateral view. E, fragment of the right tibia in posterolateral view. Abbreviations: (cd) deltoid crest, (cg) glenoid cavity, (co) coracoid, (cos) ribs, (es) scapula, (ff) fossa flexoria, (h) humerus, (la ed) anterior scapular lamina, (prs) presacral vértebra, (s1) first sacral vertebra, (v) vertebra.

al., 2000; Ortega *et al.*, 2000). Other authors suggested a similar situation in *Mariliasuchus*, a Notosuchia very related with *Notosuchus*, which also could be considered a ziphodont crocodyliform (Andrade, 2005; Andrade & Bertini, 2005b). By definition, there are two ziphodont teeth types: "true ziphodont", that possess laterally compressed crown with posteriorly recurved apex, anterior and posterior carinae bearing a number of isolated festoon-like denticles (serrations) (Fig.8D); and "false ziphodont", that possesses the anterior and posterior carinae relatively coarse and bear crenulations generally formed by anastomising, irregular ridges issued from the main body of the crown (Fig.8E) (Langston, 1975; Prasad & Broin, 2002). Molariform teeth of *Notosuchus* possess blunt apexes and they

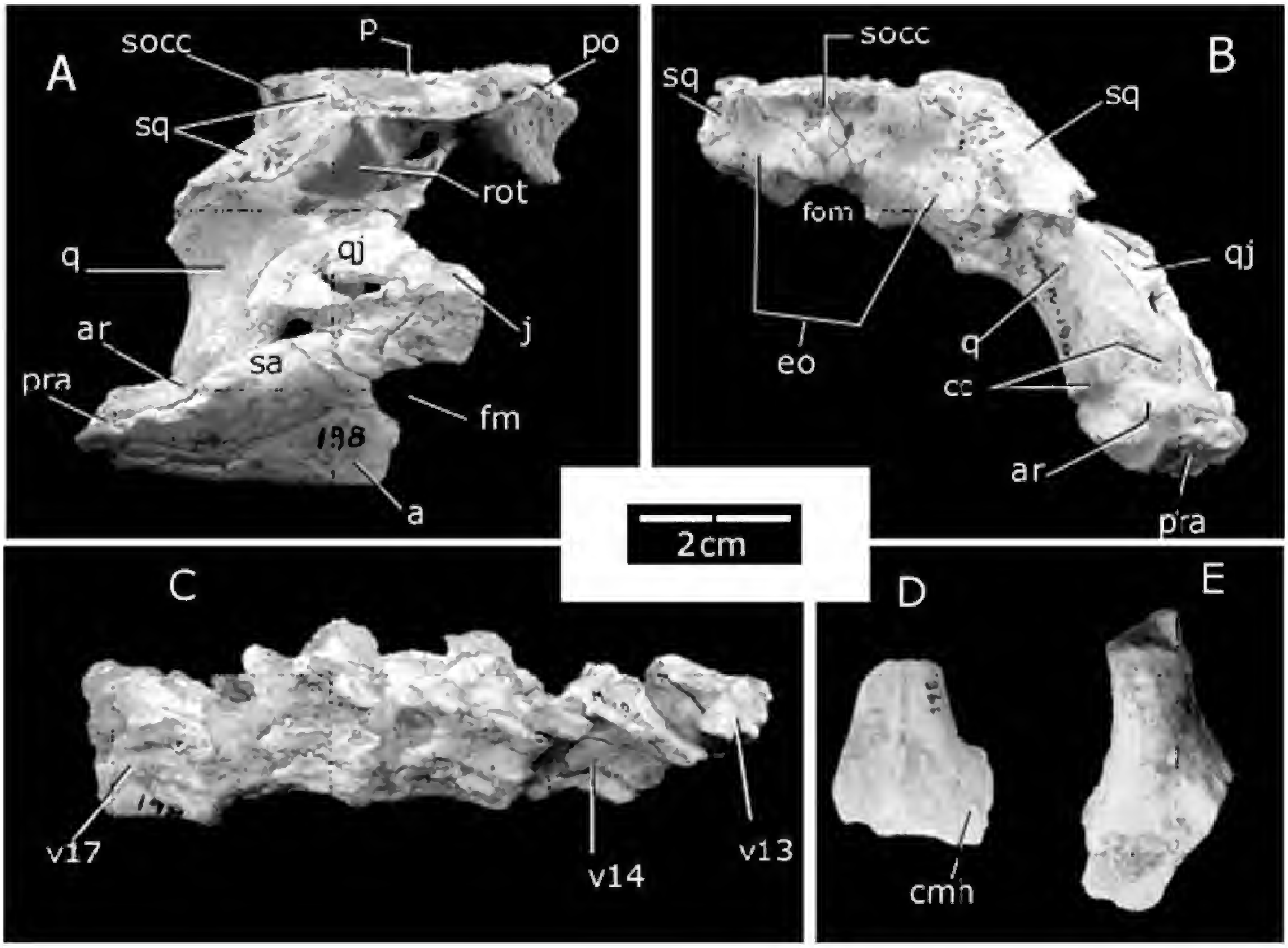

Fig.6- *Notosuchus terrestris*, MUCPv-198, referred materials. A and B, posterior section of the skull and mandible in right lateral view (A) and occipital view (B). C, anterior dorsal vertebrae in right lateral view. D, distal fragment of the left humerus in anterior view. E, distal fragment of the left tibia in anterior view. Abbreviations: (a) angular, (ar) articular, (cc) quadrate condiles, (cmh) medial condyle of humerus, (eo) exoccipital, (fm) mandibular fenestra, (fom) foramen magnum, (j) jugal, (p) parietal, (po) postorbital, (pra) retroarticular process, (q) quadrate, (qj) quadratojugal, (rot) semilunar otic groove, (sa) surangular, (socc) supraoccipital, (sq) squamosal, (v) vertebra.

are implanted obliquely to the longitudinal axis (Bonaparte, 1991; Fiorelli, 2005) (Figs.7C, 8A) with the sharpened border posterolingually located and triangular in traverse section, similar to *Sphagesaurus* (Pol, 2003), *Mariliasuchus* (Andrade & Bertini, 2005b; Zaher *et al.*, 2006), *Adamantinasuchus navae* (Nobre & Carvalho, 2006), and clearly visible in MUCPv-35 (Figs.8B, C). The diameter increases from the middle of the maxillary sequence and decreases anterior and posteriorly. By contrast, in *Sphagesaurus*, the diameters of the teeth decrease from the anterior to posterior ones. Although there is some matrix covering over the skull and jaw, the molariforms of MUCPv-147 have several spaced longitudinal carinae, as in *Sphagesaurus* (Pol, 2003) and *Mariliasuchus* (Andrade & Bertini, 2005b; Zaher *et al.*, 2006). The carinae can also be seen over the sixth left molariform of MUCPv-35. There are neither denticles on these carinae, nor the sharp posterolingual border. The anterolingual internal surface of the molariform presents, as in *Sphagesaurus* (Pol, 2003) and *Mariliasuchus* (Andrade & Bertini, 2005b; Zaher *et al.*, 2006), a worn surface extending from the apex until the lingual border of the tooth, near the alveolar border (Figs.7C, 8A). These anatomical-structural characteristics of the molariform teeth of *Notosuchus* are not framed inside the definition of "typical teeth ziphodonts true or false".

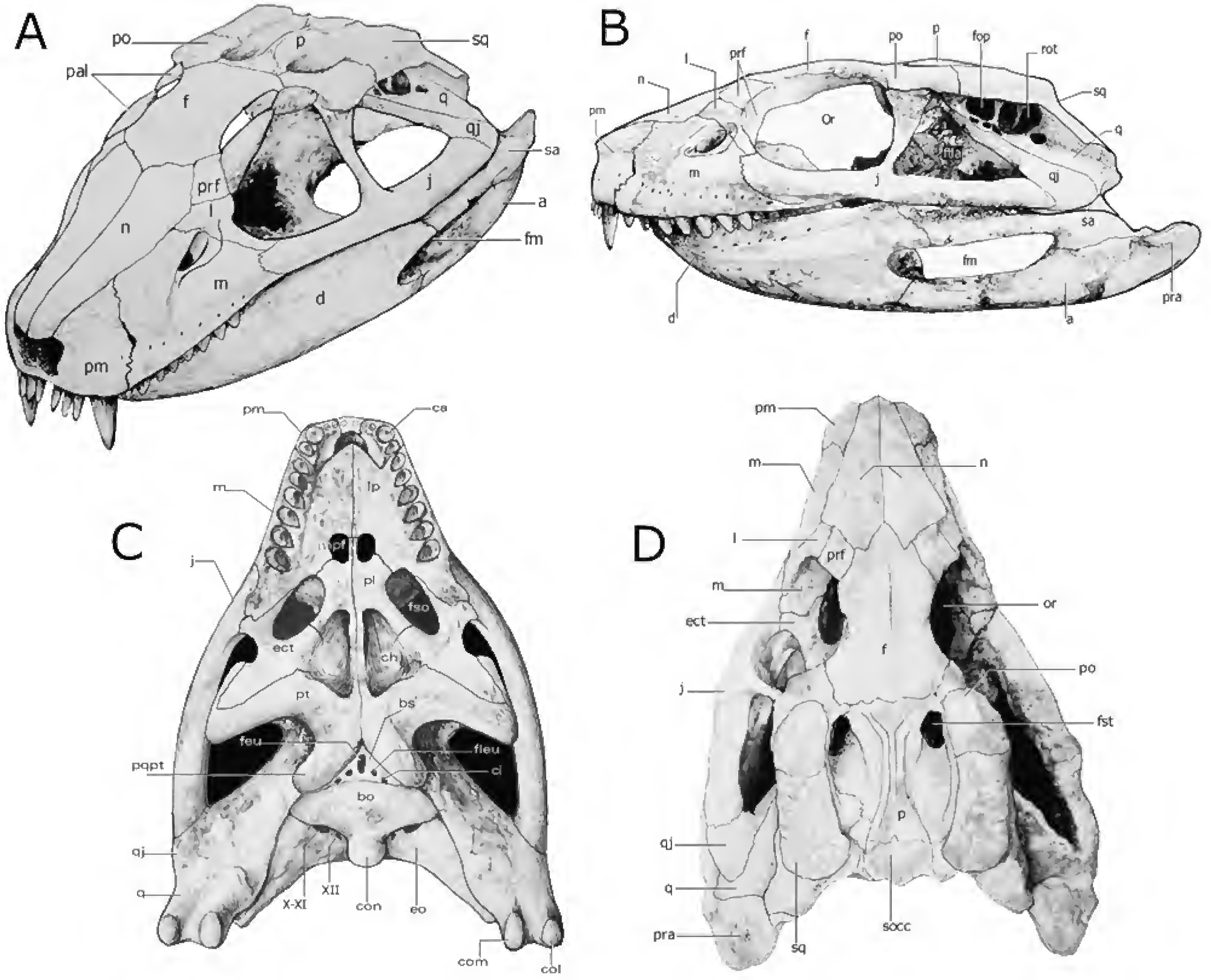

Fig.7- *Notosuchus terrestris*. Skull and jaw restoration based on the specimens MUCPv-35, MUCPv-137 and MUCPv-147. A: in left dorso-anterolateral view. B: in left lateral view. C: in palato-occipital view, without the mandible. D: in dorsal view. Abbreviations: (a) angular, (bo) basioccipital, (bs) basisphenoid, (ca) caniniform, (ch) choanal passage, (ci) internal carotide, (col) lateral condyle, (com) medial condyle, (con) occipital condyle, (d) dentary, (ect) ectopterigoid, (eo) exoccipital, (f) frontal, (feu) eustachian foramen, (fleu) lateral eustachian foramen, (fm) mandibular fenestra, (fop) preotic foramen, (ftla) infratemporal fenestra, (fso) suborbital fenestra, (fst) supratemporal fenestra, (j) jugal, (l) lacrimal, (lp) maxilo-palatal lamina, (m) maxilla, (mpf) maxilopalatal fenestra, (n) nasal, (Or, or) orbita, (p) parietal, (pal) palpebral, (pl) palatine, (pm) premaxilla, (po) postorbital, (pqpt) quadrate process of pterigoid, (pra) retroarticular process, (prf) prefrontal, (pt) pterigoid, (q) quadrate, (qj) quadratojugal, (rot) semilunar otic groove, (sa) surangular, (sq) squamosal, (x) vague nerve, (xi) spinal accessory nerve, (xii) hypoglose nerve.

For this reason, it is not appropriate the designation of the molariform teeth of *Notosuchus* as typical ziphodont teeth, made by other authors (Ortega *et al.*, 2000). The molariform teeth of *Notosuchus* clearly resemble a mammal molar, with which they have a high morphologic convergence and in some way with those observed in ornitischians dinosaurs too (Bonaparte, 1991).

In ventral view (Figs.7C, 8A), the maxilla expands medially forming a flat and horizontal surface of the palatal lamina (secondary palate). Posteriorly, each palatal lamina surrounds and embraces the maxillo-palatal fenestrae, which is in contact with the anterior projections of the palatine.

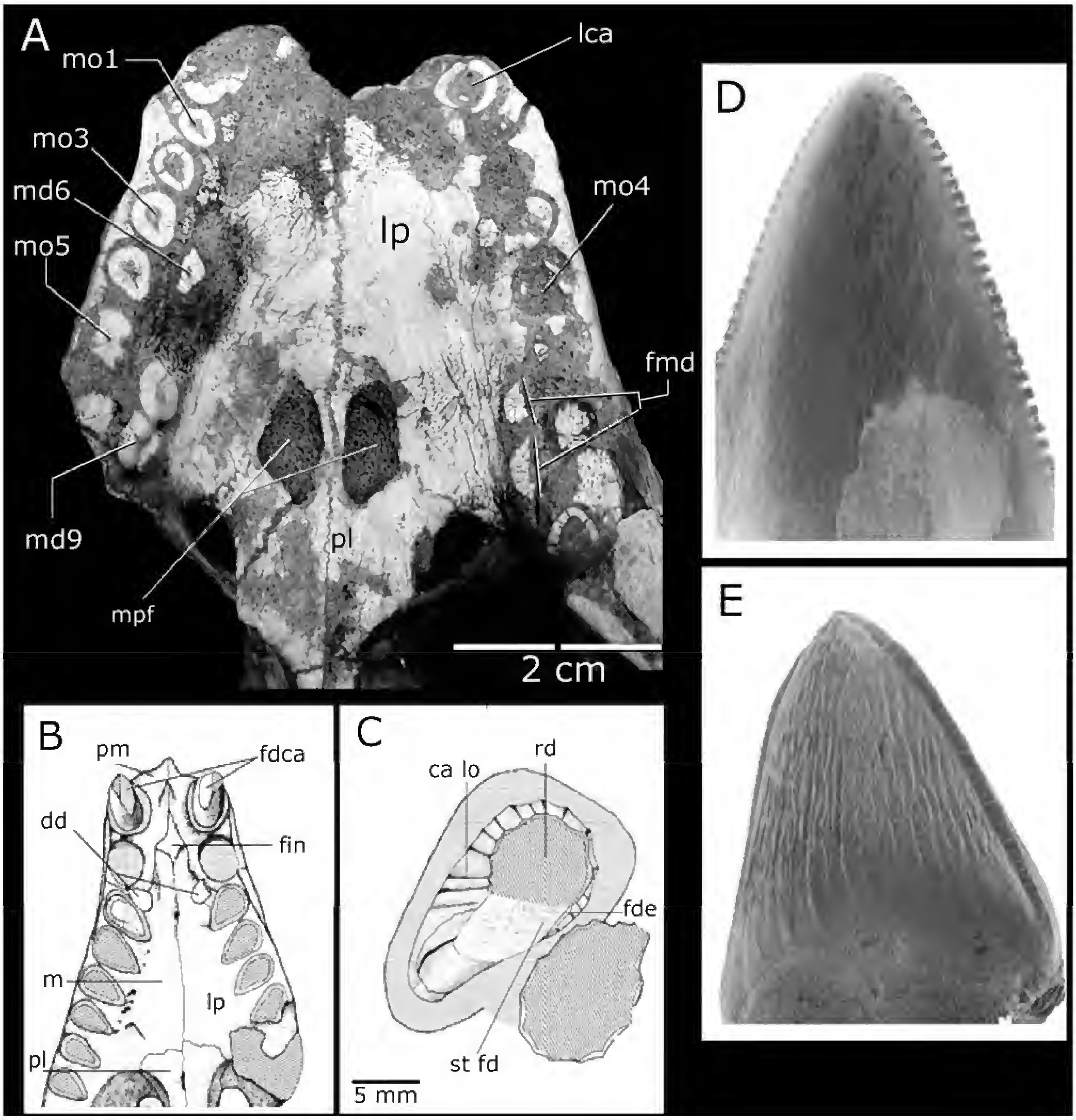

Fig.8- A, *Notosuchus terrestris*, MUCPv-35. Anterior extreme of the skull in palatal view. B and C, *Sphagesaurus huenei* (modified from Pol, 2003); B, Anterior extreme of the skull in palatal view; C, first tooth of the right maxillary. D, tooth of the "true ziphodont" type of cf. *Iberosuchus* sp. E, tooth of the "false ziphodont" type of a juvenile of *Trematochampsa taqueti* (modified from Prasad & Broin, 2002). Abbreviations: (ca lo) longitudinal carina, (dd) dentary tooth, (fd ca) waste facet of caniniform, (fde) worn surface of enamel, (fin) foramen incisivum, (fmd) waste facet of mandibular tooth, (lca) left caniniform, (lp) maxilo-palatal lamina, (m) maxilla, (md) dentary molariform, (mo) maxillary molariform, (mpf) maxilopalatal fenestra, (pl) palatine, (pm) premaxilla, (rd) broken surface of dentine, (st fd) striae on dentine worn surface.

Separating both maxillo-palatal fenestrae, there is a thin lamina formed by the union of the posterior and medial palatal projections of the maxilla. The maxillo-palatal fenestrae are exclusive of *Notosuchus* and *Mariliasuchus* (Fiorelli, 2005; Andrade, 2005; Andrade & Bertini, 2005a; Andrade *et al.*, 2006; Zaher *et al.*, 2006).

In MUCPv-35 it is possible to observe the posterior limits of the palatal lamina that form the anterior border of the suborbital fenestra (Fig.8A). At this point, the maxilla rises vertically, internally to the cavity of the orbit and, as in *Sphagesaurus* (Pol, 2003), it articulates with the jugal, lacrimal, prefrontal, the anterior process of the pterygoids, palatines, and ectopterygoids. Anteriorly, the palatal laminae possess appropriate morphology for the existence of cartilaginous conjunctive tissues embracing to the ventral premaxillary lamina in the proximal end of the snout. Considering that recently a highly descriptive work on the palate structures in Mesoeucrocodylia has been published (see Andrade *et al.*, 2006), we think that it is not necessary greater explanations in this section.

MUCPv-137 possesses both anterior and posterior palpebrals. Frontals are wide and relatively flat. The frontal does not participate of the supratemporal fenestra.

The morphology of the lacrimal, prefrontal, jugal, postorbital as well as the bones that conform the cranial roof, supraoccipital, squamosal, basioccipital and basisphenoid, have been well described in other works (Gasparini, 1971; Bonaparte, 1991; Fiorelli, 2005).

The quadrate possesses two lobular condyles, being the internal (medial condyle) slightly bigger than the lateral one (Fig.6). In Notosuchia, these condyles fit on the anterosposterior elongated channel-like of the articular. Moreover, the quadrate has a wide ventral projection that articulates with the pterygoids, basisphenoid and medially with the basioccipital (Bonaparte, 1991). The otic region is exquisitely preserved in the cranial fragment of the specimen MUCPv-198 (Fig.6) and it is possible to observe more than five fenestrae.

The unique parietal bone is narrow and possesses a longitudinal crest among both supratemporal fenestrae (Figs.7A, D); it is bifurcated posteriorly and forms an acute angle depending on the specimen (Andrade, 2005; Fiorelli, 2005). The supratemporal fenestrae do not possess an anteriorly located foramen. In occipital view (see Fig.6), the supraoccipital supports a vertical medial crest (or supraoccipital nape central crest), decreasing in height near to the foramen magnum. This crest is laterally limited by deep cavities for musculary inserts (branchiomeric muscles). The exoccipital possesses a crest laterally directed that limits the dorsal area from the ventral one. It covers the foramen magnum and the occipital condyle, separated by a greatly defined neck (Bonaparte, 1991); therefore, allowing wide cranial movements. Exoccipital possesses a large foramina of combined exits for the nerves motors and sensorial X (vague nerve) –which keeps relationship with the mouth, the pharynx, and most of the organs –, and XI (spinal accessory nerve) related with the branchiomeric muscles of the neck (Fig.7C). On the other hand, between this foramina and the foramen magnum there is a small foramen belonging to the nerve XII, the visceral motor (hypoglose nerve). The morphology of the laterosphenoid is not clear due to the state of the materials. Possibly, the foramina for the exit of nerves IV (troclear) and V (trigeminal) are in the lateral inferior of the temporary and orbital faces of the laterosphenoid (Fiorelli, 2005); only the nerves II and III would occupy a previous wide opening, axially below the olfatory nerve (Bonaparte, 1991). As in basal Crocodylomorpha, the foramen of the main branch of the trigeminal – maxillary and mandibular – would be between the union of the laterosphenoid and the prootic; meanwhile, the foramen for the exit of the ophthalmic branch of this nerve would be located ventrally in the orbital face of the laterosphenoid, above the basisphenoid (see Busbey & Gow, 1984; Walker, 1990; Gower & Weber, 1998). These characteristics of nerves IV and V are important because they are related to the facial musculature, what is extremely outstanding in *Notosuchus* and it will be discussed posteriorly.

Mandible – Splenials and dentarys on the symphysis are projected anterodorsally approximately 45° (Figs.9A, 10A). Therefore, when the mandibular occlusion takes place, the end of the jaw inserts between both superior caniniforms and the first two incisiforms in each hemimandible. This feature is present in *Chimaerasuchus*, *Sphagesaurus*, and *Mariliasuchus* (Andrade, 2005; Andrade & Bertini, 2005a; Fiorelli, 2005; Zaher *et al.*, 2006) and maybe in *Adamantinasuchus navae* (Nobre & Carvalho, 2006). In ventral view the opening of the Meckelian channel can be seen (Fig.9A). On the dentary, there is a lateral rim that separates an alveolar area from the ventral one. In both areas there are numerous aligned neurovascular foramina (even in the symphyseal region), clearly observable in MUCPv-35. This morphology agrees with the existence of thick soft muscular tissues like cheeks to avoid loss of food. The anterior 6 teeth of each hemimandible possess their alveoli on the dorsal surface of the dentary, while the posterior four teeth are implanted between the dentary and the splenial (Fig.10A).

The first incisiform of each hemimandible is implanted to 45° as that of symphysis. The crown is anterodorsally directed with the same angle, similar to that of *Mariliasuchus* (Andrade, 2005; Andrade & Bertini, 2005a, 2005b), *Chimaerasuchus* (Wu & Sues, 1996), and possibly other notosuchians (*Sphagesaurus* and *Adamantinasuchus*). The second tooth possesses a similar characteristic but its alveolus and its crown is placed more vertical. Mandibular teeth cross-section gets progressively less circular and more triangular, from the first to the fourth teeth (Fig.10A). Middle and posterior teeth are completely vertical and they are implanted obliquely to the longitudinal axis, with the sharpest border located anterolabially.

During occlusion, inferior teeth fit in the triangular space present in between superior molariforms in MUCPv-35 and in *Sphagesaurus* (Pol, 2003). In MUCPv-35, the mandibular molariform teeth possess a worn surface on their labial face and the upper molariform teeth on the lingual face (Bonaparte, 1991).

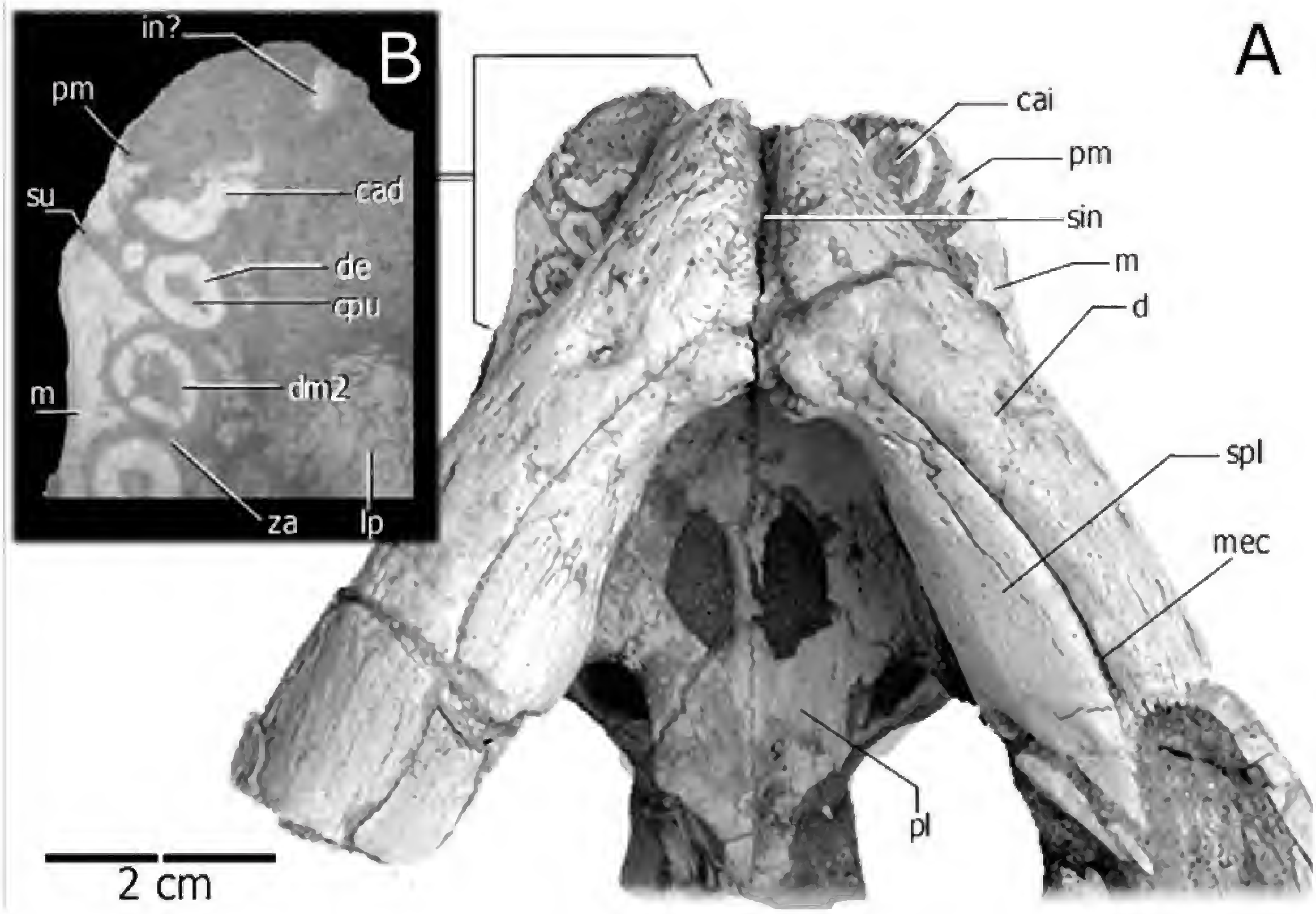

Fig.9- *Notosuchus terrestris*, MUCPv-35. A: anterior extreme of the skull and jaw in ventral view. B: right maxilla-premaxilla in alveolar view. Abbreviations: (cad) right caniniform, (cai) left caniniform, (cpu) pulpar cavity, (d) dentary, (de) dentine, (dm) maxillary teeth, (in) incisiform, (lp) maxillopalatal lamina, (m) maxilla, (mec) Meckelian groove, (pl) palatine, (pm) premaxilla, (sin) symphysis, (su) premaxilla-maxilla suture, (spl) splenial, (za) alveolar zone.

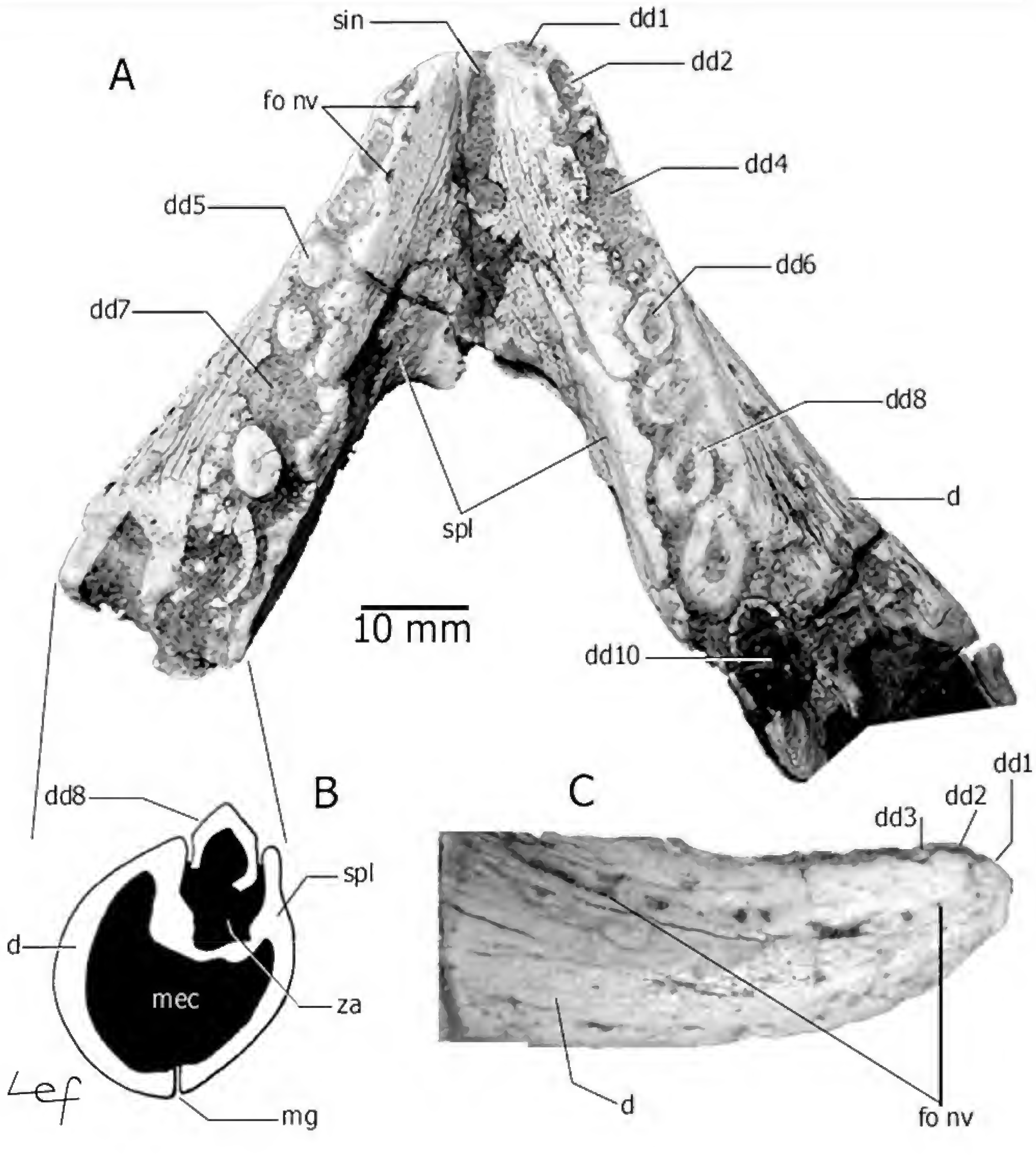

Fig.10- Jaw of *Notosuchus terrestris*, MUCPv-35. A: in alveolar (dorsal) view. B: traverse section through the left jaw. C: right jaw in lateral view. Abbreviations: (d) dentary, (dd) dentary tooth, (fo nv) neurovascular foramina, (mg) Meckelian groove, (sin) symphysis, (spl) splenial, (za) alveolar zone.

The articulate structure between the skull and the lower jaw is clearly visible and exquisitely preserved in the described specimens that conserve this structure. The angular supports the surangular and expands forming the ventral surface of the posterior retroarticular process. The surangular expands posterodorsally forming a fine thorn for the angular. In the posterior internal face of the mandibular branch, there is a clearly visible suture among the angular and articular, from where a shelf of this bone is projected medially. The articular projects posteromedially and forms the shelf for the quadrate process articulation. Condyles insert in two shallow channels directed anteroposteriorly and located in the glenoid fossa of the articular (Fig.6). The articular also lacks a posterior buttress. This morphology is clearly visible in MUCPv-198, *Araripesuchus* (ORTEGA *et al.*, 2000), *Malawisuchus* (CLARK *et al.*, 1989; GOMANI, 1997), *Sphagesaurus* (POL, 2003), *Chimaerasuchus* (WU & SUES, 1996), *Mariliasuchus* (CARVALHO & BERTINI, 1999; ANDRADE & BERTINI, 2005a; ZAHER *et al.*, 2006), and some few basal crocodylomorphs (HARRIS *et al.*, 2000). This is ambiguous in *Candidodon* (NOBRE & CARVALHO, 2002) but the quadrate characteristics and the condyles of the same one would indicate something similar. By contrast, in other Crocodyliformes the glenoid fossa is much wider than long. It is deeply concave without central crest and with a great posterior buttress. In *Notosuchus* this combination of structures indicates clearly a proal movement of the jaw during the mastication for the prosecution of the food. Posteriorly to the glenoid fossa, the articular expands and forms the "tablespoon" or dorsal face of the width retroarticular process (Figs.3, 7B) suturing toward ventral with the angular, similar to that of *Malawisuchus*, *Chimaerasuchus*, and *Mariliasuchus* (FIORELLI, 2005; ANDRADE, 2005; ANDRADE & BERTINI, 2005a, 2005b; ZAHER *et al.*, 2006).

Postcranial Axial Skeleton – An excelent postcranial study of *Notosuchus terrestris* has been published recently by POL (2005) but new observations that increase knowledge of this species contributes to give new anatomical and phylogenetic data. This is possible due to the specimen MUCPv-137, which represents the first and only record of *Notosuchus* with postcranial remains articulate to the skull (FIORELLI, 2005).

Between the skull and the first preserved cervical vertebra (axis), there were many tiny dispersed bony fragments in the matrix. They could be attributed to atlas and parts of the axis. In fact, the whole articulate cervical sequence was quite damaged and fragile preserved, hindering its description. Probably, the skull-neck articulation was located ventrally and, for this reason, the snout of *Notosuchus* is anteroventrally directed, contrary to the current Crocodyliformes.

An important morphology in *Notosuchus* opposing to other crocodyliforms is the presence of 10 cervical vertebrae (FIORELLI, 2005). All cervical vertebrae possess lightly amphicoelous centra with anteroposteriorly short and ventral keel (Fig.11). Between the keel and the parapophysis there is a shallow cavity. The diapophyses are located in the pedicelous, anteroventrally to the neurocentral suture of the anterior cervicals. Posteriorly they change being located more dorsally reaching the same level that the zygapophyses.

The curved suprapostzygapophyseal lamina extends from half of the height of the neural spines until the posterior end of the postzygapophysis.

The neural spines are high and located in a central position in the vertebra. They are rectangular in lateral view; wider in the base than in the apex.

As it was described by POL (2005), starting from the contact between the fourth and fifth vertebrae, the width at level of its zygapophysis increases notably, increasing the development of its articular surfaces (Fig.11A). It increases in the fifth-sixth and sixth-seventh vertebrae, and decreases in the seventh and eighth vertebrae. The angle formed between the right and left postzygapophysis of the posterior cervical is smaller than 90°.

The cervical centra are abnormally heptagonal, with one of its vertex developed ventrally forming a keel all along the ventral surface (Figs.11D-F). At last, pedicelous of the neural arch are placed laterodorsally to the centrum, as a consequence of this heptagonal shape. Starting from the tenth vertebra, the centrum progressively loose the heptagonal form and takes a more rounded and circular form.

The specimen MUCPv-149 possesses a very well preserved cervicodorsal sequence and the anterior to middle dorsal vertebrae (Figs.5, 12). This material presents a total of eleven articulated vertebrae; the first preserves part of the pedicelous and the zygapophysis.

POL (2005; MACN-RN 1037) described three dorsal vertebrae from the eleven to thirteen. However, their descriptions correspond from the twelve to fourteen vertebrae. They are characterized by having the tenth cervical vertebra (MUCPv-137) with a relatively short and wide center, with transitional characteristics between the ninth vertebra (MUCPv-137) and the eleventh (second vertebra in MUCPv-149 because the first vertebra of this specimen – tenth – only preserves the left superior part).

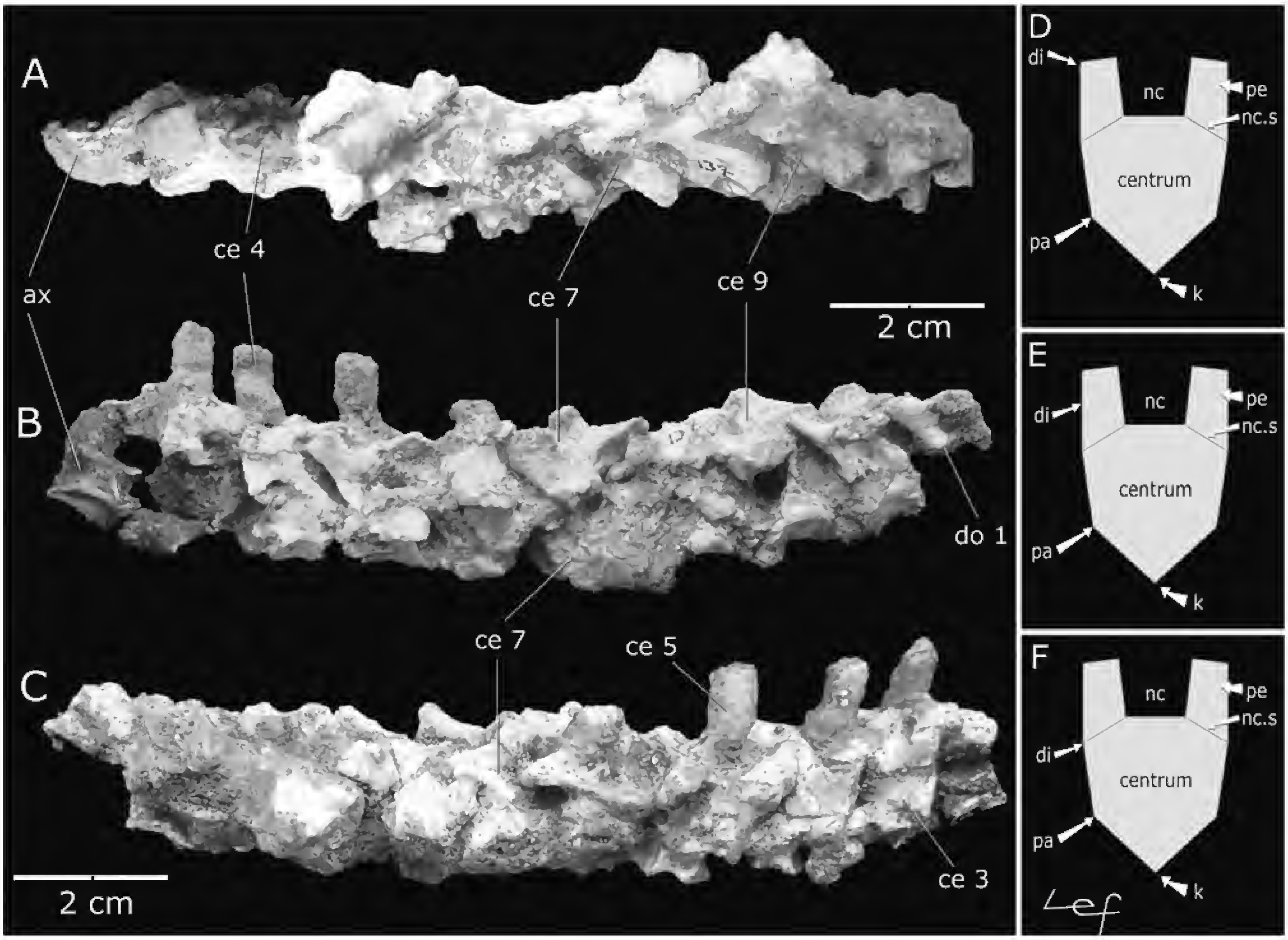

Fig.11- Cervical vertebrae of *Notosuchus terrestris*, MUCPv-137. A, in dorsal view; B, in left lateral view; C, in right lateral view. D, E and F, structures of the cervical centra in anterior view showing the variation in the position of diapophysis on de pedicelous; D, cervical III; E, cervical VII; F, cervical IX and X. Abbreviations: (ax) axis - second vertebra, (ce) cervical vertebra, (di) dyapophysis, (do) dorsal vertebra, (k) ventral keel, (nc) neural channel, (nc.s) neurocentral suture, (pa) parapophysis, (pe) pedicelous.

The centrum of the tenth vertebra is longer than the ninth (MUCPv-137) but shorter than the eleventh (of MUCPv-149). The tenth vertebra possesses a similar width to the ninth cervical, and also a posterior articular face diameter similar to the anterior articular face of the eleventh in MUCPv-149. The posterior articular diameter of the centrum in relation to the anterior one is more elongated (Fig.12).

The prezygapophyseal and postzygapophyseal articulations are horizontal and are placed practically at the same level than the diapophysis. Postzygapophysis are posterolaterally curved. Diapophysis on the 14th vertebra is robust and born at the same level that the zygapophysis, with a wide surface in dorsal view, and expands toward anterior. All characteristics of the cervicodorsal vertebrae are very similar to those present in *Chimaerasuchus* and *Mariliasuchus*.

In the last cervicodorsal vertebra (13) and in the first three dorsal vertebrae (14, 15, and 16), the pedicelous of the neural arches are lightly inclined anteriorly (more marked in 14 and 15). It is also present in dorsals 19 and 20 (Figs.3B, 5C, 6C).

On the specimens available, combining the specimens studied here and the specimen MUCPv-287 studied by Pol (1999, 2005), there is a complete vertebral sequence until the caudal vertebrae (except for the atlas). *Notosuchus* possessed a total of 29 presacral vertebrae (10 cervical, 3 cervicodorsal, and 16 dorsal vertebrae), 3 sacral (MUCPv-287), and the first 13 caudal vertebrae (MUCPv-287).

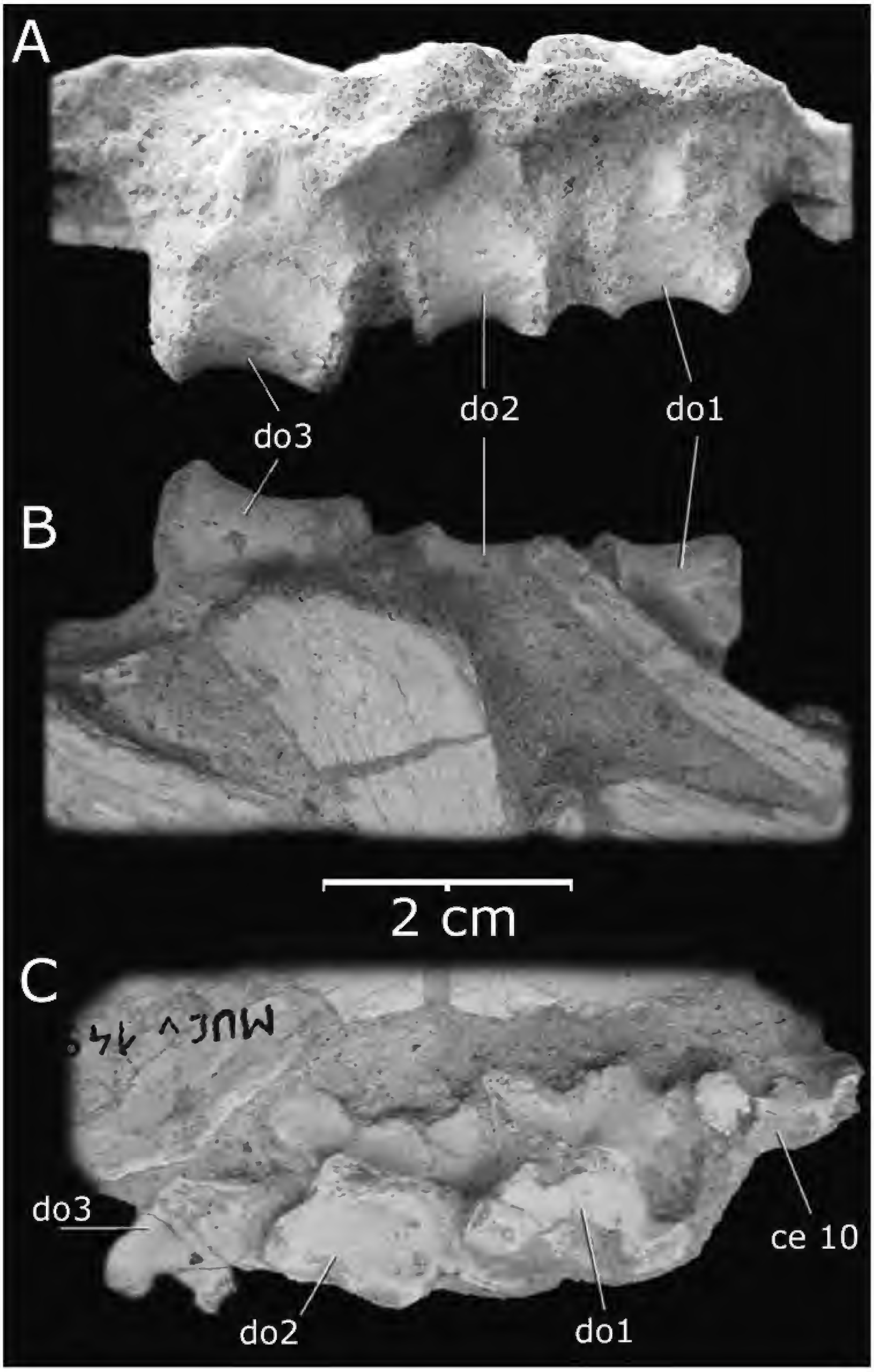

Fig.12- Cervicodorsal vertebrae of *Notosuchus terrestris*, MUCPv-149. A, in right lateral view; B, in ventral view; C, in dorsal view. Observe the size change and the longitude of the centra starting from the dorsal vertebra III. Abbreviations: (ce) cervical vertebra, (do) dorsal vertebra.

The centra of anterior dorsal vertebrae increase the length and they stay practically constant through the sequence. In posterior dorsals, the diameter of the centra increases gradually until the vertebra 28 and the presacral (29), which is wider and shorter (Fig.13). The centra are amphycoelous and they do not present hypapophysis.

Appendicular skeleton – Of the apendicular skeleton of *Notosuchus* only novel and outstanding characters are denoted because they were described minutely in previous works (Pol, 1999, 2005; Fiorelli, 2005).

The left scapula of MUCPv-149 is very well preserved (Figs.5A, 14A). A half constriction separates the dorsal expansion of the scapula of the opposed ventral expansion. This material lacks the anterior lamina of the dorsal expansion, but it possesses a great expansion backward generating a great concavity in relation to the convexity of the posterior border. This morphology is seen in *Chimaerasuchus* (Wu & Sues, 1996), *Araripesuchus* (Ortega *et al.*, 2000; Turner, 2006) and other basal crocodyliforms as *Sichuanosuchus* (Wu *et al.*, 1997). In the anterior margin it is concave while in the posterior one it is convex. The ventral expansion is shorter (practically half of the dorsal expansion) than in most crocodyliforms. The anterior border of the ventral expansion possesses a small acromial crest (acromial process), which is poor developed and located more ventrally than in other crocodyliforms (Pol, 2005).

The left coracoid is less robust than the specimen MACN-RN-1037 described by Pol (2005). The coracoid is slightly curved in all its longitude from the dorsal expansion until the ventral one (Figs.5B, 14B), contrary to other crocodyliforms that present an angular coracoid in the constriction (Pol, 2005). The great foramen of the coracoid is placed in a deep lateral cavity between the glenoid fossa and the border of the scapular process of the coracoid. As in *Chimaerasuchus*, the articular surface for the scapula is perpendicular to the surface of the glenoid cavity. It is formed by a small crest that separates the surfaces for insertion of the *M. supracoracoideus longus* and *M. s. brevis* from the insertion of the *M. biceps brachii.*

The humerus of MUCPv-149 is more gracil than the humerus of Crocodylia, but is slightly more robust and more massive that in other Notosuchia. The deltoid crest of MUCPv-149 is relatively thick and more extensive than in *Chimaerasuchus* and other protosuchians (Fiorelli, 2005).

The preacetabular process of the ilium (Fig.4F) is small and it possesses a light development (Pol, 2005), a character state that is shared with *Chimaerasuchus* (Wu & Sues, 1996), *Araripesuchus* (Ortega *et al.*, 2000; Turner, 2006), *Uruguaysuchus* (Rusconi, 1933), and *Theriosuchus* (Wu *et al.*, 1996). As it was noticed in *Chimaerasuchus* (Wu & Sues, 1996) and in the material described by Pol (2005), the specimens MUCPv-137 and MUCPv-147 lack the iliac blade present in most of the crocodyliforms, pterosaurs, and dinosaurs (inclusive in birds), related with the *M. ilitibialis*. Therefore, this muscle in *Notosuchus* is more reduced than in other crocodyliforms. The dorsal crest of the ilium is greatly expanded forming a laterally extensive acetabular roof and produce a deep acetabular cavity. The surface for insertion of the *M. iliofemoralis* is wide and horizontal in the acetabular roof of the cavity, showing that this muscle ran vertical and ventrally. It possesses a great development of the postacetabular iliac process; this goes posteriorly with the distal end directed ventrally.

The femur (Figs.4E, F) is much more robust than in other notosuchians (*i.e.*, *Chimaerasuchus*, *Malawisuchus*, *Mariliasuchus*, and *Adamantinasuchus*). In anterolateral view, it possesses a slightly sigmoid shape and is twisted. The proximal end directs anterodorsally, while the distal end does posteroventral with the shaft that is slightly curved. The fourth trochanter is wide, rounded, and located on the posteromedial surface of the proximal end of the femoral shaft. The distal end of the left femur of the specimen MUCPv-137 does not possess the condylar expansions so marked as the condition presents in *Malawisuchus* (Gomani, 1997). The fibular condyle (lateral c.) is markedly bigger than the tibial condyle (medial c.) and possesses a more ventral development. Both condyles are posteroventrally directed and possess long processes or supracondylar crests.

The tibia (Fig.4G) is also more robust than in other notosuchians and possesses a slightly smaller longitude in relation to the femur. It possesses a great expansion of the proximal end and a lateromedial expansion of the distal end. The tibial head expands excessively back and possesses a characteristic notch that separates the great process for the medial condyle of the femur; ventrally to the notch is the deep fossa flexoria. It lacks fibular crest. On the distal end, the medial maleolus is more robust and developed ventrally than the lateral maleolus. The fibula is long and smooth (Fig.4G). It possesses a porous area in the proximal portion for muscles attach and distally it is clearly visible with a deep and long medial fibular fossa.

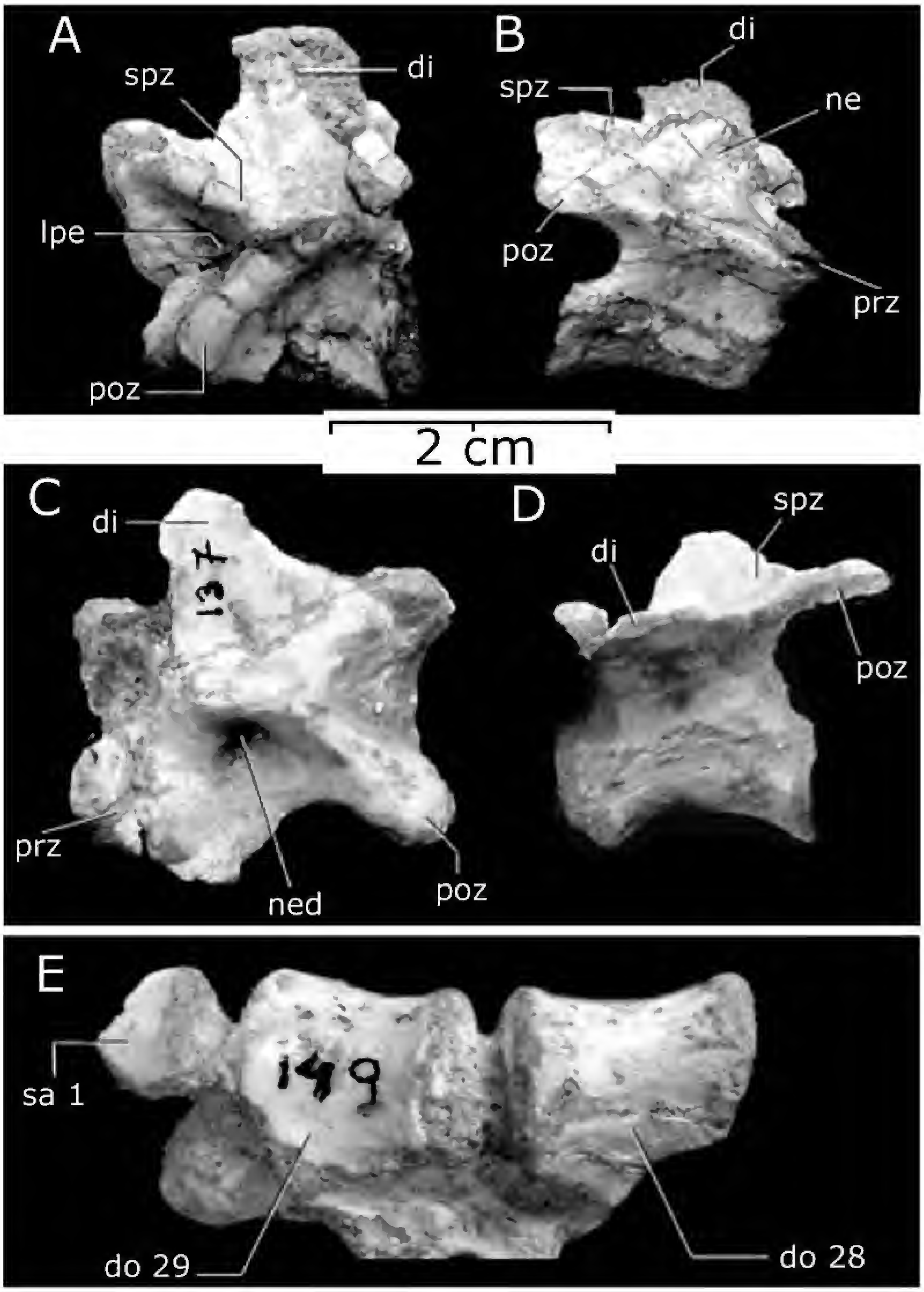

Fig.13- Dorsal vertebrae of Notosuchus terrestris. A and B, anterior dorsal vertebra (vertebra XV), MUCPv-198; A, in dorsal view; B, in right lateral view. C and D, medial dorsal vertebra (v. XXII), MUCPv-137; C, in dorsal view; D, in left lateral view. E, MUCPv-149; posterior dorsal vertebrae (v. XXVIII and v. XXIX –presacral) and fragment of the first sacral vertebra (v. XXX), in ventral view. Abbreviations: (di) dyapophysis, (do) dorsal vertebra, (lpe) postspinal lamina, (ne) neural spine, (ned) depression in the base of the spine, (poz) postzygapophysis, (prz) prezygapophysis, (sa) surangular, (spz) suprapostzygapophyseal lamina.

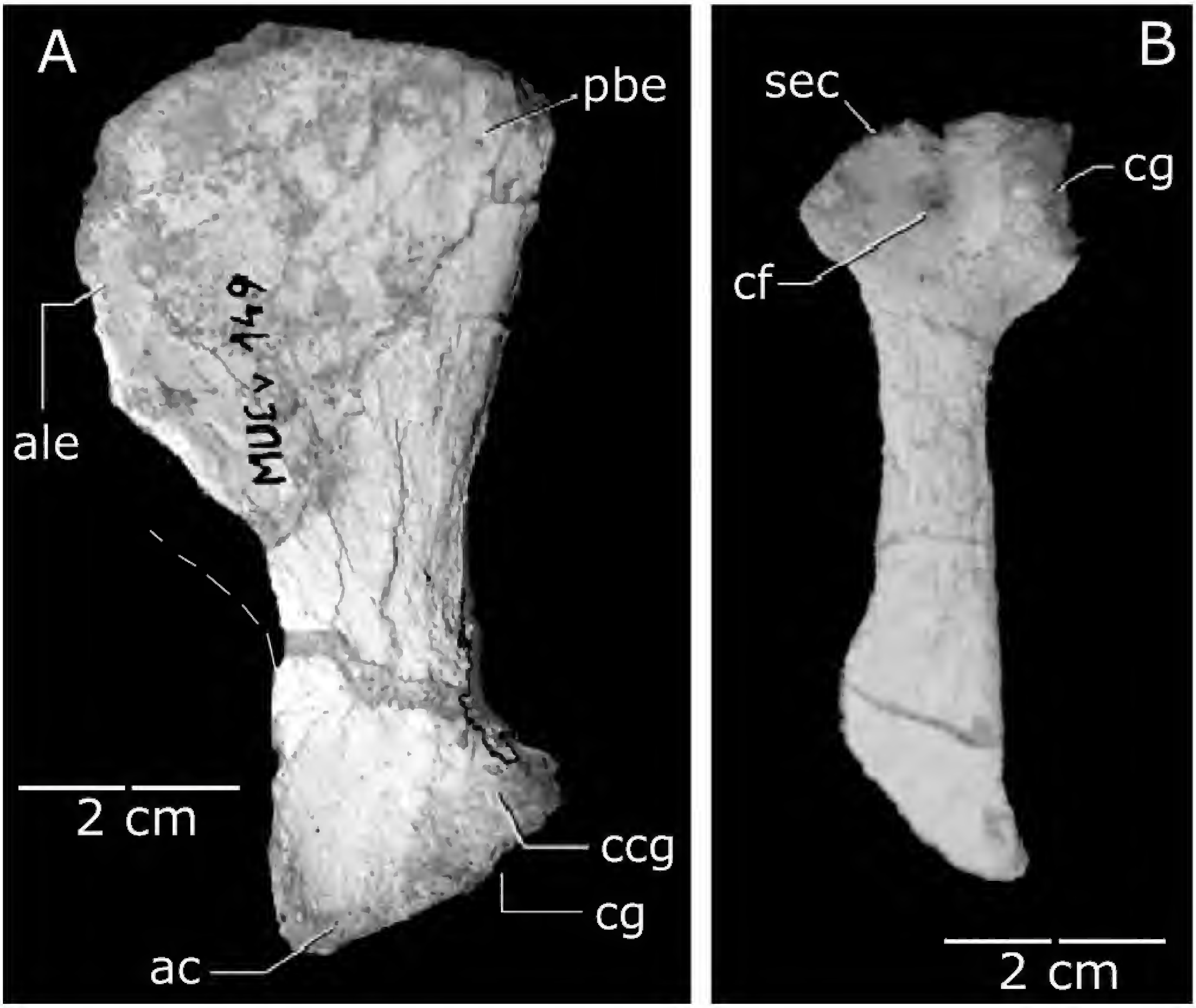

Fig.14- Pectoral girdle of *Notosuchus terrestris*, MUCPv-149. A, left scapula in laterodorsal view; B, left coracoid in ventrolateral view. Abbreviations: (ac) acromium, (ale) anterior scapular lamina, (ccg) glenoid cavity crest, (cg) glenoid cavity, (cf) coracoid foramen, (pbe) posterior scapular blade, (sec) scapulocoracoid articulation.

DISCUSSION

FORM AND FUNCTION OF THE ANATOMY OF *NOTOSUCHUS TERRESTRIS*: FUNCTIONAL ASPECTS OF THEIR TEETH AND SPECIALIZATION IN THE FEEDING

Many published works about the anatomical and functional aspects of Mesoeucrocodylia members have been done (Bonaparte, 1991, 1996; Clark *et al.*, 1989; Wu *et al.*, 1995; Wu & Sues, 1996; Gomani, 1997; Buckley *et al.*, 2000; Pol, 2003). However, few works have been dedicated to the feeding mechanism of *Notosuchus* (Bonaparte, 1991, 1996) and other notosuchian (Andrade, 2005; Andrade & Bertini, 2005a, 2005b). In general they support an herbivore habit. Specializations regarding teeth and feeding are diverse on basal Crocodylomorpha. For instance, *Phyllodontosuchus lufengensis* Harris, Lucas, Estep & Li, 2000 (Harris *et al.*, 2000) and *Edentosuchus tienshanensis* Young, 1973 (Pol *et al.*, 2004), present a heterodont dentition and a complex jag suggesting that both species had a diet not limited to meat (Harris *et al.*, 2000).

Notosuchia were perhaps the crocodyliforms that developed more variability in relation to teeth and feeding aspects. *Chimaerasuchus paradoxus* possessed very specialized teeth, with wide molariforms and three lines of longitudinal cusps, similar to the molars of tritylodontoid sinapsids (Wu *et al.*, 1995; Wu & Sues, 1996). Moreover, the mandible possessed a proal movement and "lips" to avoid the loss of food. *Simosuchus clarki* (Buckley *et al.*, 2000) has their teeth more smoothed in lingual-labial sense but they also possessed multiple cusps in the apical border. As it was suggested, *Chimaerasuchus* and *Simosuchus* were crocodyliforms highly specialized for an herbivore diet. Multicuspid teeth have also been reported in *Candidodon* (Carvalho, 1994; Nobre & Carvalho, 2002), *Malawisuchus* (Gomani, 1997), *Uruguaysuchus* (Rusconi, 1933), and *Adamantinasuchus* (Nobre & Carvalho, 2006). In the case of *Malawisuchus*, it probably fed on small sized preys (*i.e.*, insects, amphibians, gastropods), captured by the caniniforms and processed by with multicuspid molariforms (Gomani, 1997).

Undoubtedly, the dentary morphology present in *Notosuchus* indicates a feeding mechanism different to that of the other crocodyliforms, only comparable with that of *Sphagesaurus* and *Mariliasuchus* (Fiorelli, 2005; Andrade, 2005; Andrade & Bertini, 2005a, 2005b; Zaher *et al.*, 2006).

The first incisiform mandibular teeth of *Notosuchus* present a forward direction approximately at 45°. Teeth have circular section and their apexes rest on the ventral face of premaxillae when the jaw is closed. But during opening the fore and aft movement of the lower jaw made these teeth surpasses the premaxillary incisiform, producing "shovel" movement. These movements are present in varied herbivorous and insectivorous mammals such as in marsupials (Polydolopidae or Caenolestidae), in some Xenarthra, rodents, suids, camelids, notoungulans, ruminant, and lemurs. The caniniform presents a great development, with a deep root and a crown with the apex subcircular in traverse section (worn surface sensu Bonaparte, 1991).

The molariform have triangular section, oblique to the parasagital axis and worn surface similar to *Sphagesaurus* (Pol, 2003). The worn surface of molariform teeth in *Notosuchus* would also be produced by the tooth-to-tooth contact and fore and after movement of the jaw (proal movement). In *Sphagesaurus* when the jaw is closed, each tooth occluded with a single tooth of the maxilla, while the same tooth of the other hemimandible didn't reach to occlude with its corresponding one in the maxilla, being a space between them (Pol, 2003:821). In *Notosuchus* something similar is observed. The molariform increases the diameter at level of the alveolus toward posterior in the maxilla and the mandible: the first molariform possesses a diameter that oscillates, depending on the specimen, among 2.9 to 4.5mm while the diameter of the posterior molariform is 4.5 to 6.5mm. When being implanted very near to each other, the distance that occupy two teeth sum easily the longitude of mobility of the quadrate in the articular shelf, with the difference that each tooth is implanted more internally than the following one located toward posterior (Fiorelli, 2005). So, when the jaw carried out the proal movement, the waste facet was not due to the occlusion of complementary maxilla-jaw teeth, but to the friction contact of a maxillary tooth with the posterior tooth to its complementary tooth of the jaw and, in this point, a perfect occlusion tooth-tooth took place of both hemimandibles with the maxillary ones (Fiorelli, 2005). For this reason, the waste facets of the teeth not necessarily have to be explained by means of alternative hypothesis, as for example cranial kinesis or lateral mandibular movements, but to the same "proal" movement carried out by the jaw.

As it was mentioned previously, it is not appropriate the assignment of "ziphodont teeth" to the molariform or postcanines present in the maxilla or dentary of *Notosuchus* (Ortega *et al.*, 2000). The molariform teeth clearly are not ziphodont, neither "false", nor "true" (see Prasad & Broin, 2002). The characteristic aligned neurovascular foramina present in the alveolar region of the maxillary and in the surface of dentary indicate that *Notosuchus* possessed wide soft tissues like thick lips and facial and perioral musculature (*e.g.*, *m. orbicularis oris*), to maintain oral food during mastication (Bonaparte, 1991, 1996; Andrade, 2005; Fiorelli, 2005).

On the nasal surface the presence of a wide central depression, with lineal striations and similar ruggedness possibly indicate the presence of nasolabial muscles (as the *m. levator nasolabialis* in mammals) that elevates the lip or the nose. In the area of articulation of the maxillar and the nasal, another smaller depression with grooves indicates also a possible analogy with the *m. caninus*. On the lower jaw, some striations, ruggedness and numerous foramina in the base at level of the symphysis, indicates the action of a depressor muscle of the lips (Fiorelli, 2005).

On the other hand, the external nares are directed forward and they do not possess nasal sept. For this reason, at the end of the muzzle, cartilaginous tissues could exist and, together with the lips and the muscles, they will form a short trunk or "hog´s snout", similar to the characteristic muzzle of the suids (pigs) or tayassuids (pecaris), which use it for sniffing or smelling the land in food search (Fiorelli, 2005).

Notosuchus possessed a strong musculature of the neck, evidenced by the occipital inserts and very high neural spines of the cervical vertebrae. It possessed also a big suborbital fenestra for a great *m. pterygoideous anterior* (indicating a proal movement of the jaw). *Notosuchus* possessed a reduced *m. pseudotemporalis* characterized by the small size of the supratemporal fenestra, as well as a great development of the pterygoid wings for the *m. pterygoideous posterior* and a wide ventral margin of the mandibular fenestra, all evidences of a strong mandibular adduction.

Unlike other crocodyliforms, *Notosuchus* possessed a well developed and long *m. depressor mandibulae,* evidenced by the wide surface of the retroarticular process and its lack of a dorsal projection. It also possesses a good development of the posterior crests of the squamosal, suggested for *Malawisuchus* (Gomani, 1997), *Mariliasuchus* (Andrade & Bertini, 2005a; Zaher *et al.*, 2006), Squamata, and *Sphenodon* Gray, 1831 (Wu & Sues, 1996:695), as related to the control of the proal movements of the jaw and their adduction.

The cervical vertebrae of *Notosuchus* possessed diverse characteristic as for example elongated spines, wide zygapophysis, a depression among prezygapophysis, etc. It demonstrates the existence of marked arched dorsally movement on the vertebral region (Pol, 2005). *Notosuchus* possessed the head above that the neck and directed down, allowing wide cervico-cranial movements. Therefore, according to the evidence showed, *Notosuchus* distant too much of having a strict carnivore or scavenging habits. Probably, it will fit inside a description of a Suidae and Tayassuidae (Fig.15) or South American Caviidae as for example Dolichotinae (mara). These extant species have herbivore habits (or occasionally omnivorous), feeding a diverse vegetation mainly bulbs and roots, and in such case of fruits, seeds, annelids, and other worms (helped by the "hog´s snout" and incisiform) and possibly also arthropods (Fiorelli, 2005). Anyway, we do not discard the use of robust forelimb to dig and so obtain its food.

PHYLOGENETIC ANALYSIS: INTRA AND INTER NOTOSUCHIAN RELATIONSHIPS

In the last years several works that include analysis of the phylogenetic relationships within Notosuchia and related groups of crocodyliforms have been published (*i.e.*, Clark, 1994; Wu & Sues, 1996; Gomani, 1997; Wu *et al.*, 1997; Buckley *et al.*, 2000; Ortega *et al.*, 2000; Martinelli, 2003; Sereno *et al.*, 2003; Pol, 2005; Pol & Apesteguia, 2005; Pol & Norell, 2004a, 2004b; Andrade, 2005; Fiorelli, 2005; Turner, 2006; Turner & Calvo, 2005; Zaher *et al.*, 2006). In any case, and although in practically all recent analyzes, *Notosuchus terrestris* is located relatively derived within the clade, the relationships of many of his taxa are quite conflicting, and these works do not show a consensus in their results.

According to this necessity, numerous phylogenetic studies that were realized focused mainly in the relationships of Notosuchia in a general context within Paracrocodylomorpha (*sensu* Parrish, 1993; Sereno, 2005; Sereno *et al.*, 2005) and in direct

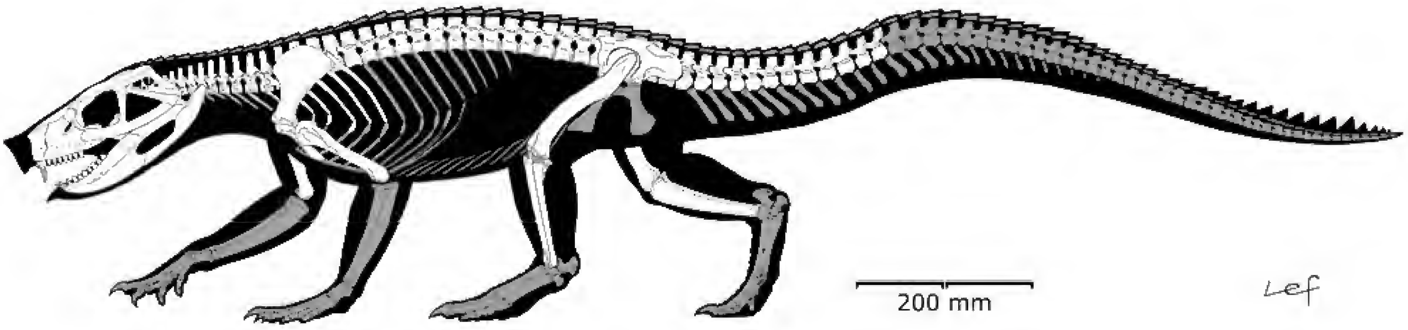

Fig.15- Skeleton restoration of *Notosuchus terrestris* based on the specimens contained in the Museum of Geology and Paleontology of the Universidad Nacional del Comahue located in the Centro Paleontológico Lago Barreales (included the specimen MUCPv-287, studied by Pol, 2005). Lacking parts in gray color.

correlation with the more influential groups of Mesoeucrocodylia. The original differences in the diverse analyses were based mainly on the number of taxa included in the different matrixes. It is interesting to observe that to incorporate different basal taxa (variant between sphenosuchians and protosuchians), the results are extremely dissimilar. Thus, the variation, inclusion and/or extraction of basal groups of Crocodylimorpha, influence markedly in the possible topology within notosuchian and neosuchian clades (see Appendix I).

The cladistic analysis by which it was chosen was lead using a modified dataset of 264 characters scored for 66 taxa of Paracrocodylomorpha plus *Gracilisuchus stipanicicorum* Romer, 1972 as outgroup. This dataset is an extension of the used by Fiorelli & Calvo (2007) which is based in previous publications and new definitions.

Additionally, in the present work new characters were incorporated (232 to 245; see Appendix II) taken from Pol & Apesteguia (2005) and new taxa included (see Appendix III). In the present analysis, this dataset was analyzed with equally weighted parsimony through of TNT (Goloboff *et al.*, 2003). A heuristic tree search was performed consisting of 1000 replicates of RAS + TBR with a final round of TBR (mult*1000; max*), holding 10 trees per replication (hold/10), followed by a final round of TBR branch swapping and zero-length branches were collapsed. The analysis resulted in ten most parsimonious trees of 1089 steps (CI: 0.278; RI: 0.636) found in all replicates. An alternative phylogeny is presented (Fig.17, see Appendix IV).

In all most parsimonious hypotheses group we observe that *Notosuchus terrestris* represents the sister taxon of the clade forming by [*Mariliasuchus amarali* + *Adamantinasuchus navae*] both from the Upper Cretaceous of Brazil. This South American clade (Fig.16, stem 11 – Notosuchidae) possesses a derived localization inside the Notosuchia clade and is diagnosed by five unambiguous synapomorphies (Character 45[2]: quadrate with three or more fenestrae on dorsal and posteromedial surfaces; Character 103[2]: articular facet for quadrate condyle close to three times the length of the quadrate condyles; Character 160[1]: forked ectopterygoid medial process; Character 176[1]: maxillopalatal fenestrae present; Character 202[0]: postcanines teeth (molariforms) triangular in traverse section). Also, the node 12 [*Mariliasuchus amarali* + *Adamantinasuchus navae*] is diagnosed by four unambiguous synapomorphies (Character 120[0]: tooth margins with denticulate carinae; Character 241[1]: ventral half of the lacrymal tapers posteroventrally, not contacting or contacting slightly the jugal; Character 242[1]: large foramen on lateral surface of anterior jugal; Character 243[1]: procumbent premaxillary –incisiform– in anterior dentary alveoli).

On the other hand, Notosuchidae (stem 11) represents the sister clade of the node conformed by *Comahuesuchus brachybuccalis* + [*Sphagesaurus huenei* + *Chimaerasuchus paradoxus*]. This node, *Notosuchus* more *Chimaerasuchus* and all his descendants (node 10, Fig.17), is diagnosed by six unambiguous synapomorphies (Character 111[1]: short and broad prefrontals anterior to orbits and oriented posteromedially-anterolaterally; Character 198[1]: ectopterygoid contact palatine excluding the pterygoid of the posterior edge of the fenestra palatina; Character 199[1]: nasal-frontal suture obliquely oriented; Character 232[1]: transversal splenial-dentary suture at symphysis on ventral surface; Character 244[1]: rodlike posterolateral palatine bar present; Character 245[1]: ectopterygoid projecting medially on ventral surface of pterygoid flanges widely extended covering approximately the lateral half of the ventral surface of the pterygoid flanges). In other phylogenetic results in which they were, extracted/included some taxa (excluding poposaurids, some "sphenosuchians" or gobiosuchids; including the *Sarcosuchus-Terminonaris* clade), *Comahuesuchus* is shared like a Notosuchidae, forming a trichotomy with *Mariliasuchus* and *Adamantinasuchus*.

Also, when excluding or including some basal taxa, the *Araripesuchus*-clade shared is paraphyletic with *A. buitreraensis* more basal within notosuchians than the other araripesuchids. Another important aspect that is derived from the present study is the intimate relationship between *Araripesuchus* with the rest of the notosuchians, occupying a relative basal place inside the notosuchian. The relationships of *Araripesuchus* are concordant with some recent publications (Pol & Norell, 2004a, 2004b; Pol *et al.*, 2004; Pol & Apesteguia, 2005; Zaher *et al.*, 2006) and in turn different from others which present its relation with the neosuchian clade (Clark, 1994; Buckley & Brochu, 1999; Bucley *et al.*, 2000; Ortega *et al.*, 2000; Andrade, 2005; Turner & Calvo, 2005; Turner, 2006).

Anatosuchus minor was described as a "notosuchian" from the Late Aptian or Early Albian, Republic of Niger. Originally it was closely related to *Comahuesuchus brachybuccalis* integrating the monophyletic Comahuesuchidae clade (*sensu* Bonaparte, 1991).

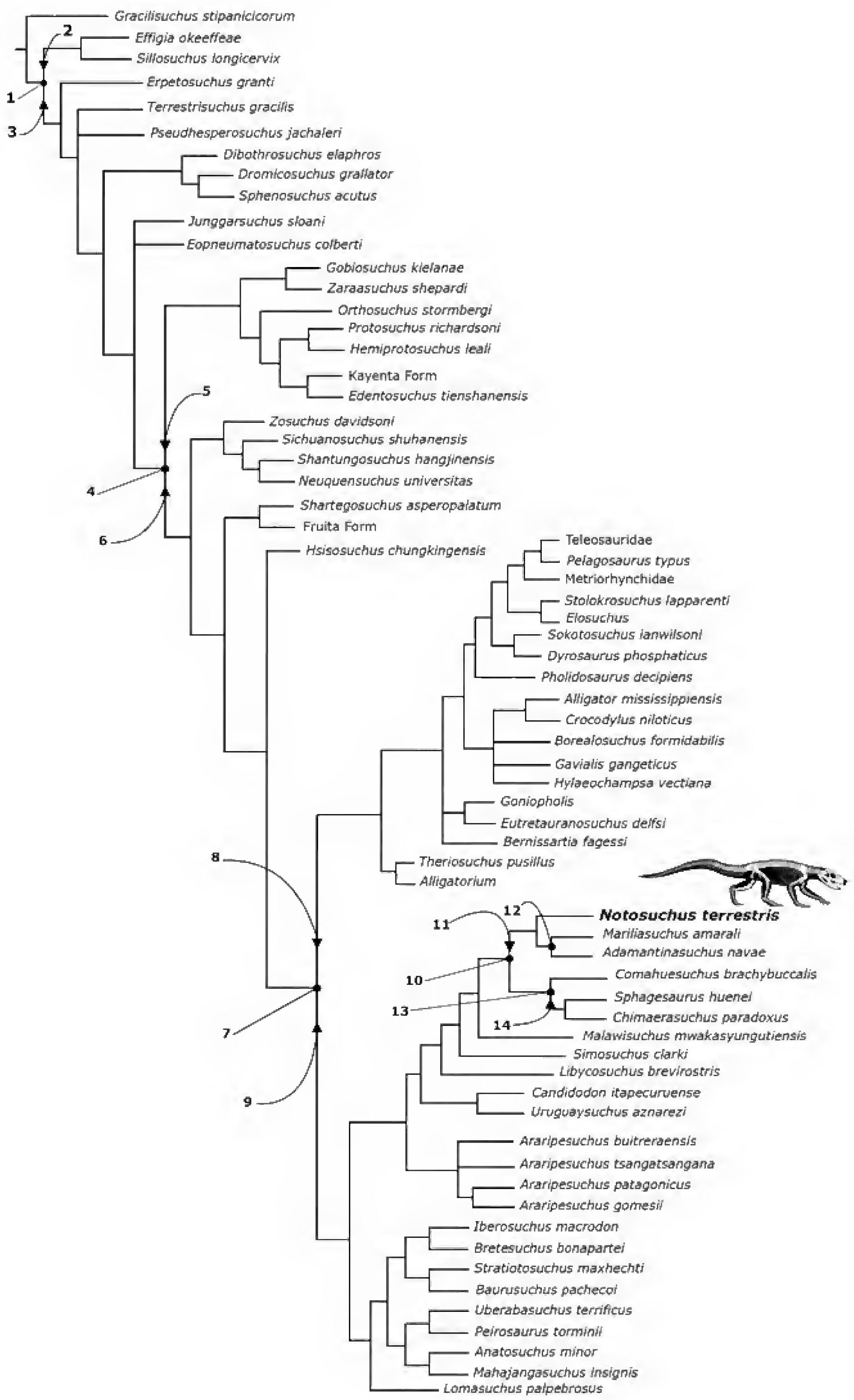

Fig.16- Strict consensus of the 10 most parsimonious topologies that resulted from a strict parsimony analysis obtained through of TNT (Goloboff *et al.*, 2003). Tree length is 1089 with a CI of 0.278 and a RI of 0.636. 1: Paracrocodylomorpha; 2: Poposauridae; 3: Crocodylomorpha; 4: Crocodyliformes; 5: Protosuchia; 6: Mesoeucrocodylia; 7: Metasuchia; 8: Neosuchia; 9: Notosuchia; Node 10, 12 and 13: Innominated. 11: Notosuchidae. 14: Sphagesauridae. Unambiguous synapomorphies for the labeled nodes 10-14: Node 10: 111(1), 198(1), 199(1), 232(1), 244(1), 245(1). Stem 11 –Notosuchidae–: 45(2), 103(2), 160(1), 176(1), 202(0). Node 12: 120(0), 241(1), 242(1), 243(1). Node 13: 11(1), 154(1). Stem 14 –Sphagesauridae–: 105(3), 121(1), 124(1).

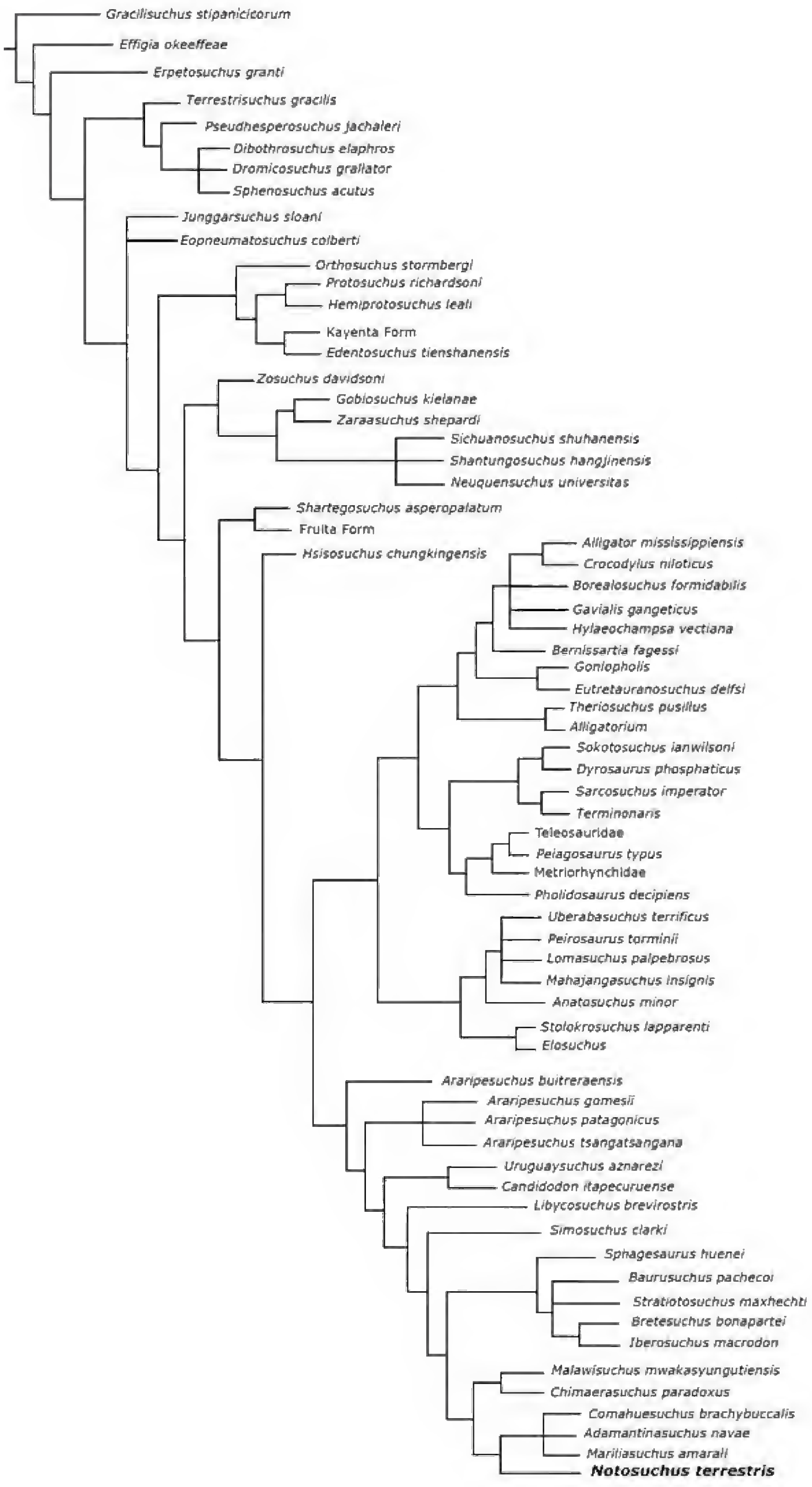

Fig.17- *(Alternative phylogeny for the appendix IV)*: Strict consensus of the 10 most parsimonious topologies that resulted from a strict parsimony analysis obtained through of TNT (Goloboff *et al.*, 2003). Tree length is 1108 with a CI of 0.274 and a RI of 0.636. This analysis result shared the different topology obtained from the exclusion of *Sillosuchus* and the inclusion of *Sarcosuchus* (Broin & Taquet, 1966; Sereno *et al.*, 2001; Gasparini *et al.*, 2006) and *Terminonaris* (Mook, 1934; Wu *et al.*, 2001; Gasparini *et al.*, 2006).

Contrary to this, in recent phylogenetic analyses carried out in another works (*e.g.*, Martinelli, 2003; Fiorelli, 2005; Fiorelli *et al.*, 2007) *Anatosuchus* is relocated outside of Notosuchia, and therefore from Comahuesuchidae, and related to peirosaurids which is similar to the present result. However, other authors related this bizarre crocodyliform to different mesoeucrocodylian or neosuchian forms (Andrade, 2005; Jouve *et al.*, 2006) which make evident that a more carefully analysis is necessary.

The notosuchian relationships presented here, especially in relation to the more derived forms, raise important paleobiogeographic questions. In fact, Notosuchia offers evidence in favor to the hypothesis of a dispersion event among Gondwana and Central Asia during the Early Cretaceous (Berriasiano–Aptiano), which took to important faunistic interchanges (Juárez Valieri & Fiorelli, 2002, 2003; Juárez Valieri *et al.*, 2004; Fiorelli, 2005; Fiorelli & Calvo, 2005). This fact is mainly demonstrated by the derived Notosuchia *Chimaerasuchus paradoxus*, of uncertain Cretaceous age of China, which represents in all parsimonious hypotheses the sister taxon of *Sphagesaurus huenei* from the Upper Cretaceous of Brazil. Such results are concordant with recent phylogenies presented by diverse authors whom they include to *Chimaerasuchus* inside his analyses (Wu & Sues, 1996; Wu *et al.*, 1995; Pol & Norell, 2004a, 2004b; Pol *et al.*, 2004; Andrade, 2005; Fiorelli, 2005; Pol & Apesteguia, 2005; Zaher *et al.*, 2006).

An interesting consequence from the phylogenetic result is the important relationships between peirosaurid and sebecosuchian crocodyliforms. This particularity, although different from the recent phylogenetic results (Pol & Norell, 2004a, 2004b; Pol *et al.*, 2004; Fiorelli, 2005; Pol & Apesteguia, 2005; Zaher *et al.*, 2006), is partially similar to the analysis carried out by Jouve *et al.* (2006) and Larsson & Sues (2007), in which these crocodyliforms represent sister groups. However, it is important to observe that in another heuristic search (excluding some sphenosuchians or the poposaurid clade) both group did not share sister relationships; thus, the sebecosuchian clade is more related to notosuchians (or inside them) and the peirosaurid clade as sister group of neosuchian crocodyliform (Pol & Norell, 2004a, 2004b; Pol *et al.*, 2004; Pol & Apesteguia, 2005; Zaher *et al.*, 2006), inside them as sister group of the [*Elosuchus* + *Stolokrosuchus*] clade or related to trematochampsid crocodyliforms (Buckley & Brochu, 1999; Buckley *et al.*, 2000; Turner, 2006; Turner & Calvo, 2005).

On the other hand, and although this does not have direct relevance with the present study, from the phylogenetic analysis derive other two very interesting aspects. First, the results confirm the position of the new basal Mesoeucrocodylia *Neuquensuchus universitas* Fiorelli & Calvo, 2007, from the same Cretaceous locality and levels of *Notosuchus*, as the sister taxon of *Shantungosuchus hangjinensis* Wu, Brinkman & Lu, 1994, from the early Cretaceous of China. However, the most parsimonious tree that depicts *Neuquensuchus* in other position, for example together with notosuchians, requires nine extra steps. Secondly, this result shared a clear paraphyly of "sphenosuchians" ratifying therefore the results offered recently by Clark *et al.* (2004). In any case, this is not confirmed since if other sphenosuchian taxa are gotten up to the analysis, like *Hesperosuchus*, *Kayentasuchus*, *Litargosuchus*, and *Macelognathus*, the monophyly of the group is guaranteed with the difference that *Junggarsuchus* would not represent a sphenosuchia. This rather represent the sister taxon of Crocodyliformes together to *Eopneumatosuchus*.

CONCLUSIONS

The new *Notosuchus* remains reported and described here increase the knowledge about the species and its characteristics. The study of the cranial and postcranial offers new information that allows understanding and confirming its relationships with the notosuchian members and the remaining crocodyliform groups. The phylogenetic analysis results demonstrate the monophyly of Notosuchia reinforcing the previous studies realized on the group (Wu *et al.*, 1995; Gomani, 1997; Pol, 2003; Pol & Norell, 2004a, 2004b; Pol *et al.*, 2004; Fiorelli, 2005; Pol & Apesteguia, 2005; Zaher *et al.*, 2006). In addition, it confirms the close existing relationships between the Argentine, Brazilian, and Chinese taxa.

This work, together with the last works on Crocodyliformes, clarifies that the heterodonty in basal crocodylomorph members (Harris *et al.*, 2000; Pol *et al.*, 2004) and Mesoeucrocodylia was not the exception but the rule, the most habitual in the mesozoic crocodyliforms. These display a great variety and dentary morphologies, doubtlessly related to its different functions, nutritional strategies, and dietary types. In addition and as it were noticed by Pol *et al.* (2004) and Ösi *et al.* (2007), the present analysis demonstrates that the heterodonty evolved independently in the different Crocodylomorpha groups (Sphenosuchia, Protosuchia, "protosuchians", Notosuchia and Eusuchia).

In the present work and on the basis of the diverse anatomical characteristics in the skull, jaw and postcranium of *Notosuchus*, it is clear the possible herbivores habits inferred for the species and other notosuchian groups.

Notosuchia would have been a remarkable group in Gondwana, very important within the faunal diversity of the Upper Mesozoic, mainly in South America. However, the presence of it outside Gondwana (*Chimaerasuchus*) during the Cretaceous demonstrates the occurrence of a paleobiogeographic land connection between Gondwana and Central Asia, by which a great migration of faunas occurred towards both continents, demonstrated by diverse vertebrate groups.

Without doubts, the least inclusive clade containing *Araripesuchus* and *Chimaerasuchus* (Fig.16) shows a great morphological diversity. It is evidenced mainly in the rostral region and in the snout, likewise on the tooth morphology and their possible nutritious specializations. Definitely, none of these taxa possesses ziphodont-like teeth ("true or false"); therefore, we do not think that the name Ziphosuchia is appropriated for this mesoeucrocodilians group (*sensu* Ortega *et al.*, 2000).

Notosuchia had to represent a great and much more diverse group than it is known at the moment, partly by the disparity of forms and the different morphotype. The recent new notosuchian notifications (*e.g.*, Novas *et al.*, 2004; Andrade & Bertini, 2005a; Garcia *et al.*, 2005; Marconato, 2006) not only confirm this hypothesis but extend the knowledge of the group and help to strengthen its phylogenetic relationships.

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APPENDIX

APPENDIX I

DATA MATRIX USED IN PHYLOGENETIC ANALYSIS

Gracilisuchus stipanicicorum
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Effigia okeeffeae
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Sillosuchus longicervix
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Erpetosuchus granti
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Terrestrisuchus gracilis
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Pseudhesperosuchus jachaleri
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Dromicosuchus grallator
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Sphenosuchus acutus
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Dibothrosuchus elaphros
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Junggarsuchus sloani
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Eopneumatosuchus colberti
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Protosuchus richardsoni
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Hemiprotosuchus leali
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Edentosuchus tienshanensis
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Orthosuchus stormbergi
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Gobiosuchus kielanae
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Zaraasuchus shepardi
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Shantungosuchus hangjinensis
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Neuquensuchus universitas
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Sichuanosuchus shuhanensis
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Zosuchus davidsoni
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Shartegosuchus asperopalatum
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Hsisosuchus chungkingensis
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Mahajangasuchus insignis
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Anatosuchus minor
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Lomasuchus palpebrosus
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Peirosaurus torminni
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Uberabasuchus terrificus
20110011211?00?11000101111?0110101022??0?00011??2????????????????11111131110?11[01]11????????2200011201?0012000???0?0????01001001?11?00?1?00001[01]101?11??0????10010??0011??1000???100?01110000000 0?0??00010010100101???1100??????????????????000000??0000??

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?????????????????????????????00?0??1??01?

Iberosuchus macrodon
1?0?00012?0?00111000111111?01?000?02??10100111?12??1?101??10?1????111??10?0?1011011??????[12][1234]00??00???00?[12][01]0?2??0000???11001101010?1?0??100?11001?0??101???[01]?0111?001101?0??01?100001000000??0??010?00????0100???????????????????????????000000?21000??

Baurusuchus pachecoi
100??0?121??00?1101????111?0110?????2?10110011112011?1000?10??10??31112101011111?????????????????????12103????1?????11011101010111001100111101 10?0111???[01]0[01]1111011101?00001?0001000000000 0???010000111?01000?????????0112202 11??0????1000000?0000011

Stratiotosuchus maxhechti
100?0??1??0000?11?111101?0???10?11???????????1?1???????????????????131?????????11???????????????????????0?2103???1??????????1111?10?1????010001101?10??1??????010??01????1??????10??010?0000????00??0??1?1??1?????????????????????????????????????0000??

Uruguaysuchus aznarezi
201?001101??00??10??1??1????1???01022?101?0011????1?????0??0???01111[12]???000110100??1?1??????0000?0??01?21002100?00?000?[01]???01?1?00????1?0111?11?????11?????1?0001????????0???10?????00????????01?001101?01100?11111?0011112021 1??0?????01????????????

Candidodon itapecuruense
201?00???1??00??110010?????0010101022?111?00????????????????????11212????????11?????????????????????????1?01????????????1011010??00????100111011????11??????1?0??21?1?1???????1?0???00?000?????01101?000??1???????????????????????????????????1???000010

Araripesuchus gomesii
20100011010000111000101111 1011[01]0010221101000111 12011?10000?0?110201121210001101[01][01]1[01]11111?1[234]000100000011110021001001010100100100 1000000100110002100001 10?0011[01]00001111010000 11100?00000000000000100100 00?01?0??????110011121021111012211001?101?000000

Araripesuchus patagonicus
201000?1010000?1[01]000101111?0111001022?10100011?12?11?1000??0?1?02?11212?0?011[01]1??1?1?????????10000?0111100???01???0?01?01101?010000??100110102?0??01????0??[01]1000111?0100001110?00000000000000010010000?01100?1?1111001112102 11??01221?01?01?1?0?0000

Araripesuchus buitreraensis
[12]01????1?1???0??10001?0111?0110?0???2?1010001??????????????????[12]??12????0??1?100????????????????????[01]???0[0123]???0?????11??1??10?100??0???0?10?02?????????01???000?1??110??01?0?0?????00?0?????010?1[01]101?010?0??????????????????????????[01]1?0100?0??000

Araripesuchus tsangatsangana
201101?1211?0011101010111100110001012110100011112?11?1000??0?1101021102100011010111111?001000???????1110002100?0000101?01001?010000011101101 02?0?001?110011[01]0000111?0100001100000100000000?000100111?02011101111111001112 1?2001100211101?010??000000

Libycosuchus brevirostris
201000?101??00??10?010?1???011000?0?2?101??0?11120?1?10?0??0???0?011??210001?1000???????????????????1[01]2010??????????01?011?????????????011000??1???01??????00000110????001?100?01??????00???0100100???01??????????????????????????????????00?1?00?????

Simosuchus clarki
10301011000000100010111110?0110001021?10100011?11011?1000010?1?02011212101011 0000??????02100?2010?10002010???01??????11011012120000101001110021100120???211[12]0001111011001[01]1?100000000000010000010110100001100?????110?????202??????????[01]1001100000000

Malawisuchus mwakasyungutiensis
101?00?1110000?[01]10001[01][01]1100?110001?22110100011??20???1000?10?1?02?111[01]2?0101110001????1??21000[02]010??01[12]2111???01?0???01100101?11000???110110101?0?0001???0?100??21110?10000111000000000000000???0100110002?1110101??11001112?0211??01221?00?001??0??000

Notosuchus terrestris
101000110101001110001111110011001102211011002111 2011?1000010?1102111112101011 10001[01]11101?210001000??0122011??01100101[01]1101[01]010010000001111111011000001110010000101110110000111011000000000000001001111121011011111110011112 0211??01221?110001?0000011

Mariliasuchus amarali
101000?1010000111000 1[01]11110001100102 2110100021?12011?1000010?1?0213011210[01]0111000??1??0??2?000????0???22111??011?010?0[01]001101001001100[01]0011110110?0011???01100010011001 00001?1010000000000 0?000100111?1?10110?11?1?????????0211??01221?110001??011111

Adamantinasuchus navae
101000?1010?00?110001???11?011??????????????????????????????????????13??1???00??10??????????????????????1??211???1??????01000101?01?0????111110?02?0?0?0????01100??211?????0????10??010?000000???01?01?0?1?1[01]10??????????????????????????????????0?1??0111??

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?11?11?111???????????????????????????1100?1??011111

Sphagesaurus huenei
1010000101??00??100?????110?????????21101?00?????011?1000????????13?2????????100????????1???????????????312????0???????111110111111111111111001110101 1?0?11?0??011?0?10??01??000000?00???????01001?1????0????????????????????????????????0?01?00000??

Chimaeresuchus paradoxus
101?0001111?00??12??0110?01010??1?1?????2100?00????11[01]?314210??00?0100111111011??????0?0110??????????10?11?????3???????????1?00???0??????????0???111?1211?101111?110011?1202????01221???0????0000???

Elosuchus
202?1111110000111100100 1?1?1010111012?101000?1?12111?1000?11?????1202?3??00?21100?????????????1110??00?0000???01?????011010110[01]1010?00000010001?11?101???00011?00011?1?0000??100001[01]??0000?0??011000101?010?????????????????????????????001000?1000000

Stolokrosuchus lapparenti
202000000010000?111001001?1?0010111012?1??0?011?1211??1000?11?1???020?1????0?21100???????????????????1?0000???01?????01?010110[01]1010?00000010001????101???000111?00?0??00000??1000011??000?????0??0001?0?010???????????????????????????0010?0?00000??

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???????0?????0???00

Dyrosaurus phosphaticus
002??1?101?010?11?00100011?1010011012?1010100111 2011?1011?10?10101302?3?00??2?000????????0?00??????1???????????????????1???????????????0??0???????????????021?0001????0??????00??1?0000000???010?00?01?010010000011001112?021111012101??0000??0??000

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

Teleosauridae
[02]02?111111001102010010000000000001100 21?01000?0011011110010 11?1?00120003?000?200002101111?0000?12000101011?0???10??01001101??1011000011000010100?0??0000??10001000011?010?01110001010000000000001000 01?12010000000011000110?0211??0???????00?0?00??000

Metriorhynchidae
[02]02?12110100111201011000?00000001100 21?0?000?0011011110010 11?1?001200?300010200002101?11?0000??????0??012?0???100?01001101??1011?000??000010102?0???000????001000011?01000?1100000100000000???0100001?1?0100000000011000110?0211??0???????00?0?000?000

Pelagosaurus typus
202?1111110011020101000000000000[01]100211010000001101111001001?10001200?3000002000011 0111?0000001200011101?00???10???????1?1??????0000??010010?0010???00????0001000011201000011000001?0000000???010000???0?1?0???000??????????????????????????000??0??000

Theriosuchus pusillus
20110111110100110000110111100110011?211010001?11?01111000?????1?20211?41001010101101111100011112001001010002?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?????????0[01]??00??0???00

Alligatorium
?0??????1?0000?1000010?111??0?100?1????0??00??11??1??1000???????20?1????00101?101?011111000???1?00100????????????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???010?00????????????????????????0?????????????0000?00?00?0

Goniopholis
203?12111100101110001001 11?0010001002?101000?1112011?1010?10?1?021312?4100[01]0[01]02011?1??1??0?00?1200?11?000002100010?1101100??101100?000010010001?1???0000110020000011001000011110?010000000000001000 0????01?????0001100?11??0211??0???????0000?0000000

Bernissartia fagessi
203??21111??00111000?00111?001000?002?????0001112?11?10100?0?1???1?1??41001010 2011?1?11??02002111011 0100000??00?????????1????1?????????0??0?10???01???0????1?12000001????0??????00??10000????0??01????????1?1?0???0001100?11?????????0????????0?????0???00

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???????????????????????????????????????0?

Gavialis gangeticus
212?121111001111110110111110010001002110101101112011110110101110[01]131003100012000001111110131112
111100?000002110?100100?101??121100?00000001000101?1?00001?0?20?00011001000011100001?000000000010
00000100100100000011 00?11??021111030111??00?0?00??000

Borealosuchus formidabilis
203?1211110010111000100111?00100010021101011111121111010010?110?1310031000110?0111111111113111?11
0?00?000002110?100100?101??11110??000000010001?1???0000110?20?00011001000011100001000000000001000
0001001001000001100?11??0211110??????00?0?00???00

Crocodylus niloticus
20301211 1100[01]0111000102111100100010021 10?011111120111101001011 10[01]1310031000100101211111101311
12021100?00000211001001 00?101??121100?000000010011010110000 1?0?2000001100100001110000100000000000 0
10000001001001000001100?1112021111030111??0000?0000000

Alligator mississippiensis
203112?101?00011100010211110 01000?0021101011111120111101001011 10[01]031203100010020121111111131112
0211?0?0000021100100100 1101??111000?00000001001[12]01011000011[01]1200000110010000111000010 00000000
0001000000100100100000 1100?1112021 11103011

APPENDIX II

LISTS OF CHARACTERS CORRESPONDING TO THE DATA MATRIX USED IN THE PHYLOGENETIC ANALYSES

Characters 1-231, not cited here, were taken and are the same from FIORELLI & CALVO (2007). The following ones, 232 to 245 characters, were taken from POL & APESTEGUIA (2005) that originally corresponded to the characters listed in the contiguous reference.

Character 232 (POL & APESTEGUIA, 2005: character 180): Splenial-dentary suture at symphysis on ventral surface: V-shaped (0), or transversal (1).

Character 233 (POL & APESTEGUIA, 2005: character 181): Posterior peg at symphysis: absent (0), or present (1).

Character 234 (POL & APESTEGUIA, 2005: character 184): Dorsal surface of mandibular symphysis: flat or slightly concave (0), or strongly concave and narrow, trough-shaped (1).

Character 235 (POL & APESTEGUIA, 2005: character 185): Medial surface of splenials posterior to symphysis: flat or slightly convex (0), or markedly concave (1).

Character 236 (POL & APESTEGUIA, 2005: character 186): Choanal septum shape: narrow vertical bony sheet (0), or T-shaped bar expanded ventrally (1).

Character 237 (POL & APESTEGUIA, 2005: character 188): Lateral surface of dentaries below alveolar margin, at middle to posterior region of toothrow: vertically oriented, continuous with the rest of lateral surface of the dentaries (0), or flat surface exposed laterodorsally, divided by a ridge from the rest of the lateral surface of the dentaries (1).

Character 238 (POL & APESTEGUIA, 2005: character 220): Flat ventral surface of internal nares septum: anteriorly broad (0), or tapering anteriorly (1).

Character 239 (modified from SERENO *et al.*, 2001: character 67 by POL & APESTEGUIA, 2005: character 222): Premaxillary palate circular paramedian depressions: absent (0), present located anteriorly on the premaxilla (1), or present located at the premaxilla-maxilla suture (2).

Character 240 (POL & APESTEGUIA, 2005: character 223): Posterolateral region of nasals: flat surface facing dorsally (0), or lateral region deflected ventrally, forming part of the lateral surface of the snout (1).

Character 241 (defined by ZAHER *et al.*, 2006: character 192 and taken by POL & APESTEGUIA, 2005: character 224): Ventral half of the lacrymal: extending ventroposteriorly widely contacting the jugal (0), or tapers posteroventrally, not contacting or contacting slightly the jugal (1).

Character 242 (defined by ZAHER *et al.*, 2006: character 193 and taken by POL & APESTEGUIA, 2005: character 225): Large foramen on lateral surface of anterior jugal: absent (0), or present (1).

Character 243 (modified from ZAHER *et al.*, 2006: character 194 and POL & APESTEGUIA, 2005: character 226). Procumbent premaxillary –incisiform– anterior dentary alveoli: absent (0), or present (1).

Character 244 (defined by ZAHER *et al.*, 2006: character 195 and taken by POL & APESTEGUIA, 2005: character 227): Rodlike posterolateral palatine bar: absent (0), or present (1).

Character 245 (defined by ZAHER *et al.*, 2006: character 198 and taken by POL & APESTEGUIA, 2005: character 230): Ectopterygoid projecting medially on ventral surface of pterygoid flanges: barely extended (0), or widely extended covering approximately the lateral half of the ventral surface of the pterygoid flanges (1).

APPENDIX III

LIST OF THE 67 TAXA USED IN THE PHYLOGENETIC ANALYSIS (TAKEN FROM FIORELLI & CALVO, THIS VOLUME).

Effigia, *Sillosuchus*, *Erpetosuchus*, *Pseudhesperosuchus*, *Dromicosuchus*, *Sphenosuchus*, *Junggarsuchus*, *Eopneumatosuchus*, *Shartegosuchus*, *Mahajangasuchus*, *Araripesuchus buitreraensis* and *A. tsangatsangana*, *Libycosuchus*, *Adamantinasuchus*, *Stolokrosuchus* and *Elosuchus*, are new taxa included by the authors for this analysis.

Gracilisuchus stipanicicorum (ROMER, 1972)
Effigia okeeffeae (NESBITT & NORELL, 2006; NESBITT, 2007)
Sillosuchus longicervix (ALCOBER & PARRISH, 1997)
Erpetosuchus granti (NEWTON, 1894; OLSEN *et al.*, 2000; BENTON & WALKER, 2002)
Pseudhesperosuchus jachaleri (BONAPARTE, 1971, 1978; CLARK *et al.*, 2000)
Terrestrisuchus gracilis (CRUSH, 1984)
Dromicosuchus grallator (SUES *et al.*, 2003)
Sphenosuchus acutus (HAUGHTON, 1915; WALKER, 1990)
Dibothrosuchus elaphros (WU & CHATTERJEE, 1993)
Junggarsuchus sloani (CLARK *et al.*, 2004)
Eopneumatosuchus colberti (CROMPTON & SMITH, 1980)
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 (FIORELLI & CALVO, 2007)
Sichuanosuchus shuhanensis (WU *et al.*, 1997)
Zosuchus davidsoni (POL & NORELL, 2004a)
Shartegosuchus asperopalatum (EFIMOV, 1988)
Fruita Form (CLARK, 1985, 1994)
Hsisosuchus chungkingensis (YOUNG & CHOW, 1953; LI *et al.*, 1994; WU *et al.*, 1994)
Uruguaysuchus aznarezi (RUSCONI, 1933)
Candidodon itapecuruense (CARVALHO, 1994; NOBRE & CARVALHO, 2002)
Araripesuchus gomesii (PRICE, 1959)
Araripesuchus patagonicus (ORTEGA *et al.*, 2000)
Araripesuchus buitreraensis (POL & APESTEGUIA, 2005)
Araripesuchus tsangatsangana (TURNER, 2006)
Libycosuchus brevirostris (STROMER, 1914)
Simosuchus clarki (BUCKLEY *et al.*, 2000)
Malawisuchus mwakasyungutiensis (CLARK *et al.*, 1989; GOMANI, 1997)
Notosuchus terrestris (WOODWARD, 1896; GASPARINI, 1971; BONAPARTE, 1991, 1996; FIORELLI, 2005; POL, 2005)
Mariliasuchus amarali (CARVALHO & BERTINI, 1999; ANDRADE, 2005; ANDRADE & BERTINI, 2005a, 2005b; ZAHER *et al.*, 2006)
Adamantinasuchus navae (NOBRE & CARVALHO, 2006)
Comahuesuchus brachybuccalis (BONAPARTE, 1991; MARTINELLI, 2003)
Chimaeresuchus paradoxus (WU & SUES, 1996)
Sphagesaurus huenei (PRICE, 1950; POL, 2003)
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)
Mahajangasuchus insignis (Buckley & Brochu, 1999)
Anatosuchus minor (Sereno *et al.*, 2003)
Elosuchus (Broin, 2002)
Stolokrosuchus lapparenti (Larsson, 2000; Larsson & Gado, 2000)
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)
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)
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 IV

ALTERNATIVE PHYLOGENY (FIG.17)

Sarcosuchus imperator
203?12?10100101?1000100110010100010 12?10101[01]01?12?1??10100?0?100?131213??00021[01]101?112????[01]00
?1200?00?010[01]0??000[01]001?0?101??121100??00000010010?1???00???110210000?1001000?1?100?010?00000000
?010000101101001001001 1000??????1?110????10000?0?0000000

Terminonaris
202?[01]2?1010010?11??01001???1010001012?1010[01]1??????11?1010??0??0??13[01][12]13?000?2100011112??0000
0?1200?10?0?0102100?1001001101??1??10??0??0?0010????1???0000111?[12]??000??00?0?0?11100?0?0??00???00?0
10000101101001000001100011220211110222 0100?000??000000

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NOTES ON A PARTIAL SKELETON OF *MOURASUCHUS* (CROCODYLIA, NETTOSUCHIDAE) FROM THE UPPER MIOCENE OF VENEZUELA [1]

(With 9 figures)

WANN LANGSTON JR. [2]

ABSTRACT: The specimen MCC 110-72V housed in the Museo de Ciencias Naturales de Caracas, Venezuela, is here described. This material, probably a specimen of *Mourasuchus arendsi*, is an associated but incomplete skeleton from the Urumaco Formation collected in 1972 by a joint field party with Venezuelan and North-american institutions. Bones are poorly preserved, all elements having suffered from chemical weathering during diagenesis and surface exposure. The lithology at the site is described as a gray, highly gypsiferous shale. The specimen consists of the skull and lower jaw, a substantial part of the vertebral column, fragments of ribs, parts of the pectoral and pelvic girdles, and some osteoderms. The estimated length of the individual is ~6.6m.

Key words: *Mourasuchus*. Crocodylia. Nettosuchidae. Miocene. Venezuela.

RESUMO: Notas sobre um esqueleto parcial de *Mourasuchus* (Crocodylia, Nettosuchidae) do Mioceno Superior da Venezuela.

O espécime MCC 110-72V depositado no Museo de Ciencias Naturales de Caracas, Venezuela, é aqui descrito. Este material, um esqueleto associado, mas incompleto, provavelmente um espécime de *Mourasuchus arendsi*, é proveniente da Formação Urumaco. Foi coletado no ano de 1972 em trabalho de campo conjunto entre instituições da Venezuela e da América do Norte. Os ossos estão mal preservados, todos os elementos tendo sofrido intemperismo químico durante a exposição em superfície e o processo diagenético. A litologia, no sítio, é descrita como um folhelho cinza com alto teor de gipsita. O espécime consiste de crânio e mandíbula, grande parte de coluna vertebral, fragmentos de costelas, partes das cinturas pélvica e escapular e alguns osteodermas. O comprimento estimado do indivíduo é de aproximadamente 6.6m.

Palavras-chave: *Mourasuchus*. Crocodylia. Nettosuchidae. Mioceno. Venezuela.

INTRODUCTION

An aberrant "duck-faced" crocodilian from the Pliocene of Brazil was named *Mourasuchus amazonensis* by Price (1964). Later, unaware of Price's work, Langston (1965) described *Nettosuchus atopus,* a similar animal from the middle Miocene Laventan stage (Honda Group) in Colombia (not the now questionable older "Friasian" South American Land Mammal Age as earlier reported by Langston, 1965): see Flynn & Swisher III (1995). Although the two taxa can be accommodated in one genus, they are significantly different at the species level, hence *Mourasuchus amazonensis* Price (1964) and *M.* (=*Nettosuchus*) *atopus* (Langston, 1966). Gasparini (1985) described *Carandaisuchus nativus,* a peculiar crocodilian with a pronounced tumescent bony occipital crest, from the late Miocene-Pliocene (Mesopotamiense) of Argentina, which is assignable to *Mourasuchus* (Bocquentin & Souza Filho, 1990). A third species, *M. arendsi*, has been recognized by Bocquentin Villanueva (1984) from the upper Miocene (Huayquariense) Urumaco Formation of northern Venezuela (Linares, 2004).

Mourasuchus is known largely from cranial material, but Langston (1965) described the scapula and coracoid, the humerus, femur, ilium, and ischium of *M. atopus*, and Bocquentin Villanueva (1984) has described an incomplete articulated neck of *M. arendsi.* Here, I report additional postcranial material including, for the first time, osteoderms, of *Mourasuchus*, probably *M. arendsi*, from the Urumaco Formation.

Institutional abbreviations: CIAAP, Centro de Investigaciones Antropológicas, Arqueológicas y Paleontológicas, Universidad Nacional Experimental Francisco de Miranda, Coro, Venezuela; MCC, Museo de Ciencias Naturales de Caracas, Venezuela; UCMP, University of California Museum of Paleontology, Berkeley,

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California; UF, University of Florida, Florida Museum of Natural History, Gainesville, Florida; TMM, Texas Memorial Museum, The University of Texas at Austin, Texas.

RESULTS

DISCOVERY, OCCURRENCE AND CONDITION OF THE SPECIMEN

The specimen, MCC 110-72V, in the Museo de Ciencias Naturales de Caracas, Venezuela, is an associated but incomplete skeleton collected in 1972 by a joint field party from the Museum of Comparative Zoology at Harvard University, led by Dr. Bryan Patterson, in collaboration with the Escuela de Geología, Universidad Central de Venezuela and the Ministerio de Minas e Hidrocarburos de Venezuela (MEDINA, 1976; WOOD, 1976). The specimen consists of the skull and lower jaw, a substantial part of the vertebral column, fragments of ribs, parts of the pectoral and pelvic girdles, and some osteoderms of an individual with an estimated length of ~6.6m. Professor Patterson's unpublished field notes record that MCC 110-V72 and...“parts of a skull, jaws, vertebrae, etc “...of a “Giant crocodile” (111-72V) were found,...” weathering out of the same small projection from the west and south and from the east sides, respectively”. Thus, as Patterson noted, ...“some possibility of confusion exists”. Indeed, an incomplete right scapula lacking a field number, but accompanying MCC 110-72V, is larger than the scapulae belonging to that individual, and a humerus bearing number 110-72V is too small to belong with the *Mourasuchus* skeleton. The “Giant Crocodilian” MCC 111-72V is not further identified in the field notes. All the bones attributed here to MCC 110-72V are, however, concordant in size. Whether the remains were articulated when found is unknown, but the postcranial material was sent to me as separate unprepared elements. Differences in preservation and coloration of the bones suggest that they were somewhat scattered, but some vertebrae may have been articulated or were closely associated.

The locality is recorded as, “$3^1/_2$km N 30°W of El Picacho, on the up side of the Chiguaje fault”, Falcon State (Patterson field notes, 1972). This places it about 6.5km N24°E of the town of Urumaco (Fig.1). The source bed may be a thin, but extensive, stratum near the top of the upper member of the Urumaco Formation, informally referred to by field geologists as the “capa de tortugas” (=”capa de huesos”) because of its profuse fossil content (ROYO & GÓMEZ, 1960; PASCUAL & DÍAZ DE GAMERO, 1969; LINARES, 2004). There is some uncertainty about this, however, because Patterson's field notes specify many of the fossil occurrences in the area as coming from the “capa de huesos”, but MCC 110 72-V is not so noted. An additional complication is that a stratigraphic column of the Urumaco Formation giving positions of fossil occurrences (LINARES, 2004, p.9-10) shows Patterson's field numbers 103-115 lying some distance below the “capa de tortugas”, in the lower member of the Urumaco Formation. Moreover, on an accompanying map (Fig.2 of LINARES, 2004), Patterson's locality 103, which Patterson states is the same geographically as locality 110-72V, is shown south of Urumaco, in the opposite direction of locality 103 described in the notes. Resolution of this discrepancy is not possible here, so I follow the information provided in Patterson's notes. The approximate locality derived from a reading of the field notes includes a small outcrop of the “capa de tortugas” shown on the PASCUAL & DÍAZ DE GAMERO (1969) map (Fig.1). The lithology at the site is described as a gray, highly gypsiferous shale, which is characteristic of much of the Urumaco Formation. The rocks are believed to be of fluvial and lacustrine origin (LINARES, 2004). For further information about the origin, age, and paleoenvironment of Urumaco deposition, see DÍAZ-DE-GAMERO & LINARES (1989), LEV (1997), and LINARES (2004). The Urumaco Formation has yielded a diverse fauna of fossil fish, crocodilians, turtles, and mammals (LINARES, 2004; SÁNCHEZ-VILLAGRA *et al.*, 2004).

DESCRIPTION

The bones of MCC 110-72V are poorly preserved, all elements having suffered from chemical weathering during diagenesis and surface exposure. Superficial detail has been largely obliterated and often only a general idea of the external form of a bone can be discerned. Some bones are partly replaced by gypsum, as is usual among bones from the Urumaco region (BOCQUENTIN VILLANUEVA, 1984).

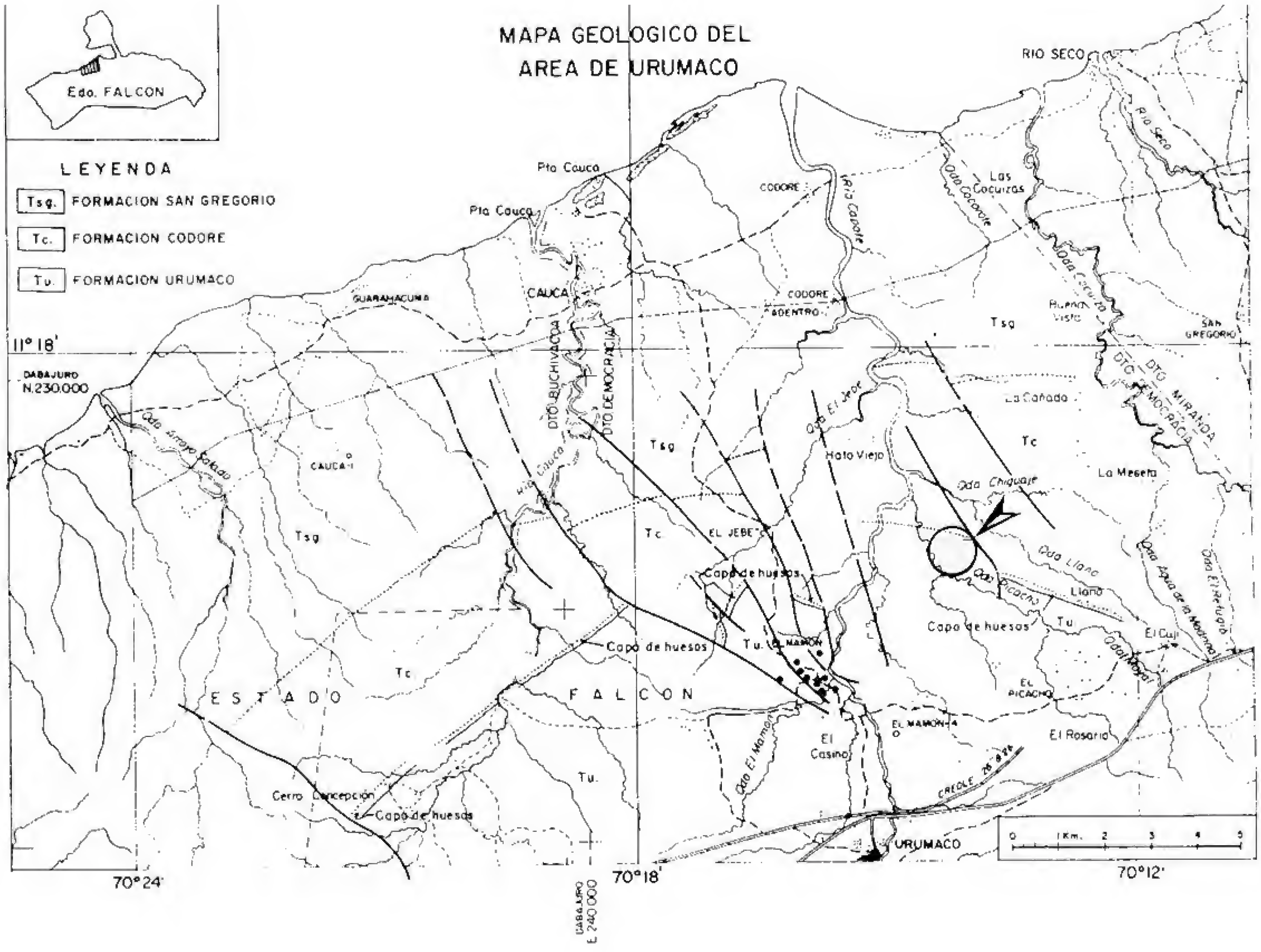

Fig.1- Simplified geologic map of the Urumaco area in northern Falcón State, Venezuela showing the “capa de tortugas” (=“capa de huesos”) and associated strata, prepared by geologists of the Texas Petroleum Company in 1958, and adapted from Pascual & Díaz de Gamero (1969). Large circle denotes approximate source area of *Mourasuchus arendsi* MCC 110-72V, deduced from field notes of Professor Bryan Patterson, 1972. Arrow points to a limited outcrop of the “capa de tortugas” which may include Patterson’s locality 110-72V. The discontinuous outcrops of the capa de tortugas at the top of the Urumaco Formation (Tu) are indicated by the solid line labeled “Capa de huesos”.

Axial Skeleton. The reconstructed skull and jaws of MCC 110-72V are currently on display at the Museo de Ciencias Naturales, Caracas, and have not been available to me. I am indebted to Dr. Ascanio Rincón (pers. comm., May 2005) for the following information about this specimen. The snout to quadrate length is 107cm (incorrectly reported as 1.25m by Langston & Gasparini, 1997), and the extreme width across the quadrates is 53cm; the width between the outer edges of the jugals is 50cm. The roof of each premaxilla is pierced by three rounded perforations.

Vertebrae are well represented, but reassembly of the vertebral column is conjectural. Only the atlas and axis, the two sacrals, and the biconvex first caudal are recognizable with certainty. Probably all of the cervical vertebrae are present, but the atlas is represented by its intercentrum only and the ninth cervical by a fragment of its neural arch. Four anterior and two posterior thoracic vertebrae, three lumbars, and thirteen caudals can be placed with some assurance. Two dissociated neural arches are likely from anterior thoracic vertebrae.

The atlantal intercentrum, viewed from below, displays the transverse constriction, or waist, observed in other eusuchians (Fig.2A). It is 49mm long and 71mm wide, caudally. The least width of the waist of the intercentrum is 53mm. On either side, caudally, a short caudolaterally projecting costal process bears a large asymmetrically reniform facet 29mm wide and 18mm high for the head of the first rib. The processes are separated by a shallow transverse emargination in the caudal edge of the intercentrum 25mm wide, suggesting that the capitula of the atlantal ribs did not meet in the sagittal plane. The cranial cotyle is narrowly reniform in plan. It is 53mm wide and at least 36mm in dorsoventral diameter. A small tubercle of unknown function occurs on either side of the intercentrum a short distance behind the cranial edge of the occipital cotyle, and here the intercentrum expands briefly to a width of 57mm.

The axis and attached odontoid bone are badly corroded, and the dens are missing (Fig.2B-2C). The length, as preserved, of the combined odontoid and centrum (excluding the posterior condyle) is 70mm. The odontoid bone bears massive dia- and parapophyses (Fig. 2C, left). The diapophysis ends in a small facet, suggesting the existence of a bicipital axial rib. The cranially-facing trochlea that supported the dorsolateral hemiarches of the atlas are flat and the articular facets are nearly vertical (Fig.2C, left). The broken base of a prezygapophysis suggests that its articular facet for the atlantal postzygapophysis faced dorsolateral at approximately 45°. The ventral keel at the cranial end of the centrum is undivided, and is arched upward longitudinally in lateral aspect (Fig.2B-2C, left). The keel descends at its cranial end, forming a small hypapophysis, which is not forked *sensu* Brochu (fig.51 of 1997).

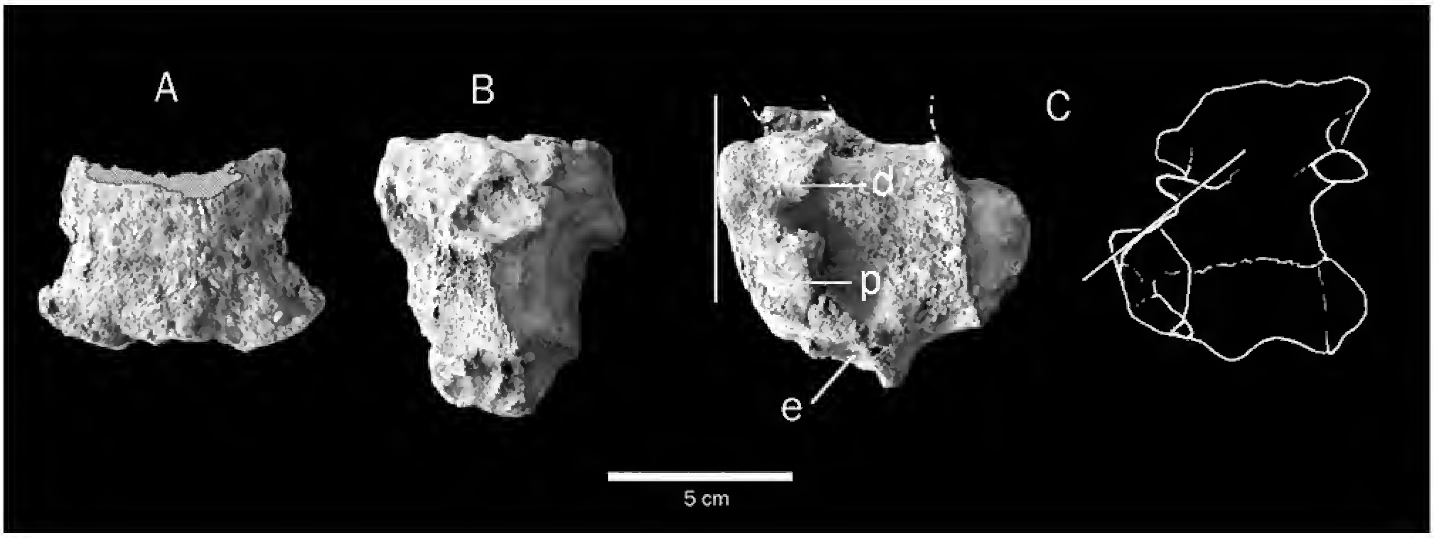

Fig.2- *Mourasuchus arendsi* (MCC 110 72-V), atlantal intercentrum, ventral view, anterior toward top (A), axis centrum with attached eroded odontoid bone, ventral view, anterior toward top (B), axis and attached odontoid seen from the left side (C, left), sketch of axis and attached odontoid bone of *Alligator mississippiensis* (C, right). d, diapophysis; e, eroded excavation at cranial end of hypapophysis; p, parapophysis. Straight lines indicate difference in inclination of the trochlear facets between *Mourasuchus* (left) and *Alligator* (right).

The cranial surface of the hypapophysis is excavated as though it lodged an ossicle, but this is probably an artifact of erosion. A lateral excavation about the size of a thumbprint occurs caudolaterally on the sides of the pedicles.

The centrum of the third cervical is 51mm long, excluding the condyle, 50mm high, excluding the hypapophysis, and 58mm wide behind the parapophyses (Fig.3A). The prezygapophyses project strongly upward, extending 10mm beyond the anterior plane of the centrum. The articular facets of the pre- and postzygaphyses slant toward the sagittal plane at an angle of 40°. The pedicle is almost as long as the centrum, excluding the condyle. A strong diapophysis bearing a hemispherical tubercular facet springs laterally from the centrum. The parapophysis, born low on the side of the centrum, is shorter and thicker than the diapophysis. The capitular facet is diagonally ovate, flat, and is larger than the tubercular facet.

The centrum of the fifth cervical is 56mm long, excluding the condyle, 59mm high, excluding the hypapophysis and 61mm wide at the cranial end (Fig.3C, left). A strong ventrolaterally-directed diapophyseal process springs from the lower part of the pedicel and the upper part of the centrum. Its relationship to the neurocentral suture is undetermined. The parapophysis, which arises from the lower part of the centrum projects laterally and is more massive than the diapophysis. The articular facets of the prezygapophyses face upward at an angle of 43° to the sagittal plane.

Intact cervical neural spines are preserved only in the presumed third and fifth vertebrae. The spine of the third cervical is a broad plate-like lamina 41mm long at the base, and expanding longitudinally to 45mm at its top (Fig.3B). Its dorsal edge is gently convex upward anteroposteriorly. The neural spine of the fifth cervical has a shorter base than that of the third cervical, and is a little more than twice as high, measured from the top of the neural canal (Fig.3C, left).

The cervical hypapophyses are relatively small and blunt, and lack a cranially-directed hook-like process distally. The largest preserved hypapophysis occurs on the sixth cervical (Fig.3C, right). All preserved hypapophyses are followed by an upwardly arched sagittal ridge on the bottom of the centrum.

The supposed third thoracic vertebra bore its dia- and parapophysis on the transverse process, which arises high upon the side of the pedicel. The parapophysis is bent slightly downward distally. The centrum of this vertebra is ~59mm long, excluding the condyle, 47mm high, excluding the hypapophysis, and ~49mm wide anteriorly (measurements are approximate owing to destruction of the cortical bone). Inclination of the prezygapophyses is 57° from the sagittal plane. Of the preserved anterior thoracic vertebrae only one bears a hypapophysis, which is small and scalene in lateral aspect, the shortest side facing craniad.

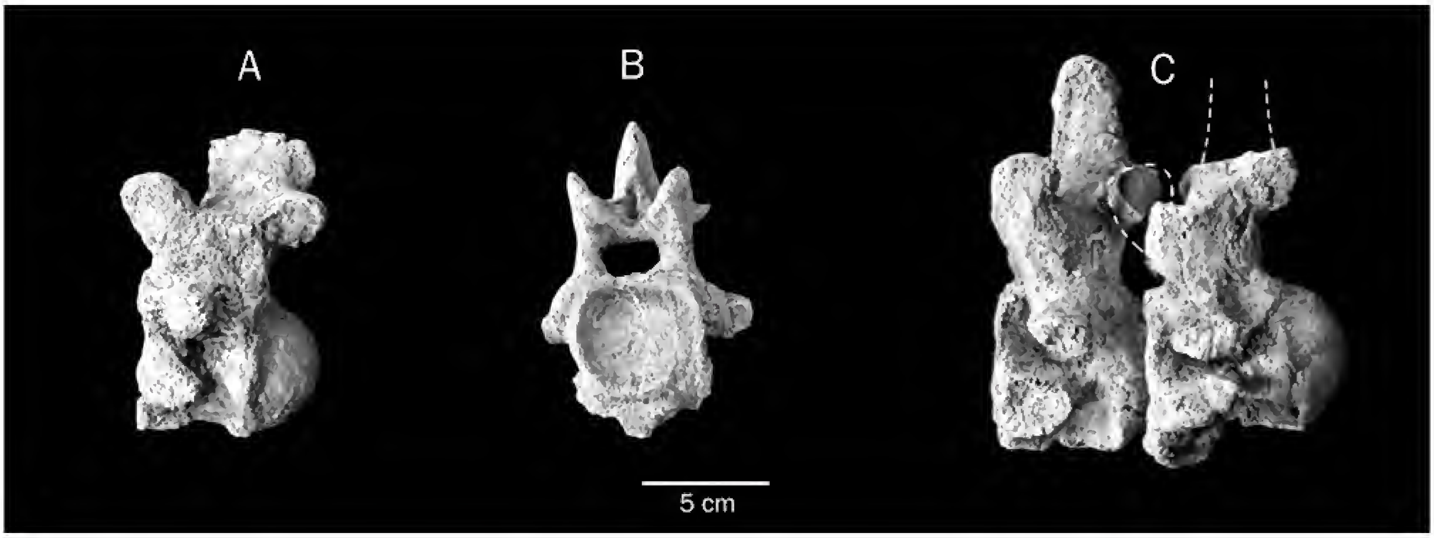

Fig.3- *Mourasuchus arendsi* (MCC 110 72-V), third cervical vertebra, lateral (A) and anterior (B) views; fifth and sixth cervical vertebrae, lateral view (C).

Two posterior thoracic vertebrae are larger than the anterior vertebrae. Their neural arches are wider and lower, and their centra are more cylindrical. The better preserved vertebra (Fig.4A) has a more gracile transverse process than the other, so was likely the more posterior of the two. It may have borne a single headed rib. The centrum is 67mm long, excluding the condyle, 60mm high anteriorly, and at least 65mm wide. The articular surfaces of the zygapophyses make an angle of 79° with the sagittal plane. There is a long shallow longitudinal excavation at about mid-height on either side of the centrum and a deeper, smaller depression on the side of the pedicel bounded posterodorsally by a pronounced caudal centrodiapophyseal buttress. The base of the neural spine is 49mm long.

The lumbar series is represented by what are believed to be the first, third and fifth vertebrae. The centra of all three vertebrae are wider than high, the condyle of the supposed fifth lumbar being significantly wider than the others in relation to its height. The centrum of the putative first lumbar retains the spindle form associated with the thoracic series (Fig.4B).

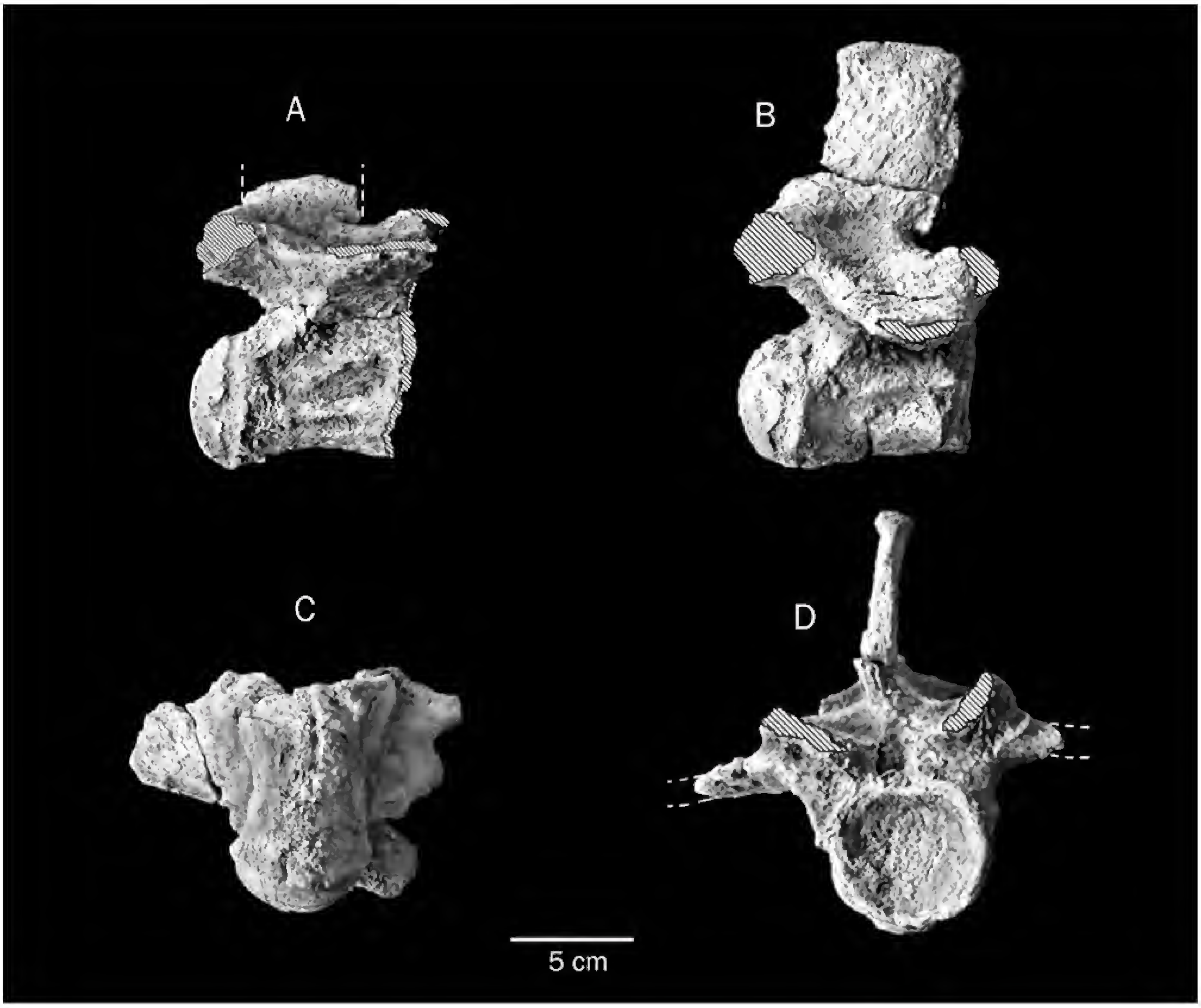

Fig.4- *Mourasuchus arendsi* (MCC 110 72-V), putative posterior thoracic vertebra, lateral view (A), putative first lumbar vertebra, right lateral view (B), ventral view, anterior toward top (C), anterior view (D). Note absence of "table top" expansion of the top of the neural spine.

It is 79mm long, excluding the condyle, 65mm wide and 55mm high cranially. It is about 57mm wide at mid-length. Corresponding measurements of the third lumbar are, respectively, 66mm, 70mm (e), and 59mm. Its width at mid-length is 62mm. The prezygapophyses make an angle of 48° with the sagittal plane in the first lumbar and of 50° in the fifth. The centrum of the first lumbar contains a shallow longitudinal fossa at about mid-height on either side (Fig.4B-4C). Larger excavations are present on the third lumber, but only shallow indentations occur on the fifth lumbar. The first and third lumbars retain intact neural spines (Fig.4B, 4D). They are long based (anteroposterior diameters of 56mm), plate-like, and like other presacral spines lack "table-top transverse expansions at the tops. The spine of the first lumbar is 97mm high, measured from the top of the neural canal. The basal diameters of the lumbar transverse processes diminish caudad.

The cranial end of the first sacral is 83mm wide anteriorly and 61mm high (Fig.5A, left). These dimensions for the second sacral are >56mm and 69mm, respectively (Fig.5A, right). Articular faces of the postzygapophyses of the first sacral are transversely ovate, but those of the second sacral are broadly triangular and wider than high. The angle of inclination of the prezygapophyses of the first sacral is 58° to the sagittal plane, that of the postzygapophyses of the second sacral is about the same. The neural arches and centra of the sacral vertebrae are firmly fused to the sacral ribs. Viewed from above, the diapophyses of the first sacral obscure the underlying parapophyses, and the tuberculum of the first rib obscures the underlying capitulum. The lengths of the two sacral centra are, respectively, 107mm, and ~72mm. The sacrum is 100mm wide across the prezygapophyses of the first sacral vertebra and 59mm wide across the postzygapophyses of the second sacral. The bases of the first and second sacral neural spines are 75mm and 61mm long, respectively.

Seen from the side, the distal (iliac) ends of the sacral ribs are as shown in figure 5A. The proximal end of the first sacral rib enters narrowly into the dorsolateral corner of the cotyl for the preceding lumbar vertebra. The second sacral rib resembles that of a large *A. mississippiensis* (TMM M-4864). The costal facets on the medial side of the accompanying ilium indicate that the ends of the sacral ribs did not meet distally. The transverse diameters across the attached sacral ribs are, respectively, 298mm and 229mm.

Thirteen caudal vertebrae, possibly constituting a continuous series, are present. In all, the neural arches and caudal ribs appear to be solidly fused to their respective centra. Transverse processes are present on the last preserved caudal. Only the first caudal retains an intact neural spine, which is 59mm long at its base and 85mm high above the roof of the neural canal. Neural spines of all preserved caudals were long-based, that of the putative fifth caudal being 62mm long. The last preserved caudal is 80mm long, excluding the condyle, and the centrum is 41mm high at the cranial end. The transverse diameter of the centrum at mid-length is 23mm. Chevron facets first appear on the second and third caudals.

A noteworthy feature of these vertebrae is the absence of a bony sagittal web extending along the cranial and caudal edges of the neural spines. The sulci that sometimes accompany these webs at the base of the neural spines in the alligators and caimans are also absent in MCC 72-V (cf. Fig.5B-5C).

The five cervical ribs preserved are unremarkable. Thoracic ribs are represented only by broken segments of the shafts. Sacral and caudal ribs are, described above.

Pectoral Arch. Both scapulae and coracoids are preserved, those of the right side being the more complete (Fig.6, right). The scapula and coracoid are robust, a quality noted in the relatively small holotype of *M. atopus* (Langston, 1965).The scapulae are missing the vertebral borders and parts of the edges of the scapular blades. When found, each scapula was connected *en matrice* with its respective coracoid, but the bones of the right side were displaced slightly at the scapulocoracoid interface. When separated in the laboratory these bones showed no evidence of bridging or fusion *sensu* (see Brochu, 1995). What remains of the right scapular blade indicates that it did not flair appreciably above (see Fig.51 of Brochu, 1999). The constricted scapular "waist" is 57mm wide anteroposteriorly in the right scapula. There is no tuber caudalis scapulae (Rossmann, 2000). The broad scapular spine (deltoid crest of Brochu, 1999 = crista cranialis scapulae of Rossmann, 2000) is thickened dorsally, but it thins rapidly toward the scapulocoracoid eminence. The edge of the spine is deflected caudally at the dorsal end, here forming a distinct tuberosity. The scapulocoracoid eminence is wide, extending 129mm from its most anterior point to the caudal edge of the glenoid fossa. The plan of the opposing articular surfaces of the scapula and coracoid is narrow longitudinally and its anteroposterior diameter is relatively long owing to the lengthening of the scapulocoracoid eminence.

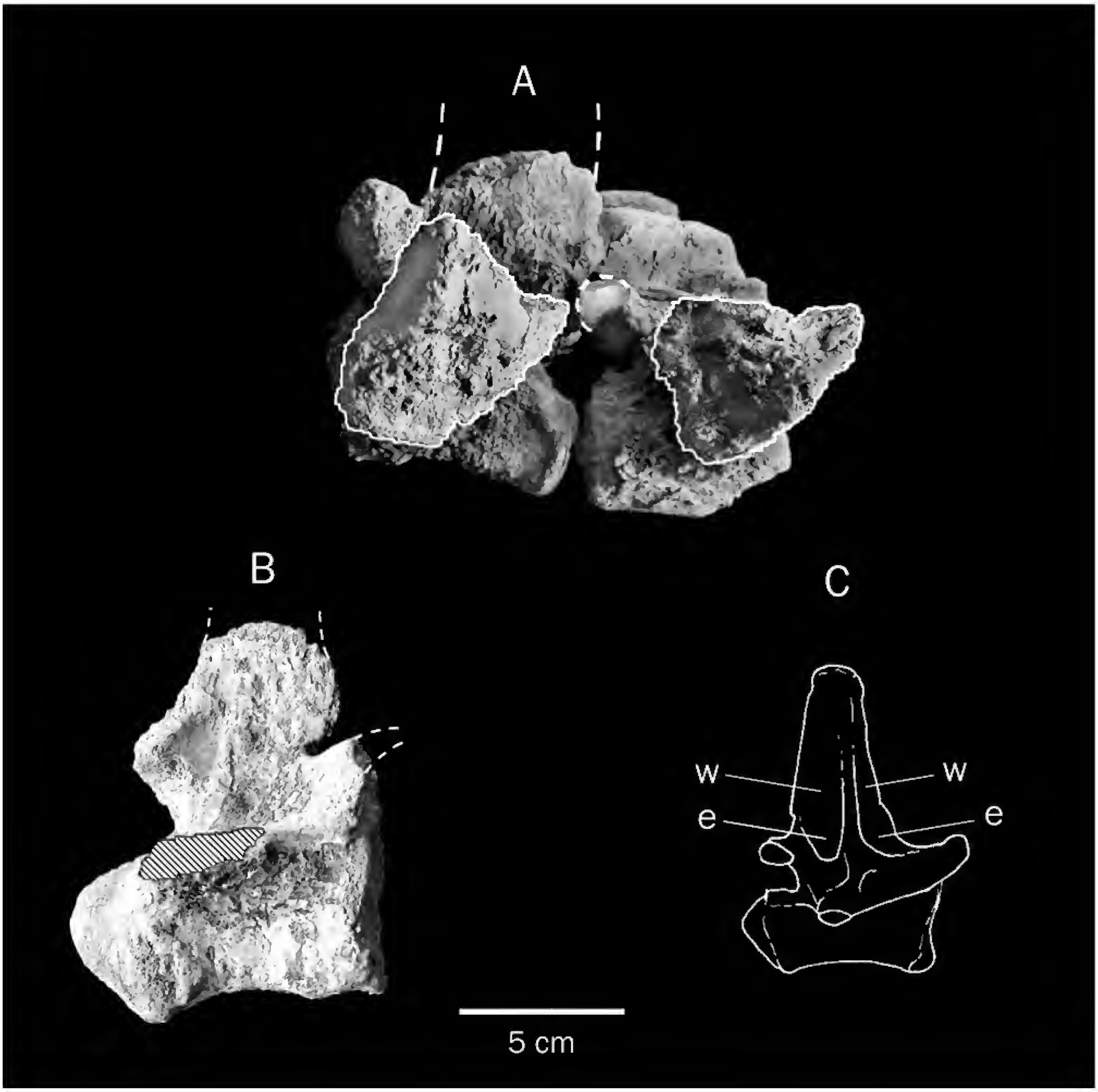

Fig.5- *Mourasuchus arendsi* (MCC 110 72-V), sacrum, left lateral view (A), the distal (iliac) articular surfaces of the sacral ribs are outlined. The narrow strip of bone seen above the broken base of the neural spine of the second sacral is the top of that vertebra's neural spine, which has been displaced and is largely hidden in this view. When restored to its natural position the spine is ~88mm high measured from the top of the neural canal, posteriorly. Right lateral view of the putative eighth caudal vertebra (B), note the absence of the spinous webs (w) and associated sulci (e) seen in neural spines of mid-caudal vertebrae of extant alligatorids, shown diagrammatically in *Alligator mississippiensis* (C).

The right coracoid (Fig.6, right) is 238mm long from the scapular edge to the sternal border. The scapular and sternal ends are, respectively, 139mm and 127mm long (anteroposteriorly). The least anteroposterior diameter of the coracoid shaft is 56mm. Viewed from below, the transition from the scapulocoracoid eminence to the cranial edge of the coracoid blade is abrupt as compared to that

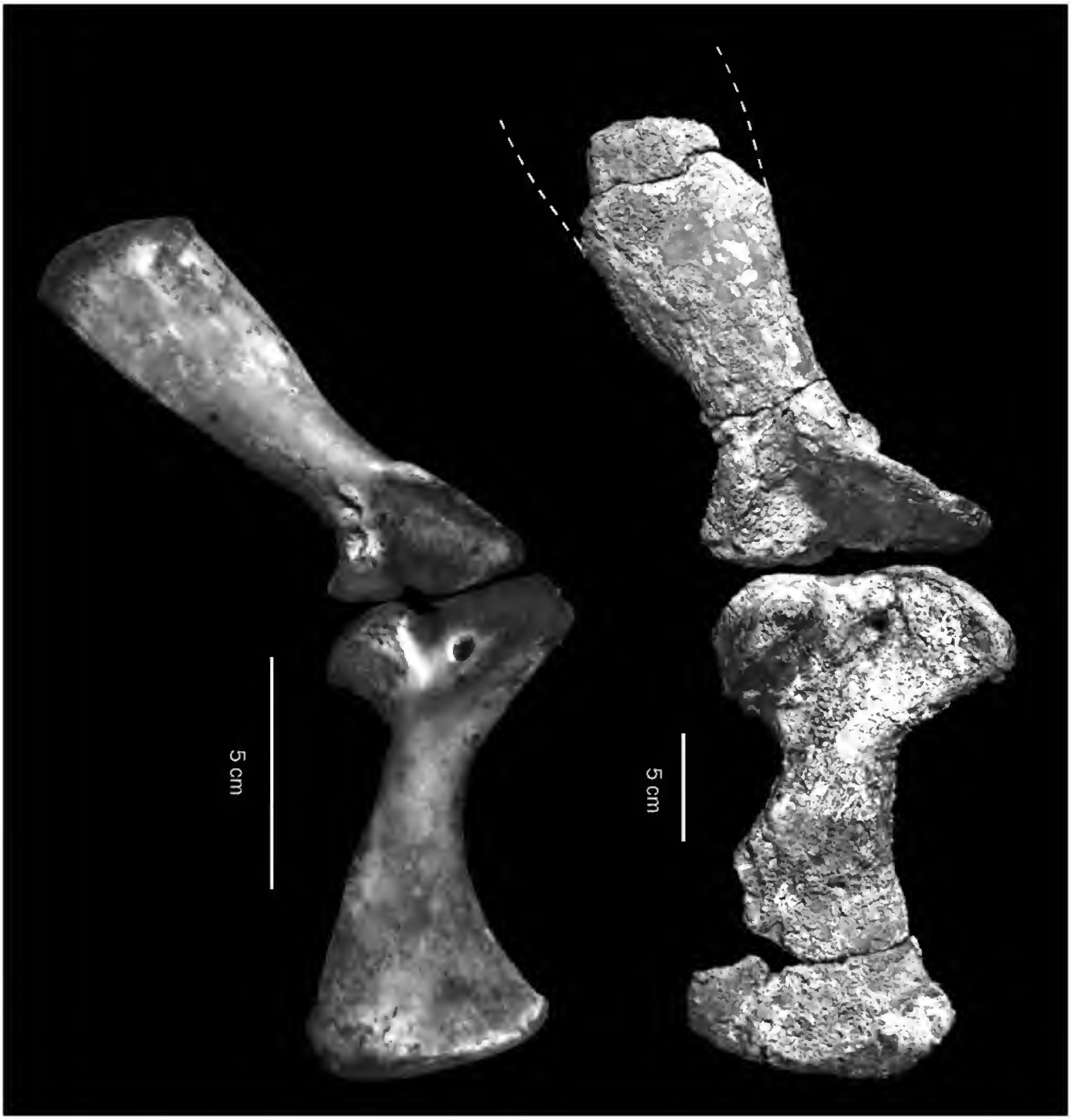

Fig.6- *Mourasuchus arendsi* (MCC 110 72-V), right scapula and coracoid. The bones are photographed in the same plane, *e.g.*, they are not in their natural articulated relationship (right image). Corresponding bones of *Melanosuchus niger* (UF 72914) enlarged to same scale (left image) to emphasize the relatively short and robust nature of the fossil.

of *Caiman crocodilus,* for example (see Fig.51c of Brochu, 1999). A round coracoid foramen with a diameter of 8mm occurs near the center of the proximal expansion of the coracoid. The coracoid forms a little more than one-half of the glenoid fossa. The saddle-shaped articular surface of the fossa is broadly and deeply concave in the transverse direction and strongly convex anteroposteriorly. It is 87mm high and 22mm deep.

Pelvic Arch. The right ilium is badly eroded, the outer surface of the bone having been almost completely destroyed by chemical weathering. An overlay of the outline of the specimen upon the perfectly preserved ilium of the holotype of *M. atopus,* UCMP 38012 (Fig.24 of Langston, 1965), shows reasonable concordance between the bones (Fig.7A). Like the ilium of *M. atopus*, there was a prominent anterior iliac process, represented by its broken base. A supraacetabular crest is essentially absent. The facets on the medial surface of the ilium for attachment of the sacral ribs are narrowly separated. The ilium is 113mm long at its narrowest diameter and 135mm high from the ischiadic peduncle to the top of the iliac blade.

An incomplete right ischium is 202mm long, but is otherwise uninformative.

Osteoderms. Fifteen osteoderms were found with MCC 110-72V. Although they convey an accurate idea of their gross form, most examples have a concretionary coating of gypsum, which obscures surface details. Gypsum has partly infiltrated and sometimes replaced the bony substance. The largest osteoderm is a broad subround plate 98mm long and 101mm wide, with a broadly rounded, 38mm high paramedian elevation caudally (Fig.8A, 8E). The elevation decreases gradually craniad. The deep face of this osteoderm is slightly arched transversely beneath the elevation, producing the "angulation" of Huxley (1860). One longitudinal edge is almost straight and is thus probably medial. Longitudinal edges are rounded dorsoventrally and are about 7mm thick. It is unclear whether either edge is serrated. The cranial edge is not noticeably beveled (faceted) for shingling by a preceding osteoderm. A slightly smaller and much thinner, weathered osteoderm has a basal plate which bears the base of a longitudinal crest lying somewhat to one side of the midline of the osteoderm.

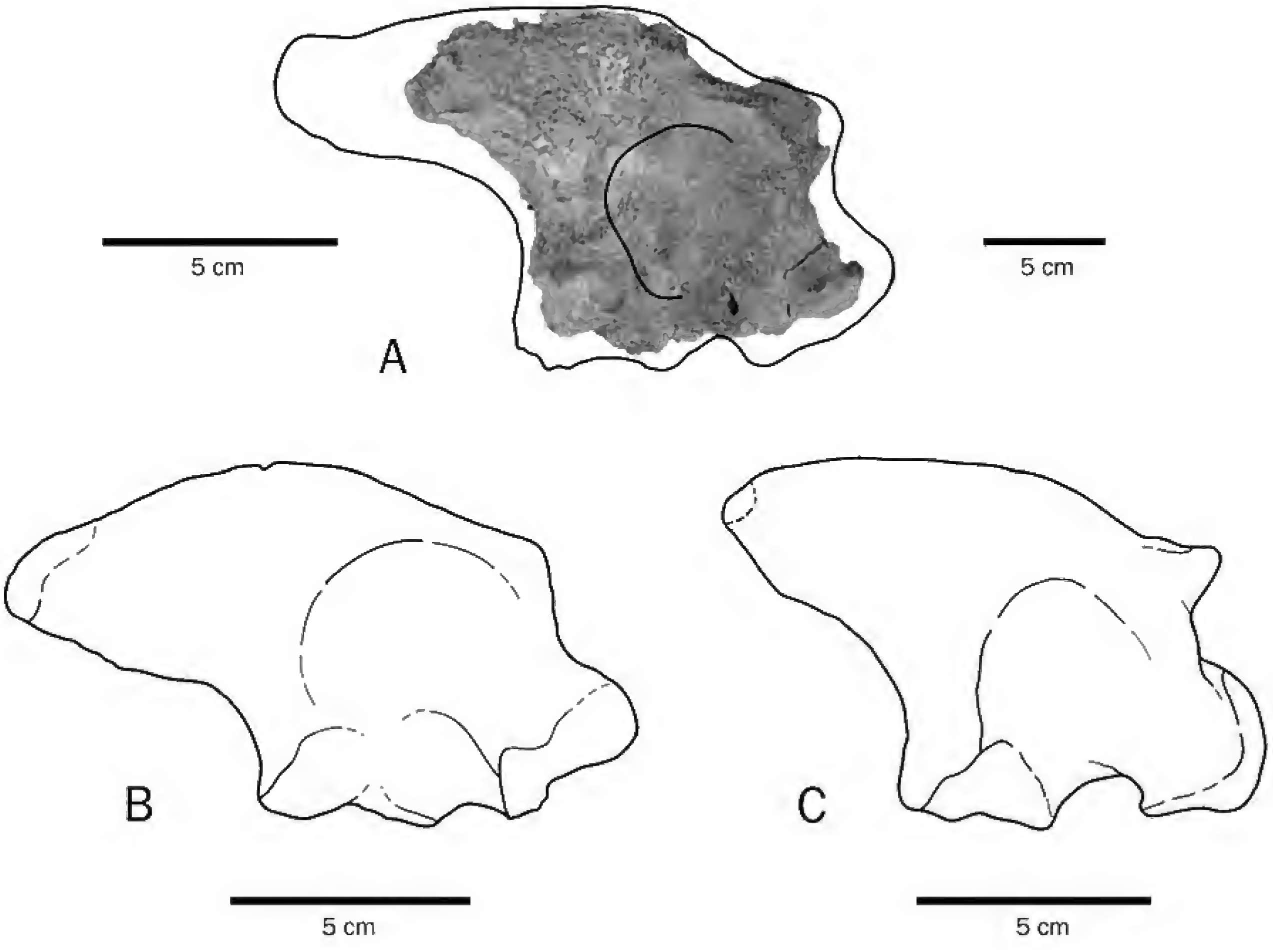

Fig.7- *Mourasuchus arendsi* (MCC 110 72-V), right ilium, lateral view, right scale, compared to ilia of *M. atopus* holotype (UCMP 38012) solid outline adjusted to best fit, left scale (A), *Alligator mississippiensis* (TMM M-8931) (B), *Melanosuchus niger* (UF 72914) (C).

One other relatively large osteoderm has an irregular cardiform basal plate which bears a massive crest (somewhat distorted by crushing). The deep side of this osteoderm is downwardly convex, having no angulation. The edges are without sutures. A fourth osteoderm, about one-third as large as the first, bears a relatively more pronounced, thick and blunt parasagittal crest on the caudal half of the plate (Fig.8B, 8F). When seen from either end, this osteoderm displays an asymmetric or "twisted" gabled appearance, thus resembling a slightly skewed peaked roof. The angulation is 130°. Edges appear to be non-sutural and lack evidence of serial shingling. The external surface of this osteoderm is marked by small shallow pits and grooves radiating from the crest.

Other osteoderms have an expanded, more or less rounded, non-sutural basal plate, and a remarkably hypertrophied longitudinal crest (Fig.8D, 8H). The deep sides of these plates are flat or slightly convex downward. Crests vary from broadly oval to laminar in planar cross section. The cranial edge of the crests is always longer than the caudal edge, giving the crest a swept-back appearance. One such osteoderm, which may be considerably altered by weathering (Fig.8C, 8G), has a relatively small basal plate bearing a wide and thin inclined crest which is 49mm long at the base, 56mm high and only 15mm thick at mid-height.

Two osteoderms are uniquely cornuted (Fig.9A-9D). The dorsal surfaces of the crests are strongly convex whereas the ventral side is flat, so the crest is bent slightly downward, distally. The crests are constricted circumferentially at their base, appearing somewhat tumid outward from the constriction and resembling a stubby horn rather than a carinated crest. The basal plate is roughly triangular in plan. In one such osteoderm the plate is expanded dorsally, forming a flange-like structure whose edges bear a few blunt serrations (Fig.9E).

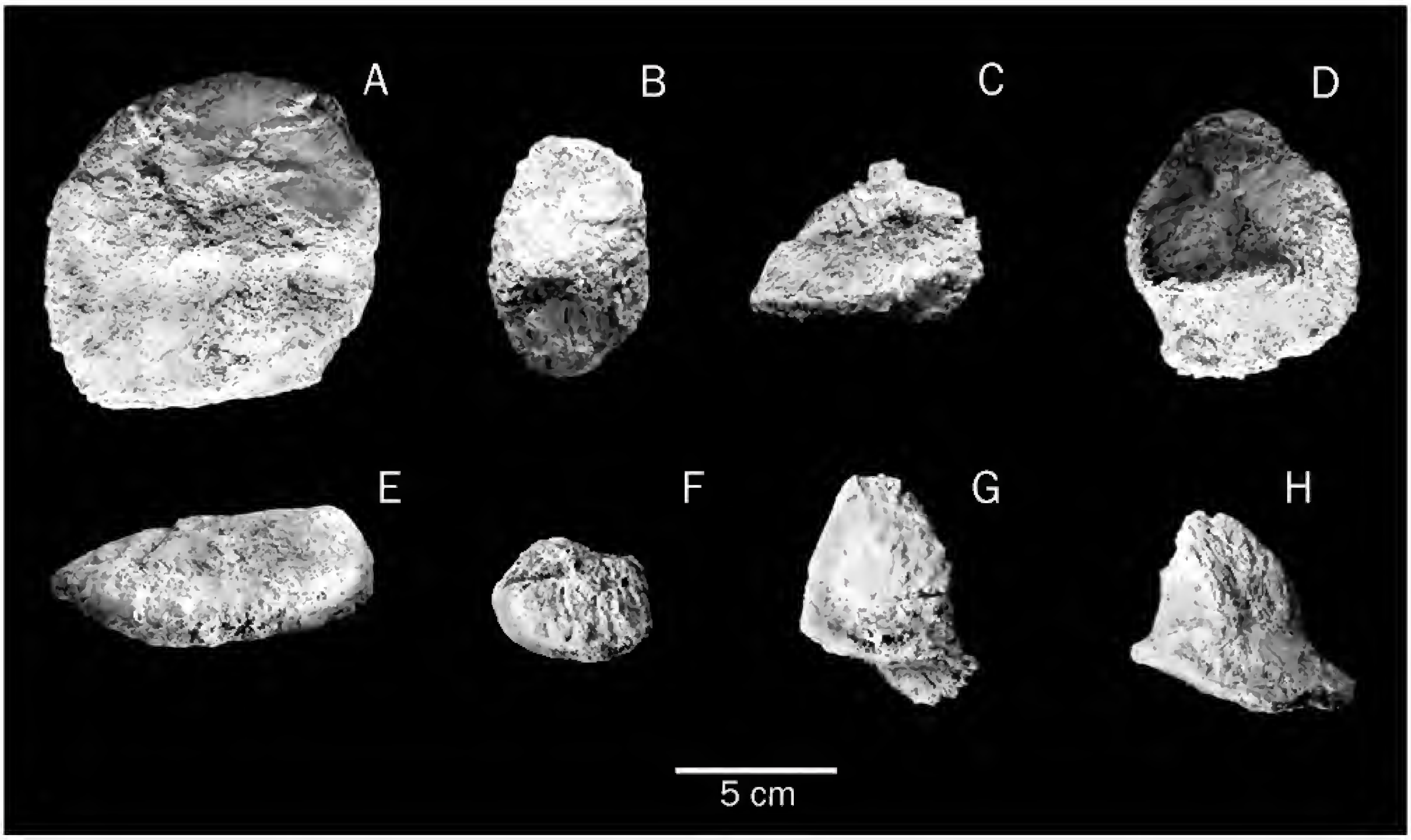

Fig.8- *Mourasuchus arendsi* (MCC 110 72-V), osteoscutes, apical view (A-D), and lateral view (E-H). Possible first median right plate of the cervical shield or rosette (A, E) -the straight edge may be medial, the apex of the broad low crest is to the right-, asymmetric "gabled" osteoderm, possibly from the occipital group or a lateral member of the cervical rosette, anterior is to the right (B, F), osteoderm of unknown position with small basal plate and large thin (tabular) crest (C,G), possible flank osteoderm with large caudally curved crest, anterior edge is to the right (D, H).

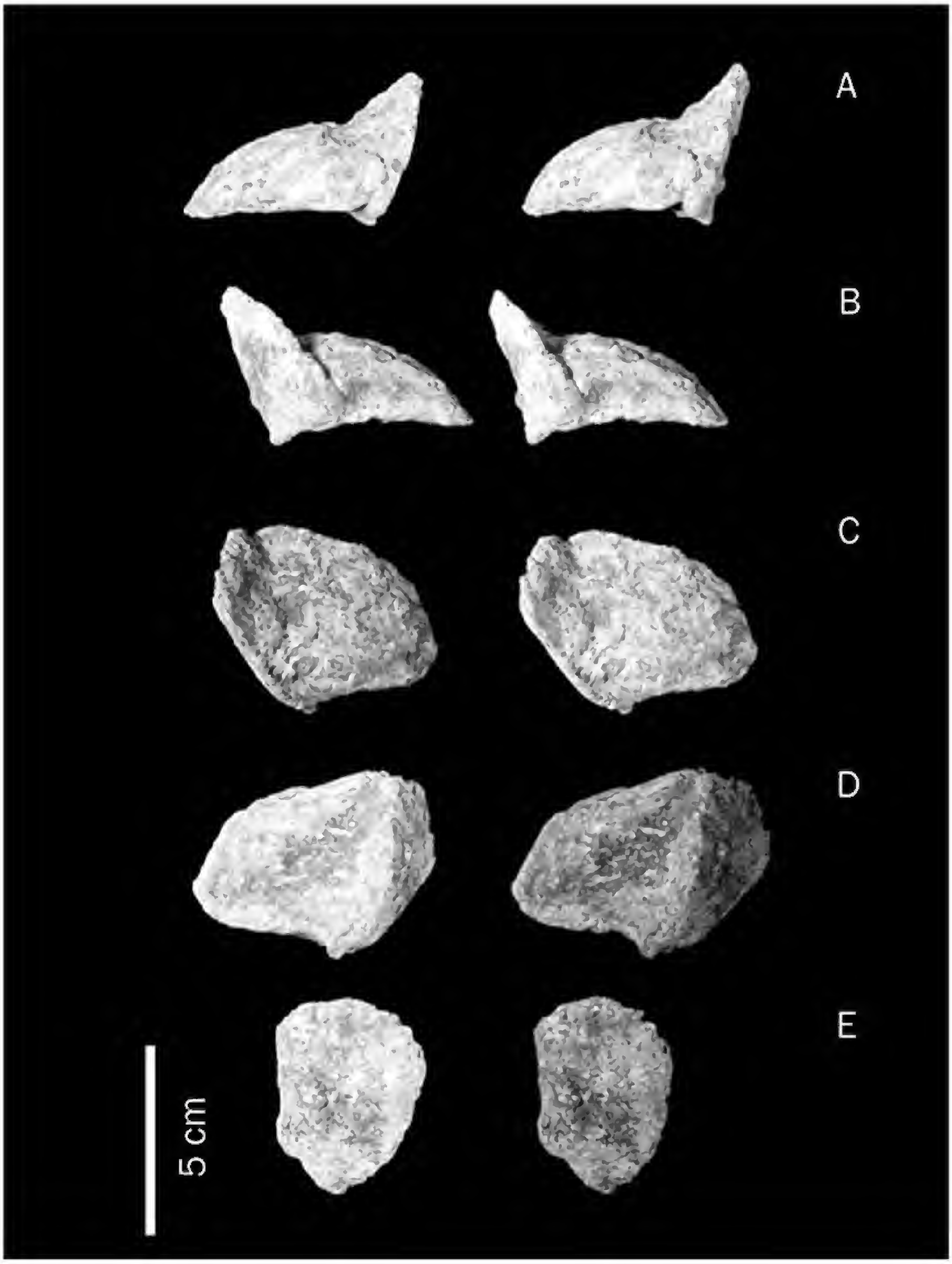

Fig.9- *Mourasuchus arendsi* (MCC 110 72-V), stereo images of an unique horn-like osteoderm, possibly from a right lateral longitudinal series, anterior view (A), posterior view (B), apical view (C), anterior is at top, ventral view (D), anterior is at top, deep surface(E), anterior is at top. Note blunt marginal processes along anterolateral edge.

The serrations, instead of forming a sutura serrata or a sutura dentata are apparently outgrowths that were imbedded in the dermis. The corresponding edges of the other horn-like osteoderm are abraded and show little evidence of serrations. The dorsal surface of the horn-like process appears to have a few short corrugations extending parallel with the long axis of the crest and exiting along the crest's lateral edge.

DISCUSSION

Systematic position. MCC 110-72V accords with 16 of 29 character states scored by Brochu (1999) as present in *Mourasuchus* (five states having to do with ribs and osteoderms are not observable in *Mourasuchus* specimens). Five states queried by Brochu owing to insufficient or absent data are clarified by 110-72V, and two scores are revised (Tab.1). Brochu (1999) scores number 34, the anterior iliac process (=Tuber cranialis iliacum of Rossmann, 2000), as virtually absent (1) in his matrix. I would score it as prominent, based upon the well preserved ilium of *M. atopus* UCMP 38012. The remnant of the process preserved in MCC 110-72V is relatively even larger than the corresponding feature in UCMP 38012. None of the findings reported here alter the placement of *Mourasuchus* within the Caimaninae proposed in Brochu's (2004) cladistic analysis of the alligators, but further study of *Purussaurus* and especially the enigmatic *Orthogenysuchus* may remove these as sister taxa of *Mourasuchus*.

Brochu (1999) scores the anterior iliac process (=Tuber cranialis iliacum of Rossmann, 2000) as virtually absent (1). I would, however score it as present, based upon the ilium of *M. atopus* UCMP 38012. The remnant of the process preserved in MCC 110-72V is relatively even larger than the process in UCMP 38012, and to my eye easily qualifies as prominent, though less hypertrophied than in *Gavialis* (Brochu, pers.com., 2007). Interestingly, notwithstanding extensive osteological evidence supporting the alligatoroid affinity of *Mourasuchus*, the ilium of *M. atopus* (UCMP 38012) and of MCC 110-72V (Fig.7A) resemble the bone in such non-alligatoroid taxa as *Gavialis gangeticus* and some species of *Crocodylus* (Fig.29A, 29B of Brochu, 1999). A robust anterior process, for example, which generally lies in apposition to, or extends a short distance beyond, the anterior dorsolateral corner of the first sacral rib described by Brochu (1999) as "almost lacking" in alligatoroids, excepting *Paleosuchus trigonatus* (Fig.29D of Brochu, 1999) and *Melanosuchus niger* (Fig.7C) is strongly developed in both *Mourasuchus* species (Fig.7A). The iliac blade in the holotype of *M. atopus* and probably also in MCC 110-72V is narrower dorsoventrally than in *A. mississippiensis*, *Melanosuchus* (Fig.7A-7C) or *Diplocynodon hantoniensis* (Fig.29E of Brochu, 1999),

TABLE 1. Modifications to Brochu's 1999 matrix of *Mourasuchus* required by the present study.

Number	Description	Brochu	110 72-v
6	Axial hypapophysis toward center (0) or toward anterior end (1) of centrum	?	1
13	Anterior sacral [rib] capitulum projects far anteriorly of tuberculum, broadly visible from above (0), or capitulum and tuberculum nearly coextensive anteriorly, capitulum largely obscured from above (1)	?	1
22	Scapular blade flares dorsally at maturity (0) or edges of blade sub-parallel at maturity (1)	?	1
24	Scapulocoracoid chondrosis closes very late in ontogeny (0) or relatively early in ontogeny	?	0
28	Dorsal margin of iliac blade rounded with smooth border (0) or rounded with modest dorsal indentation (1) or rounded with strong dorsal indentation "wasp-waisted" (2) or narrow with strong dorsal indentation (3) or rounded with smooth border, posterior tip of blade very narrow (4)	3	2
34	Anterior iliac process prominent (0) or virtually absent (1)	1	0
36	Dorsal midline osteoderms rectangular (0) or square (1)	1	?

The numbers in the left hand column correspond to the serial numbering in Brochu's Appendix 2: "List and Matrix of Characters Used in Phylogenetic Analysis". Language under DESCRIPTION has been slightly altered for the sake of brevity. The two right hand columns are the original and revised scoring, respectively, for *Mourasuchus* resulting from the study of MCC 110 – 72V and two corrections (numbers 28 and 36) based on UCMP 38012 (*M. atopus*).

and is more comparable with the ilium of *Crocodylus acutus*. It is, however broader than the blade in *P. trigonatus* (Fig.29D of Brochu, 1999), which has the narrowest blade among alligatoroids. The posterior end of the blade is deflected downward in the holotype of *M. atopus*, which resembles the condition in *C. acutus* and *P. trigonatus*. This feature is not preserved in MC 110-72V.

Comparisons. The Nettosuchidae comprises *Mourasuchus atopus* (Langston, 1965), *M. arendsi* Bocquentin Villanueva, 1984, *M. nativus* (Gasparini, 1985), and *M. amazonensis* Price, 1964. From descriptions in the literature it seems clear that the first three taxa are more similar to each other than they are to *M. amazonensis*. Bocquentin Villanueva (1984) and Bocquentin & Souza Filho (1990) have satisfactorily differentiated *M. arendsi* from the other nettosuchids.

The skull of the holotype of *M. arendsi* (CIAAP 1297) and MCC 110-72-V are approximately the same size, but the rostrum and the laterally expanded jugals appear relatively wider in photographs of MCC 110-72V than portrayed in drawings of CIAAP 1297 (Fig.1 of Bocquentin Villanueva, 1984), which seems closer to the skull of *M. atopus* (UCMP 38012) – see figure 28 in Langston (1965). Such differences may, however, result from artificial dorsoventral flattening and consequent lateral displacement of cranial bones in MCC 110-72V. The sides of the rostrum are roughly parallel, as in *M. arendsi* and *M. atopus*.

As reconstructed, each premaxilla of MCC 110-72V is pierced dorsally by three round perforations (for the tips of dentary teeth), one fewer than in *M. arendsi* CIAAP 1297, and one more than in *M. atopus* UCMP 38012. Differences in number and arrangement of such foramina may represent individual variation as seen, for example, in *Caiman crocodilus* (cf. fig.25 in Kälin, 1933), or they may be ontogenetically related.

The intercentrum of the atlas is relatively shorter than that of *Alligator mississippiensis*, *Melanosuchus* and *Caiman crocodilus*, consistent with other evidence of a relatively short neck in *Mourasuchus*.

The cervical vertebrae of MCC 110-72V are larger than those of an articulated series of cervicals found adjacent to the holotype skull of *M. arendsi* (CIAAP 1297). The least transverse diameter of the atlantal intercentrum in that specimen is 35mm compared to 53mm in MCC 110-72V. Bocquentin Villanueva (1984) records the width of the sixth cervical centrum in CIAAP 1297 as 47mm and the length of the centrum as 57mm, including the condyle. Based on the drawing and scale given by Bocquentin Villanueva (1984, Fig.2B), exclusion of the condyle would reduce this length to about 38mm. Corresponding measurements for the sixth cervical centrum of MCC 110-72V are: width, 58mm behind the root of the diapophysis (62mm at the cranial end of the centrum) and a length of 51mm, excluding the condyle, or about 1.3 times the size of CIAAP 1297.

The discrepancy in size of the cervical vertebrae between two animals with similar head lengths is difficult to explain and recalls Patterson's field notation that two specimens were found weathering from opposite sides of the same hill at his Locality 110-72V. It raises the possibility that either MCC 110-72V or CIAAP 1297 is composite. This notwithstanding, such limited morphological comparisons as can be made between MCC 110-72V and CIAAP 1297, *e.g.*, the proportionally short cervical centra, the low neural spines and the absence of cranially hooked distal ends on reduced hypapophyses supports their assignment to the same taxon. (The geographic proximity and stratigraphic context -"capa de tortugas"- upper Miocene, upper Urumaco Formation – in northern Falcón State, Venezuela, accords with this conclusion).

The scapula and coracoid are more robust than in extant Alligatoridae and Crocodylidae (Fig.6). For example, in samples of *A. mississippiensis* (n=9) and *Crocodylus* spp. (n=7) the average ratio of least anteroposterior diameter of the coracoid shaft to the length of the coracoid is .17 and .15, respectively, whereas the corresponding ratio in MCC 110-72V is .24. Corresponding ratios in *Gavialis* (n=3), *Melanosuchus* (n=1), and *Tomistoma* (n=1) are, respectively, .13, .18, and .15.

Ontogenetic stage. The large size of MCC 110 72-V raises a question about the ontogenetic stage of the individual. Attempts to "age" the specimen using growth marks in an osteoderm (Buffrénil, 1980; Erickson & Brochu, 1999) proved futile owing to diagenetic disturbance of the bone tissue. A total of 15 sequential annuli were counted in one thin section and additional fragmentary growth marks are scattered about randomly, but correlations between them are impossible.

Except, possibly, on the axis vertebra, neurocentral sutures are not discernable. Although some of the neural arches were found separated from their centra, the separation occurs at fractures through the pedicels, suggesting that the neurocentral sutures were closed or fused (Brochu, 1996).

The articulation between the damaged odontoid bone and the centrum of the axis vertebra is either closed or fused to the axial centrum, forming a unitary epistropheus. These facts suggest that MCC 110 72-V was ontogenetically mature at time of death.

Size and proportions. *Mourasuchus* was a large crocodilian. Known skulls of *M. arendsi* are approximately 1m long, depending upon the definition of "total skull length" used by various authors. Among several proposed methods for estimating total body length of crocodilians based upon skull length (*e.g.*, Meyer, 1984; Cott, 1961; Woodward *et al.*, 1995), a graphical solution by Wermuth (1964, Fig.5) is useful in the absence of conclusive information about the shape of the post-cranial body of *Mourasuchus*. Wermuth arranged all extant crocodilian species into six groups based upon the length of the head relative to total body length. Although the shape of the rostrum of *M. arendsi* is unique, the skull as a whole is proportionally comparable in length and trans-quadrate width to the skull of *Gavialis gangeticus* with a similar trans-quadrate width. It should therefore fall into Wermuth's Group VI, comprising *G. gangeticus, Tomistoma schlegelii,* and *Crocodylus johnsoni.* From Wermuth's graph it is seen that MCC 110-72V should have been in the neighborhood of 6.6m long at the time of death. This estimate is slightly below values obtained from commonly used ratios of head length: total body length as, *e.g.*, 1:7.48 for *C. porosus* (Wermuth, 1964) and 1:7.5 for *C. niloticus* (Bellairs, 1970). It is worth noting here that Bellairs (1970) obtained a head: length ratio of about 1:5 for *G. gangeticus*, owing to its relatively long rostrum.

Estimation of body mass for MCC 110-72V is even more conjectural as it depends upon the determination of body length. Recent work (Farlow *et al.*, 2005) shows that the relationship between body length and mass based on *Alligator mississippiensis* predicts sizes of extant crocodilian species reasonably well, and may be used to estimate the mass of related species in the fossil record. An extrapolation from a Farlow *et al.* (2005) graph, figure 7A, yields a mass value of 1,400kg for the 6.6m long MCC-110V. Farlow's regression (pers.comm., June 13, 2005), based on data from 58 captive alligators yielded a mass of 1,634kg ($R=0.995$, $P<0.001$). Webb & Manolis (1989) quote an "average" body weight of 6m long *Crocodylus porosus* from tidal rivers as 900kg. Crocodilians in captivity may bulk larger than wild animals of similar lengths, so mass values between 1,400kg and 1,634kg for MCC 110-72V seem reasonable.

Head and neck motility in *Mourasuchus*. The character of the cervical vertebrae described above bespeak of a relatively weak and less motile neck than that possessed by extant crocodilians. As noted by Bocquentin Villanueva (1984) the cervical vertebrae are, indeed, relatively shorter than those of extant crocodilians. Measurements of MCC 110-72V show that the average ratio of least width of centrum to length of centrum, excluding the condyle, for cervicals 3-6, is 0.95. The largest value for any cervical in this specimen is 0.98. Corresponding ratios for available extant taxa are: *Alligator mississippiensis*, 1.29 (n=5), *Melanosuchus niger,* 1.49 (n=1), *Tomistoma schlegelii,* 1.31 (n=2), *Crocodylus acutus*, 1.28(n=5), and *C. cataphractus*, 1.24 (n=1). The average ratio among these taxa is 1.36, no value for an individual being less than 1.0. The more nearly vertical trochlear surfaces on the odontoid bone indicate a shorter vertical excursion of the head than is achieved in extant crocodilians. The small non-hooked hypapophyses suggest less development of the M. longus colli, which is involved with flexing and lateral movement of the neck (Richardson *et al.*, 2002). The low cervical spines suggest that the epaxial antagonists were also less powerful than in extant taxa. Consistent with the foregoing, Bocquentin Villanueva (1984) states that the occipital condyle is small in *M. arendsi* (CIAAP 1297).

Thus, *Mourasuchus* was likely less capable of the violent head movements during capture and dismemberment of prey than are observed in large contemporary crocodilians.

Prey and Feeding. The present study offers added support to previous speculations (*e.g.*, Langston, 1965) on possible feeding strategies of *Mourasuchus*. The animal was likely a "lie in wait" predator inhabiting quiet waters and subsisting on "sluggish" fish (*e.g.*, *Lepidosiren,* some catfish), whose remains have been encountered in the vicinity of *Mourasuchus* sites in Colombia, especially in the Fish Bed in the lower part of the Villavieja Formation of the Honda Group (Langston, 1965; Lundberg, 1997), and freshwater crabs, in the Urumaca area (Patterson, 1972, field notes; Langston, 2005, personal observation).

Osteoderms. The exact positions of the fossil osteoderms in the living *Mourasuchus* are, of course, unknown. The two largest osteoderms found with MCC 110-72V may, however, belong to the cervical shield or rosette (Richardson *et al.*, 2002), which contains the largest osteoderms in extant crocodilians. The larger of the two plates is substantially more massive than any others recovered with MCC 110-72V. Its proportions, its apparently non-embrocating caudal edge, and its single straight longitudinal edge suggest that it may be the first median right osteoderm of the rosette. A slightly smaller, flatter plate with a more laterally placed crest may be the left medial osteoderm of the second transverse series of the rosette. A much smaller, angulated and "twisted" plate (Fig.8B, 8F) may be from the edge of the rosette as it is thick, has only a low, broadly rounded crest, lacks sutural edges and shows no evidence of shingling. But, these features might also place it among the occipital osteoderms which lie in the soft skin between the transverse occipital crest of the skull and the cervical rosette.

The osteoderms with more elevated crests arising from more or less discoid bases without angulations, sutural or imbricated edges, may represent accessory plates, but their elevated crests render them considerably more spinose than osteoderms in extant crocodilians. The crests are more in keeping with the articulated transverse series of osteoderms in the dorsal shield of extant crocodilians. If these are, in fact, from the dorsal shield, their lack of sutured edges and shingling indicate that they did not form a cohesive armor like that of extant caimans, s.l. (*vide* HUXLEY, 1860).

The remarkable horn-like osteoderms of *Mourasuchus arendsi* described above may represent a lateral fringe extending longitudinally along the flanks of the animal – an aëtosaurian model springs to mind. This analogy cannot be drawn too narrowly, however, as the *Mourasuchus* osteoderms were non-embrocating and without sutures.

Of known crocodilians, only the Paleocene eusuchian *Acanthosuchus langstoni* O'Neill, Lucas & Kues, 1981, and the tiny, poorly understood Upper Cretaceous *Pinacosuchus mantiensis* Gilmore, 1942 possessed osteoderms with spike- or horn-like osteoderms. The only known specimen of *A. langstoni*, includes among others, more than 120 osteoderms with spike-like crests, evocative of aëtosaurian architecture. The horn-like osteoderms of *Mourasuchus* resemble somewhat those of *Acanthosuchus*, but they are more rotund than in the smaller taxon. They agree in the absence of embrocating facets, however. *Acanthosuchus* osteoderms do not have the annular constriction seen at the base of the crests in *Mourasuchus*. The basal plates of the spiked osteoderms in *Acanthosuchus* are square to round and display a radiating system of buttresses around the base of the spikes not seen in *Mourasuchus*. The *Acanthosuchus* plates bear limited sutures on one parasagittal edge, suggesting coupled pairs, arranged into transverse rows. O'NEILL *et al.* (1981) supposed, however, that the spiked osteoderms formed a single, "...row of paired scutes along each side of the dorsal surface of the body and tail", in *Acanthosuchus*.

The spike-like crests on *Pinacosuchus* osteoderms are often placed asymmetrically and sometimes extend beyond the edges of the basal plates, unlike the crests of *Mourasuchus*, and spikes are described as having sculptured surfaces (GILMORE, 1942). Associated vertebral centra are biconcave, so the animal is not likely a eusuchian.

In his detailed account of crocodilian armor, especially that of *Melanosuchus (=Jacare) niger*, HUXLEY (1860) observes that the osteodermal armor of the Caimaninae (*Caiman, Melanosuchus* and *Paleosuchus*) is more extensive than that of other extant crocodilians. All laterally contiguous osteoderms of both the dorsal and ventral armor (the latter extensively present in extant crocodilians only in Caimaninae) are joined laterally by suture, the tail being completely encircled by articulated osteoderms. Excepting some osteoderms in the skin of the neck, the dorsal and ventral osteoderms are slightly imbricated in Caimaninae, posterior edges moveably overlapping narrow smooth transverse anterior facets on each succeeding osteoderm. Even the limbs [of *M. niger*] are, "...covered with articulating scutes..." (HUXLEY, 1860).

Although *Mourasuchus* is related to alligators and caimans, its armor seems, from the limited information available, to deviate substantially from the norm for those taxa. There is no evidence that *Mourasuchus* possessed ventral or appendicular osteoderms. Evidence that the osteoderms were joined by parasagittal suture, or that they overlapped is also lacking. Reduced armor as seen in *Crocodylus porosus* (Fig.7 in WERMUTH, 1953) has long been correlated with that taxon's aquatic habits where the weight of armor might be disadvantageous, and increased trunk flexibility would be an advantage in swimming. By contrast, the supporting function of massive articulated osteoderms and the expanded tops of the neural spines to which the sagittal osteoderms are attached by ligaments (SALISBURY & FREY, 2001), as seen in some caimans and *A. sinensis* (*vide* HUXLEY, 1860; ROVERETO, 1912; MÜLLER, 1924), but absent in *Mourasuchus,* would seem unnecessary in a crocodilian that only occasionally travels on land. Oddly, gain in freedom of movement in the trunk by reducing the dorsal armor seems counterintuitive to the idea of a longitudinal series of horn-like lateral osteoderms as proposed above. In life, however, lateral tensing of the trunk would have been governed by the space intervening between serially aligned osteoderms. The small size of the basal plates of the horn-like osteoderms of *Mourasuchus* suggests there may have been considerable separation between them in the skin, and lateral bending of the trunk would have been unrestricted.

Taphonomy. Early work by vertebrate paleontologists and later by GONZALEZ DE JUANA *et al.* (1980) implied that vertebrate fossils of the upper Urumaco Formation were largely concentrated in the "capa de tortugas", but it is now known that fossils are more widely distributed both stratigraphically and geographically in a variety of lithologies (LINARES, 2004). It is still unclear, however, where in the section most of the Urumaco crocodilians have been found. More taphonomic information including the relationships between *Mourasuchus* and other organic remains, including trace fossils, is necessary for a better understanding of the behavior of *Mourasuchus*. For example, what were the makers (lungfish, catfish, crabs, etc.?) of the frequent vertical burrows reported by DÍAZ DE GAMERO & LINARES (1989) in the upper member of the Urumaco Formation. The environmental conditions that produced the "capa de tortugas" and the diversity of crocodilians within the region, and an analysis of individual burials in the upper Urumaco are other questions that should be addressed.

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DISCUSSING A MYTH: BIOMECHANICAL COMPARISONS BETWEEN *DINODONTOSAURUS* (SYNAPSIDA, DICYNODONTIA) AND EXTINCT GROUND SLOTHS [1]

(With 5 figures)

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ABSTRACT: Dicynodonts possess a mosaic of features that includes the development of a differentiated posture in some genera: while the forelimbs remain abducted, in a sprawling posture, the hind limbs became fully improved. In the lack of modern analogues, comparisons with extinct ground sloths lead some authors to proposals of a bipedal posture, only facultative, which could enable the animal to rise on the hind limbs to reach higher vegetation. To test this hypothesis, some biomechanical aspects required to a bipedal posture were analyzed, regarding to specimens of the genus *Dinodontosaurus*, a medium-sized dicynodont from the Middle Triassic of Rio Grande do Sul State, Brazil. From observations of general morphology, location of the center of mass, estimation of moments of resistance of the vertebral column, and calculation of indicators of athletic abilities, we conclude that, at least in what concerns *Dinodontosaurus*, there are no evidences to support the morphofunctional analogies with the ground sloths.

Key words: Synapsida. Dicynodontia. *Dinodontosaurus*. Ground sloths.

RESUMO: Discutindo um mito: comparações biomecânicas entre Dinodontosaurus (Synapsida, Dicynodontia) e preguiças terrícolas extintas.

Dicinodontes possuem um mosaico de características que incluem o desenvolvimento de uma postura diferenciada em alguns gêneros: enquanto os membros anteriores permanecem abduzidos, em uma postura esparramada, os posteriores se tornam totalmente eretos. Na falta de análogos modernos, comparações com preguiças terrícolas extintas levaram alguns autores a propor uma postura bípede, ao menos facultativa, que permitiria ao animal erguer-se nas patas traseiras e alcançar vegetação mais elevada. Para testar essa hipótese, foram abordados vários aspectos biomecânicos envolvidos na postura bípede, aplicados em espécimes do gênero *Dinodontosaurus*, um dicinodonte de porte médio do Mesotriássico do estado do Rio Grande do Sul, Brasil. Através de observações morfológicas gerais, localização do centro de massa, estimativa de momentos de resistência da coluna vertebral e cálculo de índices de capacidade atlética para os membros, conclui-se que, ao menos no que concerne a *Dinodontosaurus*, não há evidências que apóiem as analogias morfo-funcionais com as preguiças terrícolas.

Palavras-chave: Synapsida. Dicynodontia. *Dinodontosaurus*. Preguiças terrícolas.

INTRODUCTION

The Dicynodontia comprises an extinct lineage of synapsids, originated in Late Permian and probably disappeared at the end of the Triassic, that developed into dominant primary consumers worldwide at least in two separate moments. Among a mosaic of peculiar features presented by them, we can enumerate: extreme dental reduction, presenting in most taxa only a pair of superior caniniform tusks, while the pre-maxilla and the anterior part of the dentary normally adopt the shape of a beak, being probably covered by a horny process (several forms during the Triassic lost the dentition completely, presenting just

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caniniform processes over the maxilla); the jaw articulation, which permits propalinal motion, is recorded even in basal forms through tooth striation (Rybczynski & Reisz, 2001), indicating the possibility of some oral food processing; broad anterior and posterior paws, of equal dimensions; fore and hind limbs plesiomorphically adducted and disposed laterally, but presenting considerable variation in orientation among later dicynodont taxa (Ray & Chinsamy, 2003), in which the anterior limb can dispose closer to a parasagittal plane, but remaining adducted, while the hind limbs became fully abducted; and a barrel-shaped trunk, in some forms becoming very robust. Several taxa can also present some extend of cranial ornamentation, with thick and sculptured rostral regions, probably covered at some extend by horny sheets, indicated by the presence of nutrient foramina (Morato *et al.*, 2005).

The lack of modern analogues to some of these characters presents difficulties to interpretations in functional basis. Nonetheless, to comprehend the success of Dicynodontia during their time span, it is necessary to investigate their adaptations to withstand in their habitat. This success is generally credited to their food-processing capabilities (Crompton & Hotton III, 1967; Cox, 1998), associated to their ecological flexibility (Hotton III, 1986; Rayner, 1992); in that topic, an increasing mobility in the hind limb could also deserve some attention (King, 1981; Fröbisch, 2003).

Hotton III (1986) describes the general dicynodont body form as "roughly comparable to that of such robust mammals as beavers (*Castor*) and New World badgers (*Taxidea*)", but with robust limbs. Dicynodonts lack the same specific adaptations as badgers or beavers for their burrowing lifestyles, although fossorial capabilities in several degrees were proposed, particularly in small Permian forms (*e.g.*, Cluver, 1978; Ray & Chinsamy, 2003).

Cox's (1965) classification of triassic dicynodonts, particularly in respect to the families Kannemeyeriidae and Stahleckeriidae, takes in account some comparative proposals. He noticed among other characters that some forms present narrow beaks, while others have broad and robust beaks; similar differentiation was observed in the muzzle shape of rhinoceroses, distinguishing browsers, with pointed and prehensile lips and straight oriented occiputs in relation to the palate, of the grazers, with broad lips and tapering occiputs. However, as Cox himself observed, comparisons of feeding habits between them are not straight forward, as the dicynodonts with narrow-shaped beaks possessed tapering occiputs, while in the broad-shaped forms, the occiput is vertical. Other attempt of comparisons in size and body form were made by Cruickshank (1978), with modern Suidae, in which sloping occiputs were found in animals feeding close to the ground, as selective grazers, while upright occiputs are found in browsers and omnivorous forms. Although this seems to fit better with the dicynodont skull morphology, Cruickshank (1978) is careful to extend these comparisons, as the suids in discussion are relatively more active animals, and their feeding behaviors transferred for the dicynodonts would ignore the available vegetation above the head heights of these animals.

Finally, the analysis of the morphology of extinct ground sloths (Xenarthra: Tardigrada) lead Cruickshank (1978) to propose several inferences about feeding habits in dicynodonts, including the possibility of a bipedal posture, only facultative, for the animal to rise over the hind limbs and reach higher vegetation. The comparisons described by Cruickshank (1978) refer more to the general external morphology, with emphasis in post-cranium, specially to the broad pelvic girdle, with high number of sacral vertebrae (some dicynodonts present up to 6), and the shape of the femur, which is transversally expanded, as well as other appendicular bones. Cruickshank thus could find a reason for the apparent dichotomy that developed in the limbs, with the hind ones becoming fully erect, with higher mobility in relation to the plesiomorphic pattern, and apparently under-used in respect to the restrictions imposed by the forelimbs, in a primitive sprawling posture (Vega-Dias & Schultz, 2004).

These last comparisons, however, never were tested in a biomechanical basis. Here, a first attempt of biomechanical reconstruction is made, investigating several aspects involved in the bipedal or quadrupedal posture in a dicynodont species.

MATERIAL AND METHODS

Among dicynodont fossils collected in the Rio Grande do Sul State, the most complete and abundant remains belong to the genus *Dinodontosaurus* Romer, 1943 (Fig.1), a medium sized animal with up to 1.8m in length, from the Middle Triassic Santa Maria Formation. The paleovertebrate sector of the Universidade Federal do Rio Grande do Sul (UFRGS/PV) counts with fairly complete skeletons of ten juvenile individuals

(UFRGS/PV0111T-UFRGS/PV0120T) and one adult (UFRGS/PV0121T) attributed to this taxon, in which it was made the bulk of the following measurements and analyses. Additional material, for further comparisons, used mainly in the skeletal reconstructions, included well preserved skulls and partial skeletons, found in the collections of the Museu de Ciências e Tecnologia of the Pontifícia Universidade Católica do Rio Grande do Sul, in Porto Alegre, and of the Museu Municipal Guido Borgomanero, in Mata (RS).

A fundamental variable for a series of biomechanical analyses is the mass of the animal, which can be estimated from the volume of scale models. For the confection of the models, it was first effectuated skeletal reconstructions and accurate morphological restorations, trying to minimize the errors of the mass estimative. The restoration of soft tissues is also important subsequently, for the understanding of muscular action and for the interpretation of rest posture for the dicynodonts.

The volume of the model can be obtained through immersion in water, utilization of sand (Colbert, 1962), or approximated from its lateral and dorso-ventral silhouettes. This last principle is utilized by the software PaleoMass (Motani, 2001), available at the World Wide Web, and was used here for the adult *Dinodontosaurus*. As the models were constructed in unfired water-based potter's clay, water could dissolve the model, and the use of sand is time-consuming and the results are also approximate. For the juvenile individuals, the clay model was digitalized through a laser 3D-scanner, and the volume of the digital model was calculated from the CAD (Computer Aided Drafting) software Rhinoceros® (trademark of Robert McNeel & Associates), after its conversion to non-uniform rational Bézier splines (NURBS) surfaces. With the volumes, the mean density for terrestrial vertebrates used for calculation of the mass was $1.0 g/cm^3$, according to Alexander (1985).

From the clay models, the center of mass can be located through the suspension by wires (Fig.2), in two positions, presuming that it is located in a point at the sagittal plane (Alexander, 1985). Knowing the center of mass, it is also possible to estimate the distribution of corporal mass supported by each limb (Fariña, 2001) (Fig.2). For the digital model, the center of the volume could also be located with the software Rhinoceros (Fig.3), corroborating the location got from the real models.

Slijper (1946) argues that the moments of resistance for the vertebral column can be estimated only from dimensions of breadth and height of vertebral centra, using their posterior border for measurements. The resulting data can be plotted in a line graphic, in which the abscissas axis gives the position of the vertebra in the column, by its number, while the product of the breadth by the height at the square (bh^2) is plotted in the ordinates axis.

Fig.1- Skeletal reconstructions of *Dinodontosaurus*, showing the morphotypes of a juvenile (based mainly on UFRGS/PV0113T and partially on UFRGS/PV0115T) and an adult (skull based on Mata 367-99, skeleton based on UFRGS/PV0121T and modified from Cox, 1965). Scale bar = 20cm.

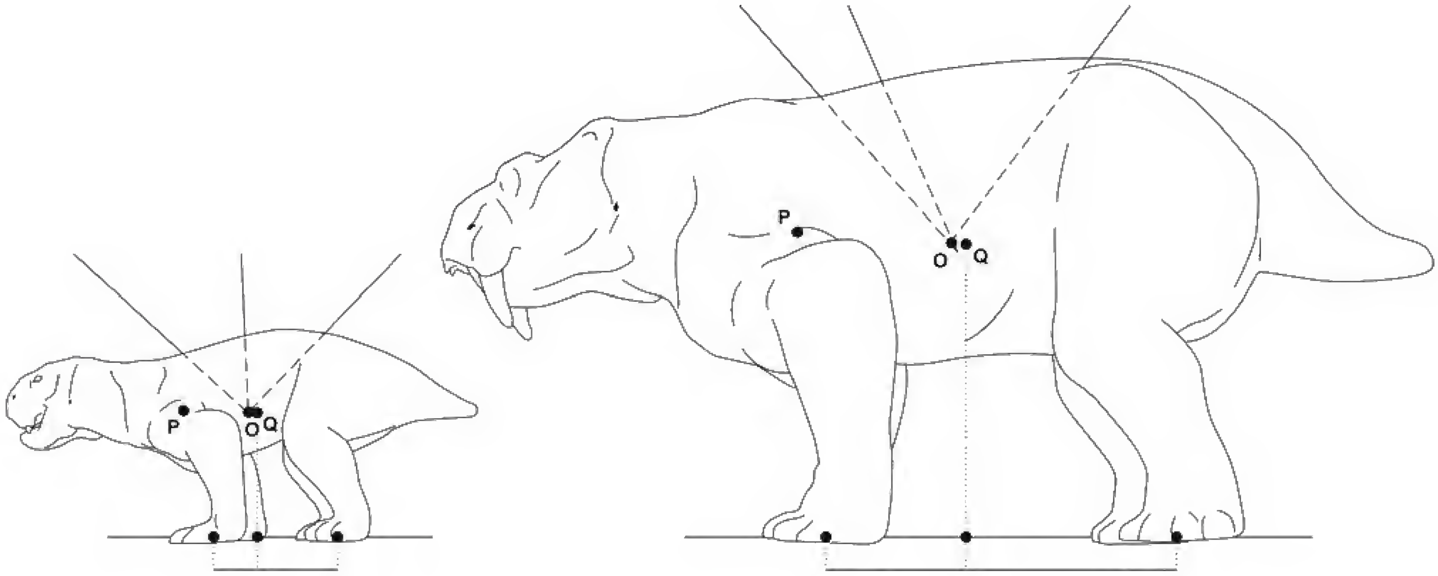

Fig.2- Location of the center of mass for juvenile and adult individuals of *Dinodontosaurus*. *O* represents the center of mass from suspension of clay models, *P* is the approximate location of lungs center of buoyance, and *Q* is the corrected location of the center of mass. In the base of the figures are the projections of the center of mass in the ground and the points of support for front and hind limbs, represented by dots, to allow the estimate of mass percentages sustained by each limb.

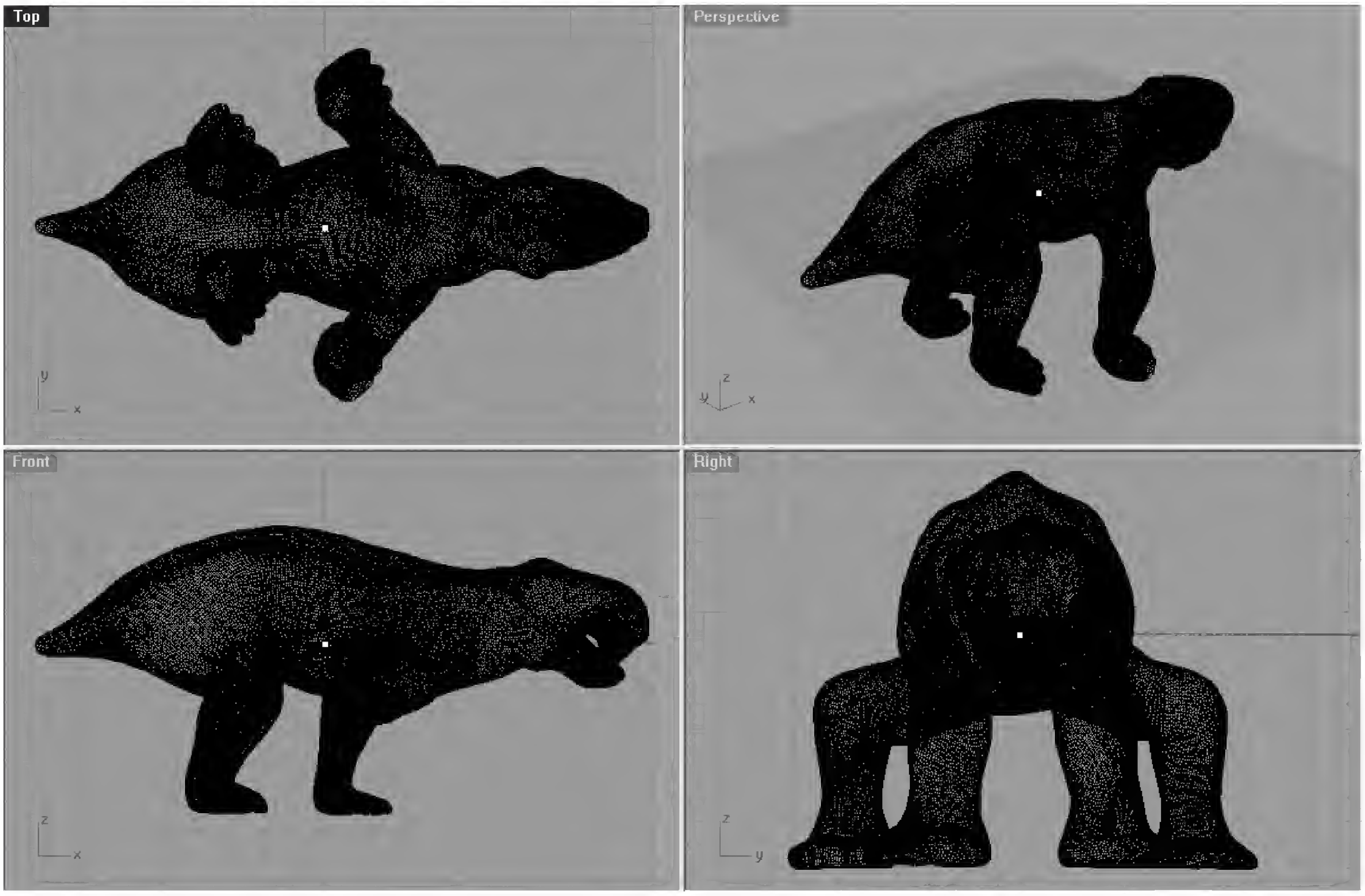

Fig.3- Screen capture image (from software Rhinoceros) of the location of the center of mass (white dot in the center of each figure) for a juvenile individual of *Dinodontosaurus*, from a digitalized model obtained with 3D-scanner.

Indicators of athletic ability for the limbs can be calculated from measurements of the transverse and sagittal diameters, as well as the length, of long bones (as the axial strength indicator, given by the expression A/amg, and the long bone strength indicator (LBSI) given by $Z/amgx$, where A is the section area, Z is the section modulus, amg is the fraction of weight supported by the respective limb, and x the half of the bone length; see Alexander, 1983; 1985) (Fig.4).

The indicators of athletic ability were calculated using a solid cylinder model, not subtracting the corresponding amount occupied by the medullar channel (as made in Casinos, 1996). This was preferred to allow comparisons with other values available in the literature, even though broken bones in the specimens allowed measuring of their walls thickness and could be possible to obtain a mean percentage of bone diameter occupied by cortex.

Some considerations must be made on the applicability of some of these indicators, once the posture and gait of dicynodonts is distinct from any living vertebrate. Even when compared with sprawling animals, there are no modern parallels for evaluations of athletic capabilities, as is usually made with such indexes (Morato *et al.*, in press).

RESULTS AND DISCUSSION

In a general observation, the comparisons between dicynodonts and xenarthrans don't seem to proceed biomechanically, as several ground sloth taxa may have walked effectively in a bipedal gait, presenting various adaptations to facultative bipedalism. Their centers of mass are displaced caudally, being near the pelvic girdle (see, for example, Blanco & Czerwonogora, 2003, for percentage of weight supported by each pair of limbs, and Fariña, 2001, for its relation to the center of mass). To this feature, contributes the relatively reduced skulls, anteriorly narrowed trunks, vigorous hind limbs and broad muscular tails. Besides that, the pes is normally larger than the manus, giving them a stable base while walking on two limbs. Measurements for *Megatherium* (Casinos, 1996) revealed that the vertebrae present the height of the centra improved towards the sacrals, increasing the resistance of the vertebral column at the lumbar region, which is necessary for a bipedal stance; the hindlimb bones presented also axial strength compatible with bipedal animals, and LBSI values superior to that of the front limbs. The sloths also possess transversally expanded femora, probably in reflection of the latero-medial stresses generated by the traviportal gait.

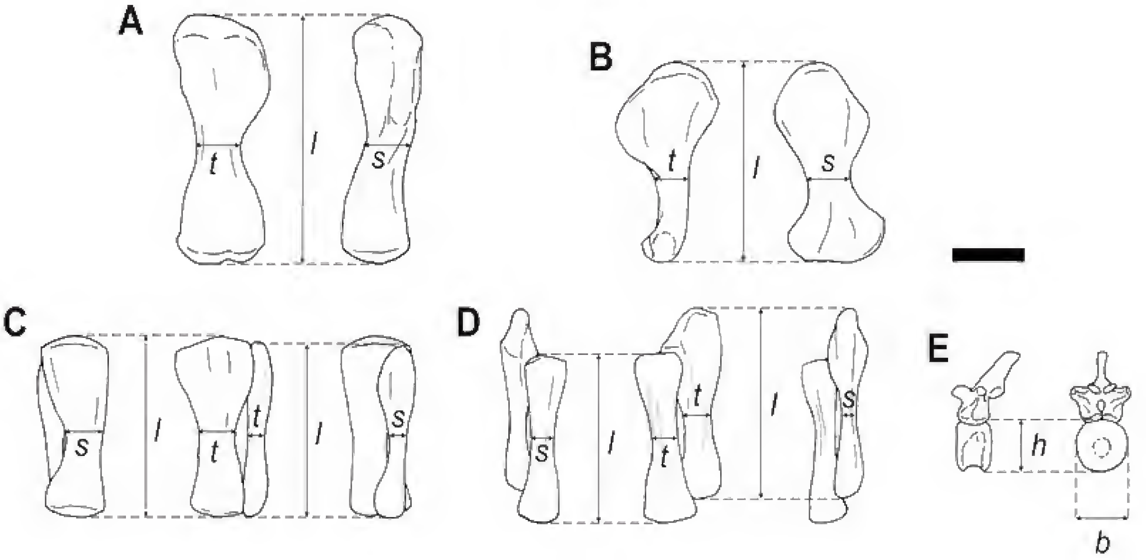

Fig.4- Key for the measurements taken from the bones of *Dinodontosaurus*: (A) left femur in dorsal and lateral views; (B) left humerus in anterior and dorsal views; (C) left tibia and fibula in medial, anterior and lateral views; (D) left radius and ulna in medial, anterior and lateral views; (E) dorsal vertebra (twentieth) in lateral and posterior views. All the long bones of the appendicular skeleton were measured for length (l), and width near midshaft, in sagittal (s) and transverse (t) diameters (in the case of the humerus, these diameters were related respectively to the antero-posterior and dorso-ventral bending stresses). Vertebrae were measured for breadth (b) and height (h) of the posterior border of their centra. Scale bar = 5cm (all drawn in the same scale).

The center of mass of *Dinodontosaurus* was located in a point in the sagittal plane about half the distance between the stylopodials, closer to the front limbs (Figs.2-3). This location was corroborated by the suspension of the sculptures as well as by the digital models. Although the center of mass have been stipulated for models composed by homogeneous matter (clay), the displacement of its position due to lungs volume would be of little significance (ALEXANDER, 1985), as it will remain closer to the forelegs. To attain a bipedal stance, any animal must adopt a posture in which the center of mass rests over or after the hindlimbs (ALEXANDER, 1985), and, in the case of *Dinodontosaurus*, such a posture would be achieved momentarily, during copula; however, the location found for its center of mass suggests that a bipedal posture would not be easily maintained without support, and a bipedal walk would be absolutely impracticable. The bipedalism in giant ground sloths is unequivocal, as it is indicated even by ichnofossils (*e.g.*, CASAMIQUELA, 1974; BLANCO & CZERWONOGORA, 2003), while the likely candidates for dicynodont's trails (*e.g.*, ELLENBERGER, 1970; HUNT *et al.*, 1993; NESBITT & ANGIELCZYK, 2002) show only quadrupedal gaits.

The estimates of the moments of resistance for the vertebral column of *Dinodontosaurus* resulted in a graphic that is also compatible with a quadrupedal animal (Fig.5), according to SLIJPER (1946). The pattern of the graphic has a lumbar peak, as well as a horizontal level near the scapular region. For *Megatherium*, the graphic presents a tapering line from the second vertebra to the end of the lumbar region (Fig.5), in keeping with a graphic for bipedal animals, except for the lack of a lumbar peak (CASINOS, 1996). This absence could be related to the xenarthrous lumbar vertebrae.

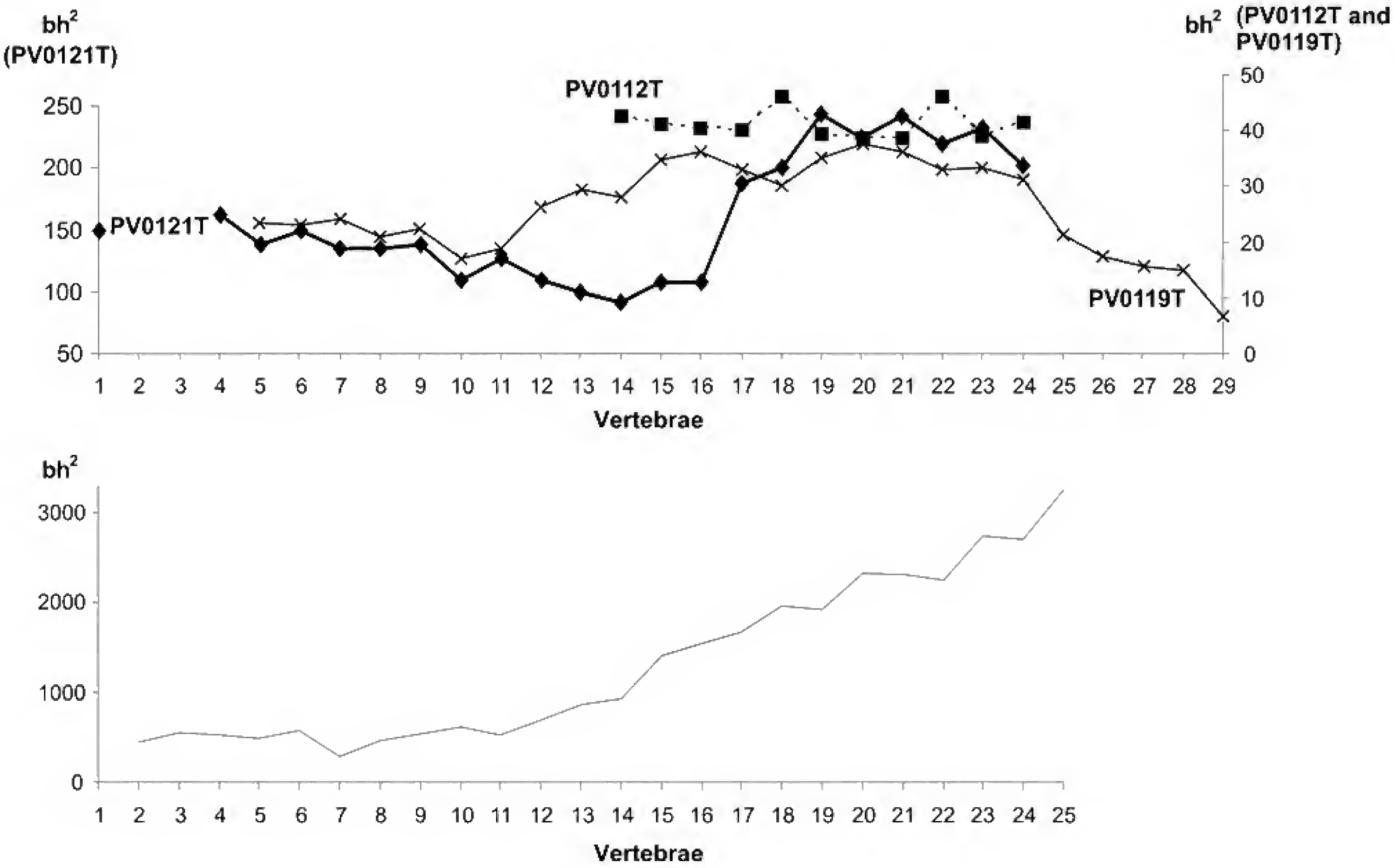

Fig.5- Moments of resistance for the different vertebrae of (above) three *Dinodontosaurus* specimens (indicated inside the graphic; UFRGS/PV0112T and UFRGS/PV0119T are juvenile individuals, while UFRGS/PV0121T is an adult), compared with (below) data for *Megatherium* (modified from CASINOS, 1996). On the *y*-axis are plotted values for the moment of resistance estimates (bh^2); on the *x*-axis, the number of the vertebrae (initiating with cervicals). In *Dinodontosaurus*, the last lumbar vertebra is number 24, and for *Megatherium*, 25.

Slijper (1946) already noticed that not only the vertebral centra are involved in the resistance of the column: tendons, muscles and aponeuroses also have a role in stress support, and the presence of additional zygapophyseal articulations could account for part of this support, liberating the charge over the centra. *Dinodontosaurus* does not have supplementary articulations on vertebrae, resulting in a lumbar peak in the graphic, although the zygapophyses seem well packed, and neural spines are close to each other. Also, the shallow angle that the zygapophyses made in relation to the axis of the vertebrae does not permit large amounts of dorso-ventral movement, uniformly increasing the column strength.

The axial and bending strength parameters were calculated for the long bones for anterior and posterior limbs, but first, this calculation needed body mass estimations, obtained from the models. The mass of juvenile individuals of *Dinodontosaurus* ranged from 23 to 32kg, for animals between 0.8 and 1m in length, while the adult individual could not surpass 300kg. The last value is an overestimate, as the silhouettes used are incorrect in the shape of the autopodials, caudal and cervical regions. A more likely value could reside near 250kg.

The superficial resemblance noted by Cruickshank (1978) between femora of dicynodonts and ground sloths proceeds only partially, because the femur in dicynodonts is transversally expanded in the proximal end, but narrows in the midshaft, showing an elliptical section, while in sloths the transverse expansion extend all the length of the femur.

TABLE 1. Indicators of athletic ability (*A/amg* and *Z/amgx*) calculated for the limb bones of *Dinodontosaurus* (specimens identified by cataloguing numbers), compared with values for mammals (from Casinos, 1996).

	Femur		Tibia		Fibula	
Taxon	*A/amg*	*Z/amgx*	*A/amg*	*Z/amgx*	*A/amg*	*Z/amgx*
Megatherium	194	42.08	742	31.40	-	-
Buffalo	-	17.74	569	21.77	-	-
PV111T	18800	164	16000	276	6990	79.4
PV112T	* 21900	* 249	-	-	-	-
PV113T	23300	259	* 12300	* 138	* 3490	25.9
PV115T	16100	146	12100	143	2580	16.5
PV116T	20700	231	-	-	-	-
PV117T	* 26100	* 315	15300	202	* 3300	* 28.0
PV118T	27500	277	14900	208	4350	37.5
PV119T	* 19200	* 204	* 14400	* 195	* 3350	* 28.2
PV120T	22100	218	-	-	-	-
PV121T	7630	73.8	5610	73.8	2380	23.4

	Humerus		Radius		Ulna	
Taxon	*A/amg*	*Z/amgx*	*A/amg*	*Z/amgx*	*A/amg*	*Z/amgx*
Megatherium	421	13.85	-	-	-	-
Buffalo	380	16.93	-	-	-	-
PV111T	-	-	5230	51.0	5060	39.4
PV112T	11600	139	-	-	-	-
PV113T	-	-	-	-	-	-
PV115T	* 20900	* 329	* 4660	* 49.0	* 9680	* 98.5
PV116T	14000	231	7380	91.4	6820	59.5
PV117T	-	-	3000	25.0	-	-
PV118T	25200	347	3560	29.7	* 5340	* 31.3
PV119T	10700	124	4760	40.6	6420	45.9
PV120T	10700	148	3980	37.7	5500	42.9
PV121T	7680	90.3	2080	25.8	2570	17.4

Values are given in GPa^{-1}, calculated for the direction of motion (for antero-posterior bending stresses), from measurements from bones of the left side; when this was not possible, values from the right side are given (indicated with asterisks).

This compromises the strength of the bone exactly where it is more demanded. Even then, the values obtained for the *A/amg* parameter, an indicator of strength in opposition to axial stresses, already show that *Dinodontosaurus* limbs were extremely resilient, even when compared with bipedal animals (see Table 1). LBSI values (the *Z/amgx* parameter) are also much superior to values for other animals (*e.g.*, ALEXANDER, 1985, 1989; FARLOW *et al.*, 1995; and CASINOS, 1996). But it must be noted that values for humeri and femora are in the same order of magnitude, at least, which supposes a quadrupedal posture (see values for *Megatherium*: CASINOS, 1996).

Finally, it is worth to note that pes and manus of dicynodonts are all of similar dimensions, therefore the pes do not have any advantage to provide a substantial support for a continuous bipedal posture.

CONCLUDING REMARKS

The results of the present analysis suggest that, at least in what concerns *Dinodontosaurus*, there are no strong evidences to support the morphofunctional analogies with the extinct ground sloths. The comparisons made by CRUICKSHANK (1978), paraphrasing himself about previous analogies (p.122), are “tenuous to say the least”. The author, for instance, discredited comparisons with modern rhinoceroses in basis of a much larger size of the latter, but if one opens space for comparisons with an extinct taxon of which there is no direct evidence of feeding behavior, why not to consider the extinct rhinocerotids or suids, whose size range varies considerably? In the other hand, there are no remarks of that matter to the much larger megatheriid sloths, some of the few sloths with extensive evidence for facultative bipedal stance to reach higher vegetation and furthermore been able to walk in this stance. Of course there won’t be a perfect equivalent for dicynodont morphology, in living as in extinct mammals, but criterion for comparison cannot be ruled only by superficial and subjective observations.

There is another syllogism in CRUICKSHANK (1978) that doesn’t have strong basis for argumentation. He suggests that tusks in Dicynodontia were used for display and/or threat purposes, therefore implying that tuskless forms were either nocturnal or lived in deep undergrowth. However, the absence of tusks does not imply in absence of ornamentation, as caniniform processes in the maxillae of tuskless forms may as well have played a role in visual signaling, what may be done by several other characters present in Middle to Late Triassic tuskless dicynodonts (MORATO *et al.*, 2005). Loss of tusks could be only an apomorphic morphological differentiation (VEGA-DIAS *et al.*, 2004), and not a complete life habit indicative.

However, in order to investigate the main comparisons of Cruickshank’s paper, other questions emerged. The values of LBSI found, incomparable to other animals described in the literature, can be a reflection of the demands of a differentiated posture adopted by dicynodonts, but this hypothesis still must be investigated throughout. Although these values can not be used in direct correlations with living creatures, they appear at least to be comparable with other Triassic amniotes, including non-mammalian cynodonts referred as quadrupedals (MORATO *et al.*, in press).

Some authors (including WALTER, 1986) admit that the differentiation in postures between fore and hindlimbs can imply in a differentiated functionality for the limbs, with the forelimbs more adequate for support, while the hind ones are more involved with effective thrust. Nevertheless, similar values for LBSI of fore and hind members can indicate that they were both effectively utilized in the locomotion, and, although they had dynamically distinct motions, they were subject to similar bending stresses; by other hand, the extreme bone strength can mask a sum of locomotory and body-support stresses, due to the arrangement of the limbs itself.

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FOSSIL BATS FROM MESOAMERICA [1]

(With 1 figure)

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ABSTRACT: Recent bats (Mammalia, Chiroptera) represent one of the most diverse mammalian orders, with more than 1,000 species, but the fossil record is poorly known. To date, records are for 41 species from 17 Mesoamerican localities in México (15) and Central America (2). This number corresponds to 24.8% of the 165 currently-known living bats for the region, pertaining to six out of eight known families. Most of the records are from Rancholabrean age deposits, with only one extinct species known for Pliocene sediments and two Pleistocene extinct vampire bat species. All other species presently range in the same region, but two of them. Most localities are cave deposits that correspond to the cave roosting habits for most of the species, either exclusive or temporal; only six are open spaces. Most of the fossils represent species that are insectivores (24), while others are frugivores (6), nectarivores (5), blood-eaters (4), and carnivores (2). The most dramatic change is with the blood-eater bats. While in the past there were three species within the genus *Desmodus*, only one is extant at present. Finally, future fieldwork should include the recovery of microremains from cave deposits to increase the findings of bats and other small vertebrates.

Key Words: Chiroptera. Fossils. Mesoamerica. Bats.

RESUMEN: Los murciélagos fósiles de Mesoamérica.

Los murciélagos (Mammalia, Chiroptera) conforman uno de los órdenes de mamíferos más diversos en el mundo, con más de 1,000 especies, pero no es el caso en el registro fósil por diversas razones. Hasta el momento, se han registrado 41 especies procedentes de 17 localidades fosilíferas mesoamericanas de México (15) y Centroamérica (2). Dicho número corresponde al 24.8% del total de especies que actualmente se conocen para la región (165) y representan a seis de las ocho familias de murciélagos registradas en la misma. La mayor parte de los registros corresponden a restos óseos procedentes de depósitos de Edad Rancholabreana; una sola especie ha sido registrada para el Plioceno, así como dos especies extintas de vampiros pleistocénicos. Las demás especies se distribuyen actualmente en la misma región de donde proceden los restos fósiles, con excepción de dos de ellas. La mayor parte de las localidades corresponden a cuevas y sólo seis son depósitos abiertos; lo mismo corresponde a los hábitos de reposo de las especies identificadas, la mayoría son cavernícolas exclusivas o eventuales. Con respecto a los gremios alimentarios representados, hay 24 murciélagos insectívoros, 6 frugívoros, 5 polinívoros, 4 sanguinívoros y 2 carnívoros. Lo más notorio es el registro de los sanguinívoros, el que ha cambiado de manera significativa, pues en el pasado se conocieron tres especies dentro del mismo género, *Desmodus*. Finalmente, es indispensable que las exploraciones en las cuevas sean planificadas de tal manera, que esto permita la recuperación y el estudio tanto de los mamíferos voladores como de otros vertebrados pequeños presentes en los depósitos.

Palabras clave: Chiroptera. Fósiles. Mesoamérica. Murciélagos.

INTRODUCTION

Recent bats (Mammalia, Chiroptera) are one of the most diverse mammalian orders with more than 1,000 species. Such diversity should be found in the past, but the fossil record for these animals is very poorly known (Teeling *et al.*, 2005). In this report, fossil bats from Mesoamerica (México to Panamá) are documented, an area in which 165 bat species live at present (modified from Hutson *et al.*, 2001). Such species pertain to 8 families and 83 genera, with mixed affinities for Neartic and Neotropical regions.

MATERIAL AND METHODS

Published reports have been reviewed and a regional map with the locality records was prepared. All the records are from deposits of Holocene or older age, mostly Pleistocene.

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LOCALITIES

The known localities (Fig.1 - numbers correspond to the following list; Tab.1) are:

MÉXICO (modified from ARROYO-CABRALES & POLACO, 2003)

(1) Yepómera, Chihuahua
The deposit is near the town of Yepómera, at 1,500masl, in northern México. As one of the most important Pliocene localities in México, it contains the Hemphillian and Blancan faunas. All 37 mammal species known in the Yepómera fauna are extinct at present.

(2) Cueva de Jiménez, Chihuahua
This cave is 14 km southeast of Jiménez, at 1,450masl. The locality has remains of extinct and extant vertebrates and molluscs. Several rodents are no longer found south of the southern United States. Only two extinct species are known: an undescribed antilocaprid and the rabbit *Aztlanolagus agilis* Russell & Harris, 1986. Neither radiocarbon dating nor stratigraphic controls during excavation have been undertaken. The fauna is assigned to the Pleistocene/Holocene interface based on its composition.

(3) Cueva de La Boca, Nuevo León
The cave is 3km east of Santiago, at 540masl, in a region with scrubland. The fossil bone is from a tunnel below the main chamber. Among the remains are many reptiles and mammals, including shrews, bats, rodents, and artiodactyls. Most of the identified species are similar to the present regional mammal fauna. The few extinct species like the Pleistocene shrub ox *Euceratherium* sp. allow assigning this fauna to the late Pleistocene.

(4) El Cedral, San Luis Potosí
The site is on "La Amapola" Ranch, El Cedral at 1,700masl. The materials from the excavations are similar to those from Rancho La Brea, California, USA, containing about 40 species, mainly birds and mammals, as well as 20 molluscs species. Radiometric dating indicates a range between 40,000 to 10,500 years before present (BP).

Fig.1- Map with the fossiliferous localities of bat remains in Mesoamerica

TABLE 1. Bat species found in fossiliferous deposits in Mesoamerica (locality numbers correspond to text localities).

SPECIES/LOCALITIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Balantiopteryx io									x								
Peropteryx macrotis														x			
Mormoops megalophylla			x		x		x					x		x			
Pteronotus parnellii													x	x			x
Anoura cf. *A. geoffroyi*						x											
Artibeus jamaicensis								x	x				x	x	x		
Artibeus lituratus																x	
Carollia subrufa/brevicauda																x	
Centurio senex																x	
Chiroderma villosum														x			
Choeronycteris mexicana					x												
Chrotopterus auritus														x			
Dermanura sp.																x	
Desmodus cf. *D. draculae*														x		x	
Desmodus rotundus														x			
Desmodus stocki			x		x		x					x					
Diphylla ecaudata														x			
Glossophaga soricina														x			
Leptonycteris curasoae							x										
Leptonycteris nivalis					x				x								
Macrotus californicus							x										
Mimon cozumelae													x				
Sturnira lilium														x			
Sturnira lilium/mordax																x	
Tonatia saurophila																x	
Antrozous pallidus		x															
Corynorhinus townsendii					x												
Eptesicus furinalis													x	x			
Eptesicus fuscus					x												
Lasionycteris cf. *L. noctivagans*									x								
Lasiurus blossevillii																x	
Lasiurus cinereus					x												
Lasiurus ega														x		x	
Lasiurus intermedius														x			
Myotis californicus					x												
Myotis thysanodes					x												
Myotis velifer			x														
Myotis cf. *M. yumanensis*									x								
Myotis sp.		x		x			x								x		
Plionycteris trusselli	x										x						
Eumops perotis									x	x							
Nyctinomops aurispinosus									x								
Nyctinomops laticaudatus									x					x			
Tadarida brasiliensis			x						x								
Tadarida sp.		x															
TOTAL	1	3	4	1	9	1	5	1	9	1	1	2	4	15	2	9	1

(5) Cueva de San Josecito, Nuevo León

San Josecito Cave is southwest from Aramberri, Municipio de Zaragoza, at 2,240masl. Research in the cave has been conducted since the middle 20th century. The cave deposits are well-stratified, and some strata have been radiocarbon dated, with a range of 16,000 to 44,000 years BP. The 120 vertebrate species constitute the most important Pleistocene fauna for México. Recently ARROYO-CABRALES & JOHNSON (2008) documented new findings for the cave mammal fauna, including the additions to the known bat species.

(6) Cueva de Infiernillo, Tamaulipas
Subfossil bone remains were found in this cave within the Gómez Farías region, including seven bat species (Koopman & Martin, 1959). The studied material was associated with a Pleistocene fauna.

(7) Cueva de La Presita, San Luis Potosí
The locality is 21.4km south of Matehuala, at 1,540masl. The fauna consists of 36 mammal taxa, of which 11 are extinct, including five bat species. This fauna is assigned to the late Pleistocene based on its high proportion of extinct components.

(8) Gruta de Quintero, Tamaulipas
This cave is located 6km south of Ciudad Mante, at 200masl. The deposit includes some extinct large mammals. Based on these taxa, the fauna is considered to date to the Pleistocene/Holocene interface.

(9) Cueva de El Abra, Tamaulipas
This cave is near the previous one, within the tropical area of the state, 9km northeast from Antiguo Morelos, at 300masl. An important tropical vertebrate microfauna comes from a travertine layer. The fauna is composed primarily of bats (9 species) and rodents, and is assigned to the late Pleistocene. All of the species are extant, but the extinct mouse *Perognathus huastecensis* Dalquest & Roth, 1970 is known only from this cave.

(10) Cuencas de Chapala-Zacoalco, Jalisco
Several fossil vertebrates, either complete or incomplete, have been found on the shore line of both Lake Chapala and Lake Zacoalco. Most of those remains are not stratigraphically controlled. During the initial excavations, however, it was possible to identify two distinct Pliocene/Pleistocene and late Pleistocene faunal components.

(11) Rancho El Ocote, Guanajuato (Carranza-Castañeda & Miller, 2004; Carranza-Castañeda & Walton, 1992)
This place is the most important late Hemphillian and Blancan locality in central México, with more than 50 taxa known and several others under study. Another possible bat Hemphillian record was reported for the State of Hidalgo, east from Guanajuato (record not shown in the map).

(12) Tlapacoya, Estado de México
Tlapacoya Mountain is a small volcanic hill located 26km southeast from downtown México City, at 2,240masl. The known mammal fauna consists of 22 taxa from a period between 33,150 to 9,000 years BP. The fauna includes both extinct and extant species. Among the extant forms, some still live in the region and others are extralimital.

(13) Actún Spukil, Yucatán
This large cave is 6km south of Hacienda Calcehtok, at 60masl. A mylodont and other tropical mammal remains have been collected at the deepest portion of the cave. It has been assigned to it a late Pleistocene age.

(14) Gruta de Loltún, Yucatán
The cave is located 7km south of Oxkutzcab, at 40masl. The vertebrate remains come from archaeological excavations and were assigned to deposits from late Pleistocene and early Holocene. The fauna includes several extinct taxa, like dire wolf, extinct llama, and gomphothere.

(15) Cueva Encantada de Chimalacatlán, Morelos
The cave is found 2km east of Chimalacatlán, Municipality of Tlaquiltenango, at 1,200masl. The fauna is composed mainly of tropical animals such as ground sloth and gomphothere, but includes extinct temperate taxa, like bison and horses. The fauna is assigned to the late Pleistocene.

BELIZE

(16) Cebada Cave, Chiquibul System, Cayo District (Czaplewski *et al.*, 2003)
This cave is part of an extensive cave system formed by 65km of tunnels and chambers. The fauna contains mammals (including human), reptiles, and a young spectacled bear *Tremarctos floridanus* Gidley, 1950; the bear previously was reported from San Josecito Cave. The fauna is assigned to the late Pleistocene or Holocene.

EL SALVADOR

(17) Barranca de Sisimico, Department of San Vicente
This open site shows the presence of Neotropical animals that crossed over the Panama Isthmus, including *Megalonyx*, *Eremotherium*, *Mixotoxodon*, *Cuvieronius*, and an extinct cervid. Webb & Perrigo (1984) suggested that this fauna needed further study because it might represent the early Pleistocene (Irvingtonian). The bat skeleton comes from diatomaceous deposits below the sandstone; it has not been studied in detail, but it should be since it may represent a new species.

RESULTS AND DISCUSSION

Currently, records consist of 41 bat species from 17 fossil localities in Mesoamerica: México (15) and Central America (2). Such a number represents 24.8% of the total current species known at the region (165), and includes six out of eight families [Emballonuridae (2 species, 4.9% fossil total), Mormoopidae (2 species, 4.9%), Phyllostomidae (20 species, 48.8%), Antrozoidae (1 species, 2.4%), Vespertilionidae (12 species, 29.3%), and Molossidae (4 species, 9.8%)]. The same families are respectively represented as follows: 11 (6.9%), 5 (3.1%), 72 (45.3%), 2 (1.3%), 47 (29.6%) y 22 (13.8%). Gruta de Loltún is not only the most diverse locality based on bat species found at the fossiliferous deposits in the studied region, but also the place where most abundant remains were collected.

Only one bat species is known at a pre-Pleistocene deposit, being the oldest bat in Mesoamerica. It is *Plionycteris trusselli* Lindsay & Jacobs, 1985, an extinct genus that comes from one locality in northern México (type locality), and two probable occurrences in central México (Carranza-Castañeda & Miller, 2004); further study of those Central Mexican specimens is needed to corroborate the taxon identity. All other species are from deposits assigned to the late Pleistocene, and to the Rancholabrean land mammal age (300,000 to 10,500 years BP; Tab.2), although the El Salvadoran specimen may be older. Only two other extinct species come from those deposits, *Desmodus draculae* Morgan, Linares & Ray, 1988 and *D. stocki* Jones, 1958. The other species are extant, and all but two occur at present at the same geographic region where they were found. Two extralimital species, *Balantiopteryx io* Thomas, 1904 and *Eumops perotis* Schinz, 1821, are currently not known from northeasten Mexico where they were found.

Most of the known fossil localities are caves, and only six were open deposits. The same is true for the species' roosting habits, most of them being cave bats, either exclusively or temporally (at least 80%). In regard to food habits, the composition consists of 24 insectivorous bats (57.5%), six frugivorous (15%), five nectarivorous (12.5%), four blood-eaters (10%), and two carnivorous (5%). The piscivorous habit is not represented, but is known for fossil specimens in South America. For the modern bat fauna, food habits follow a different distribution pattern: 108 insectivores (65.5%), 33 frugivores (20%), 15 nectarivores (9.1%), three blood-eaters (1.8%), four carnivores (2.4%), and two piscivores (1.2%).

TABLE 2. Fossil bat localities in Mesoamerica and their absolute or relative age.

Locality	Age
Yepómera	Late Hemphillian
Cueva de Jiménez	Pleistocene – Holocene
Cueva de La Boca	Rancholabrean
El Cedral	40,000 – 10,500 years BP
Cueva de San Josecito	44,000 – 16,000 years BP
Cueva de Infiernillo	Rancholabrean
Cueva de La Presita	Rancholabrean
Gruta de Quintero	Rancholabrean
Cueva de El Abra	Rancholabrean
Cuencas de Chapala-Zacoalco	Rancholabrean
Rancho El Ocote	Latest Hemphillian
Tlapacoya	33,150 – 9,000 years BP
Actún Spukil	Rancholabrean
Gruta de Loltún	Rancholabrean
Cueva Encantada de Chimalacatlán	Rancholabrean
Cebada Cave	Pleistocene – Holocene
Barranca del Sisímico	Early Pleistocene?

Some of the reasons for the low numbers of fossil bat species known from Mesoamerica are: 1) the lack of detailed collecting methodology for small vertebrates, that has been improved in the recent years by using archaeological excavations methods; 2) the researchers interest in pursuing studies of macrofauna rather than the overall faunal components; and 3) the actual preservation of small mammal remains, that seems more difficult in open spaces than in caves. As for the bat fossil record in Mexico, the presence of three species of the genus *Desmodus* in the Pleistocene is outstanding, as currently only one is extant, *D. rotundus* Geoffroy, 1810. The large size of the extinct species, *D. draculae* and *D. stocki*, may be due to the large-sized animals, like ground sloths and many other megafaunal mammals, on which they fed. These large "mega-vampires," then, were depleted of their food supply at the time of megafaunal extinction. Small sized species such as *D. rotundus* and *Diphylla ecaudata* Spix, 1823 could survive feeding on smaller herbivorous animals.

CONCLUSION

Enhancing the collecting efforts for microvertebrates is critical to gaining a deeper knowledge of the evolutionary pathways for the bats. The same is true for all other microvertebrates. Since caves seemed the best site for fossil bat collecting, the development of cave research protocols for small vertebrate paleontology is needed.

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MAMMALS FROM THE LATE PLEISTOCENE/EARLY HOLOCENE OF SAN LUIS PROVINCE (ARGENTINA) AND PALAEOENVIRONMENTAL INFERENCES [1]

(With 15 figures)

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ABSTRACT: This report informs about the findings of extinct mega-mammals of the Late Quaternary in San Luis Province, produced between 1993 and 2003. They constitute the first descriptions with geographic and stratigraphic references correctly identifiable. The remains are dominated by *Equus (Amerhippus) neogeus, Stegomastodon platensis, Sclerocalyptus ornatus, Megatherium americanum*, and *Scelidotherium leptocephalum*. This association establishes its link to the Lujanense Mammalian Age recognized in the Pampean region; it also suggests a strong similarity with the climatic conditions prevailing during the Late Maximum Glacial Ice. The relatively scarce and partially fractured presence of fossil mammals as well as some stratigraphic evidences suggests a larger severity in the environment taking into account its closeness to the area of contribution of arenas and Patagonian slimes and the Andean glacial fronts.

Key words: Megafauna. Late Quaternary. San Luis Province. Climatic conditions.

RESÚMEN: Los mamíferos fósiles del Pleistoceno Tardío-Holoceno temprano en la Província de San Luis (Argentina). Inferencias paleoambientales.

Se dan a conocer los hallazgos de megamamíferos extintos del Cuaternario Tardío de la provincia de San Luis, producidos por el autor y colaboradores entre 1993 y 2003, los que constituyen las primeras descripciones con referencias geográficas y estratigráficas correctamente identificables. Los restos están dominados por *Equus* (*Amerhippus*) *neogeus, Stegomastodon platensis, Sclerocalyptus ornatus, Megatherium americanum* y *Scelidotherium leptocephalum*. Dicha asociación establece su vinculación con la Edad Mamífero Lujanense reconocida en la región pampeana, a la vez que sugiere una fuerte similitud con las condiciones climáticas dominantes durante el Ultimo Máximo Glacial. La relativamente escasa y parcialmente fracturada presencia de los restos fósiles, sumada algunas las evidencias estratigráficas, sugiere una mayor rigurosidad en el ambiente, considerando su cercanía al área de aporte de arenas y limos patagónicos y los frentes glaciares andinos.

Palabras claves: Argentina. San Luis. Cenozoico. Mamíferos. Paleoambiente.

INTRODUCTION

San Luis Province is located in the center-west of Argentina between 31°50' and 36°00'S and 64°69' and 67°22'W. It is 700km west of the Atlantic Ocean and 250km east of the Andes Mountains. The largest area of the relief is a plain with a height between 600 and 700m above sea level, whereas in the highland zone there are 2,200m above sea level. The fossil remains recognized in this report were exhumed at Depresión Oriental, Planicie Medanosa Austral and Sierra de San Luis (Fig.1).

Field references and comparative quotations about the presence of Quaternary fossils in isolated areas of this region are known since the end of the XIX century. However, the first work of description, illustration, and cataloguing of the remains was produced at the end of the last century (Tognelli *et al.*, 1993). Additionally, radio carbon dating of those remains improved the quality of these records (Chiesa, 2005).

The objective of this contribution is to submit a present-day condition about the knowledge of the presence of Quaternary fossil mammals in San Luis Province as well as producing a general characterization of bearing sediments and paleoenvironmental conditions prevailing during the Late Pleistocene and Recent Holocene.

Antecedents

The major stratigraphic and paleontological contributions related to the Upper Quaternary of

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San Luis have been produced in the last 30 years. In this context, the most significant antecedents referring to the stratigraphy of Quaternary deposits of San Luis Province is attributed to Santa Cruz (1979) whose proposal was debated by Latrubesse & Ramonell (1990) who put forward a new lithostratigraphy. Pascual & Bondesio (1981) and Costa *et al.* (1997/2002) published important compilations on the sediments and scarce fossils of the area. Several other published and unpublished studies at a zonal range generated significant advance in the knowledge of sedimentary characteristics of the main geomorphologic units. Their most highlighting contribution was the progressive clarification about the space and/or temporal distribution with the detailed descriptions of the outcrops, sometimes associated with microflora and megafauna.

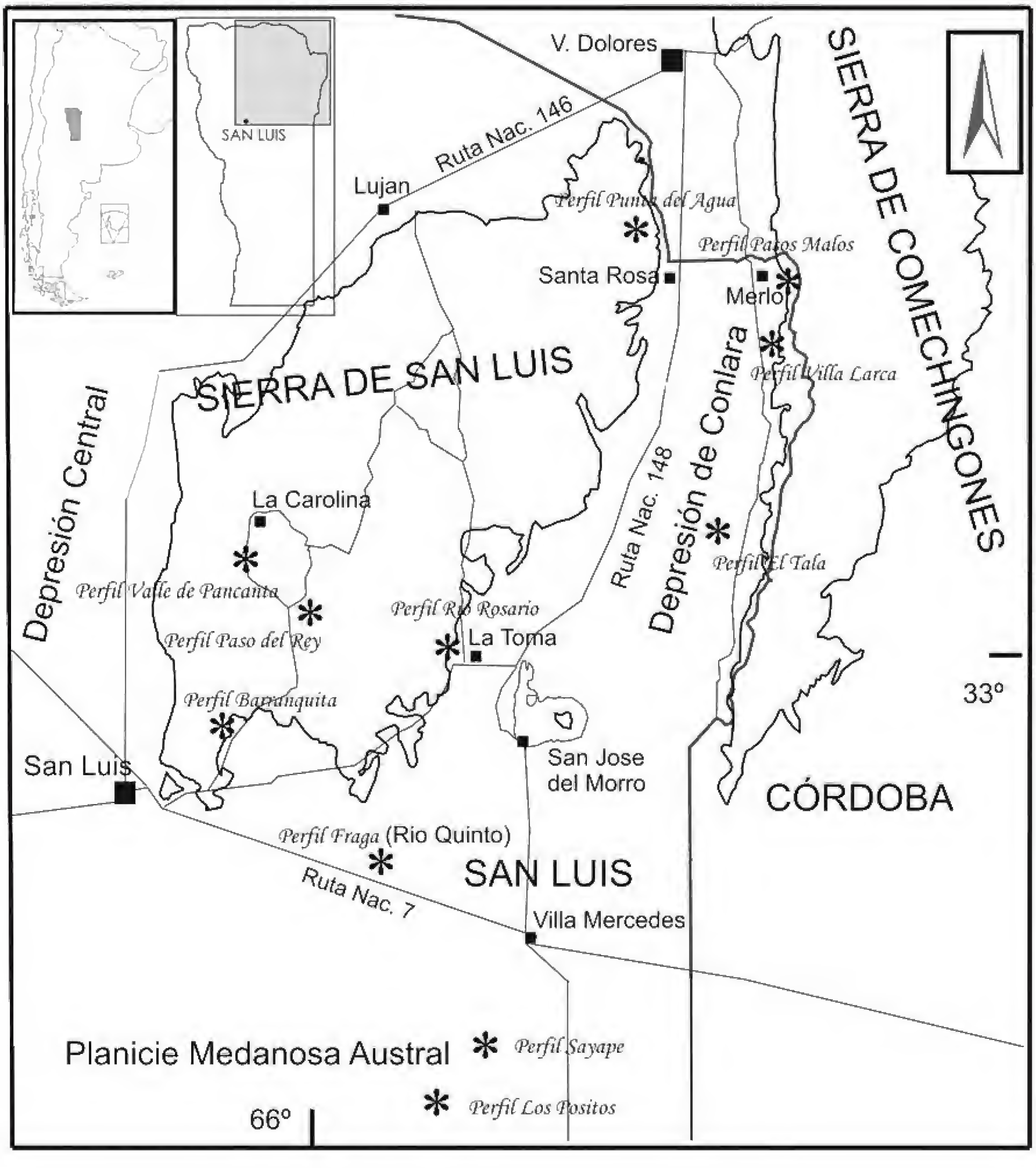

Fig.1- Map of the location of the main quaternary fossiliferous localities (*) of San Luis Province.

Finally, Costa *et al.* (1997/2002) presented contributions with a detailed compilation and description of stratigraphic profiles representative of the Quaternary of the central and northern region.

From the paleontological point of view, the first historical and synthetic review linking geology and Quaternary fossils from San Luis corresponds to the study of Strasser *et al.* (1992). In this respect, the oldest citations belongs to De Moussy (1860) who mentioned, "it is told that in some plains of Sierra de San Luis there are very voluminous fossil skeletons. All our searches have been fruitless and we have not been able to gather evidences". A similar situation was commented by Ave Lallemant (1875) in Cañada de Zavala. Although he pointed out having found "a rib", it is not presented a further description of the fragment.

Adaro (1917) was the first researcher that presented descriptions and illustrations of the Pleistocene xenarthra and ungulates of San Luis remains. The author referred at the point 1 (:4) "the first fossil that came to our hands was a *Megatherium* dorsal vertebra found on the left shore of Río Quinto" without providing the date of such finding, whereas in the point 2 (:7) he mentioned that "later, in 1901, we received another bone that was better fossilized, colored in black as if it were coal and found by our friend Antenor Orueta on the left shore of Río Conlara and on the alley that departs from San Pablo to La Riojita. It is the ileum of a *Megatherium*". Adaro went on describing the finding of fossil remains in the Quaternary successions of different spots close to Sierra de San Luis supplied by villagers from 1910 until 1926. The finding of a *Megatherium* vertebra in the zone of El Morro was presented by Pastore (1915). A very important reference for the time is Frenguelli (1931). The author registered the occurrence of *Megatherium americanum greslebini*, *Scelidotherium* sp., *Lestodon* sp., "*Eumylodon*" sp. (*Mylodon* sp.), *Panochtus sp.*, "*Auchenia*" sp. (*Lama* sp.), *Macrauchenia* sp., *Equus* sp., and "*Arctotherium*" (*Arctodus*; *Arctotherium* sp.). New quotations referred to Quaternary fossils correspond to Gez (1938), who pointed out to remains assigned to "*Panochtus*, *Sclerocaliptus*, *Toxodon*, *Equus argentinus*, *Pachyrucos*, *Megatherium americanum* (the big one) and *M. lundi* (the small one), *Scelidothoerium*, *Lycodon*, *Lama* and *Paraclotherium parodi*", found in several zones of the province isolated among them. Subsequently, different geologic analyses in San Luis Province (Tapia & Rigal, 1933; Pastore & Ruiz Huidobro, 1952; Pastore & González, 1954) mentioned the presence of Quaternary fossils without producing a study of them. Those fossils were assigned to *Scleroclyptus*, *Glyptodon*, *Megatherium*, *Mylodon*, *Panochtus*, *Toxodon*, and *Equus argentinus* remains.

Finally, during the last decade studies such as those of Chiesa *et al.* (1999) and Tognelli *et al.* (2000) provided a significant advance in the description, illustration, and chronostratigraphy of Quaternary fossil remains from peripheral basins of the province highland region.

Geology

The Quaternary sediments take up the largest area of the province, approximately 85%, distributed in the plains. They overlie without agreeing with the rocks of the basement, Neopaleozoic, Cretaceous, and Neogene continental sedimentary rocks. Although units assigned to the Lower to Middle Pleistocene are proposed in some sections taking into account the fossil findings and radio carbon datings, the most ancient ones involve the Lujanense Mammalian Age or the Late Pleistocene.

From the geomorphologic point of view, San Luis Province presents two contrasting environments: the highland one and the plain one (González Díaz, 1981). The highland environment is located in the northern half like stretched strips in north-south direction and is distributed from east to west in Sierra de Comechingones, Sierra de San Luis, and Serranías Occidentales; whereas the plains take up the Planicie Austral and the inter-highland northern depressions known as Depresión Oriental with the Valle del Río Conlara, Depresión Central, and Depresión Occidental with the Valle del Río Desaguadero.

In the geomorphologic units mentioned above, the Quaternary sediments present peculiar characteristics for the region and contrast with those that are close to them including the "high pampas" where the evolution of paleosoils highlights. In general, the Planicie Austral is a stretched and monotonous sandy unit, softly wavy with dunes associated with trays of deflation sometimes occupied by bodies of water and bordered on the north by the basin of the Río Quinto.

The Depresión Oriental is a loessoid plain with outcrops isolated of the basement and bordered on the east by the softly tilted basement of Sierra de San Luis, the Valle del Río Conlara on which basin it is possible to identify fluvial psephites and psammites. On the eastern side it developed alluvial fans beginning from the steep piedmont of the Sierra de Comechingones.

The Depresión Central is a sandy loessoid semidry unit with two saline trays as depositional centers to the north (Pampa de las Salinas) and to the south (Salinas del Bebedero), and which draining is organized by a dorsal at the center of the depression. Finally, the Depresión Occidental is a wide area with a sandy cover; its fluvial-lacustrine evolution associated to Río Desaguadero is linked to the glaciers of Río Mendoza and Río San Juan of the Andes Mountains.

REGIONAL STRATIGRAPHIC SETTING

During the last 15 years, there have been contributions referred to the paleontology and the stratigraphy of the Quaternary in different areas of the provinces bordering on San Luis, fundamental to generate a paleoenvironmental model. This model allows us to come up with a biostratigraphic scheme relatively coherent for the center-west of Argentina because of its similarities and differences with other regions that have been further studied. Some contributions are related to the Córdoba region such as those of CANTÚ (1992), TAUBER (1997), and CARIGNANO (1999), whereas RODRÍGUEZ & BARTON (1993) and ZÁRATE (2002) produced significant advances in the description of the Quaternary of Mendoza.

Up to the present, the general biostratigraphic scheme for the Quaternary of Argentina corresponds to the Pampean region, especially Buenos Aires Province (ZANCHETTA, 1995; CIONE & TONNI, 1995). In general, that scheme foresees that the identified units correspond to different depositional environments where the fossil remains exhumed enable a chronology based in part on the extinct megafauna. Thus, in the alluvial environment Luján Formation, the lower unit denominated Guerrero Member is assigned to the Late Pleistocene and characterized by the exclusive presence of *Megatherium americanum* and *Equus (Amerhippus) neogeus*, whereas the upper unit or Río Salado Member belongs to the Holocene and is linked to the presence of *Lagostomus maximus*.

The so-called Platense with lake characteristics and the Aeolian deposits of La Postrera Formation also correspond to the Holocene. It is possible to identify the presence of two paleosoils, Puesto Callejón Viejo (Late Pleistocene) and Puesto Berrondo (Middle Holocene), both inserted among the successions mentioned above in different areas.

Recently, DANGAVS & BLASI (2003), based on their own researches and antecedents, hold the acknowledgement of La Chumbiada Member and Lobos Member as part of Luján Formation.

In San Luis, a stratigraphic scheme of the Quaternary was recently proposed by CHIESA (2005) (Fig.2). The geographic position of the actual area of study justifies in part the sedimentary differences with respect to the wide Pampean region, but with stratigraphic units more spatially enclosed probably as a response to the prevailing geomorphologic environments linking the relations proposed by LATRUBESSE & RAMONELL (1990), TOGNELLI *et al.* (1993), STRASSER *et al.* (1996), and CHIESA *et al.* (1999).

MATERIAL AND METHODS

The fossil material presented here is deposited in the Museo de Historia Natural of the Universidad Nacional de San Luis and registered under the reference 'MHN-UNSL-V' plus the accession number.

The data about the findings of extinct mega-mammals of the Late Quaternary in San Luis Province, here described and discussed, were produced by the author and associates between 1993 and 2003.

RESULTS AND DISCUSSION

PALEONTOLOGY

Among the mammal megafauna remains of the Late Quaternary in San Luis Province, we recovered elements of *Sclerocalyptus ornatus* (Owen, 1845) (Figs.3-4), *Scelidotherium leptocephalum* Owen, 1840 (Figs.5-8), *Megatherium americanum* Cuvier, 1796 (Figs.9-10), *Stegomastodon platensis* (Ameghino, 1888) (Figs.11-14) and *Equus (Amerhippus) neogeus* Lund, 1840 (Fig.15).

Class MAMMALIA Linnaeus, 1758
Super-order XENARTHRA Illiger, 1811
Order CINGULATA Illiger, 1811
Family Glyptodontidae Burmeister, 1879
Subfamily Sclerocalyptinae Ameghino, 1895
Tribe Sclerocalyptini Ameghino, 1895
Genus *Sclerocalyptus* Ameghino, 1891
Sclerocalyptus ornatus (Owen, 1845)

Localities and descriptive aspects – Pasos Malos, El Tala, Arroyo Mundo Nuevo (La Carolina), and Cerro El Morro. An almost complete shell with part of the caudal shield and the pelvis were exhumed in Pasos Malos.

TIME	AREA	SAN LUIS SIERRA			AUSTRAL DEPRESSION		ORIENTAL DEPRESSION		
		West Region	East Region	South Region	Plain	Río Quinto Basin	Río Conlara Basin	Comechingones Sierra	El Morro Hill
HOLOCENE		Algarrobito			El Chulengo	Puerta Negra	San Luis / Río Conlara	La Estanzuela	Algarrobito
		Los Toldos				Los Filtros			Los Toldos
PLEISTOCENE		Barranquita				San Luis			Barranquita
		Alto Grande				Fraga		Uspara	La Unida
		Units III / IV	El Pantano / Olguín	Donovan / del Potrero / Las Chacras			Renca	Merlo	
						La Petra	San Felipe	Papagallos	Los Pozos

Fig.2- Stratigraphic correlation of the Late Pleistocene - Holocene units at San Luis province.

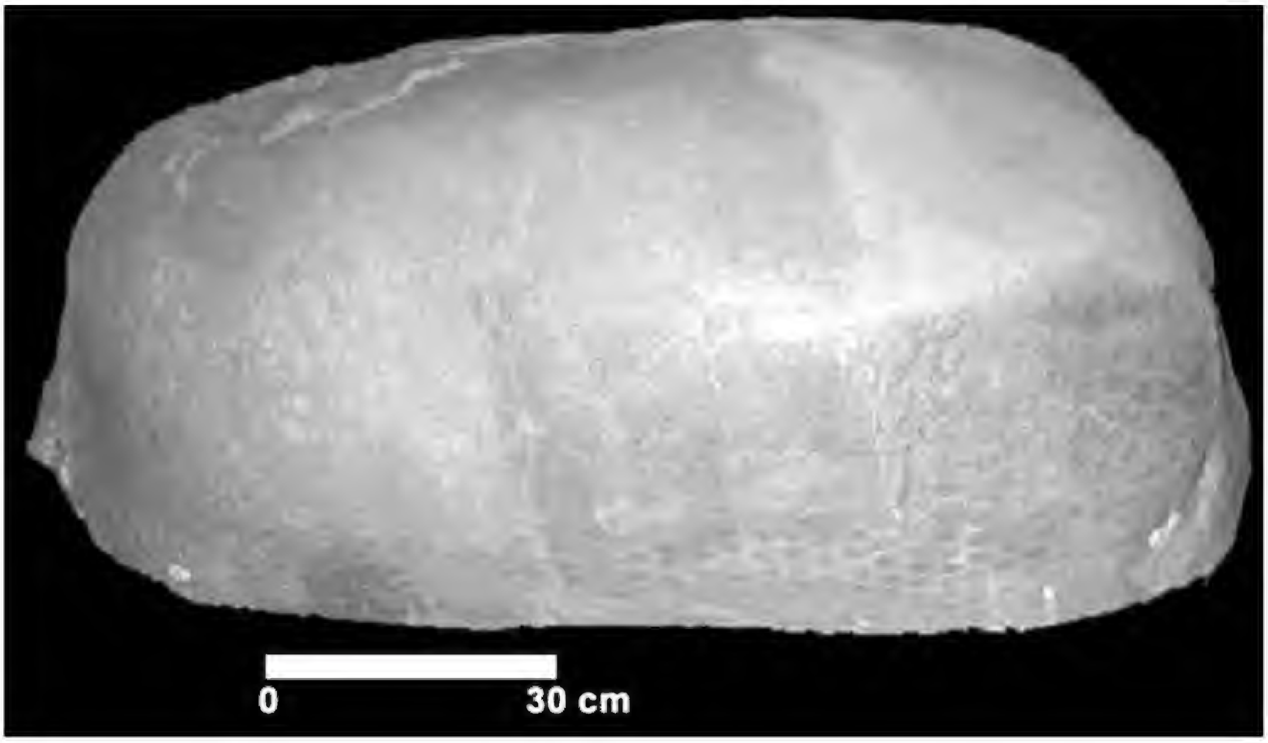

Fig.3- *Sclerocalyptus ornatus* – carapace.

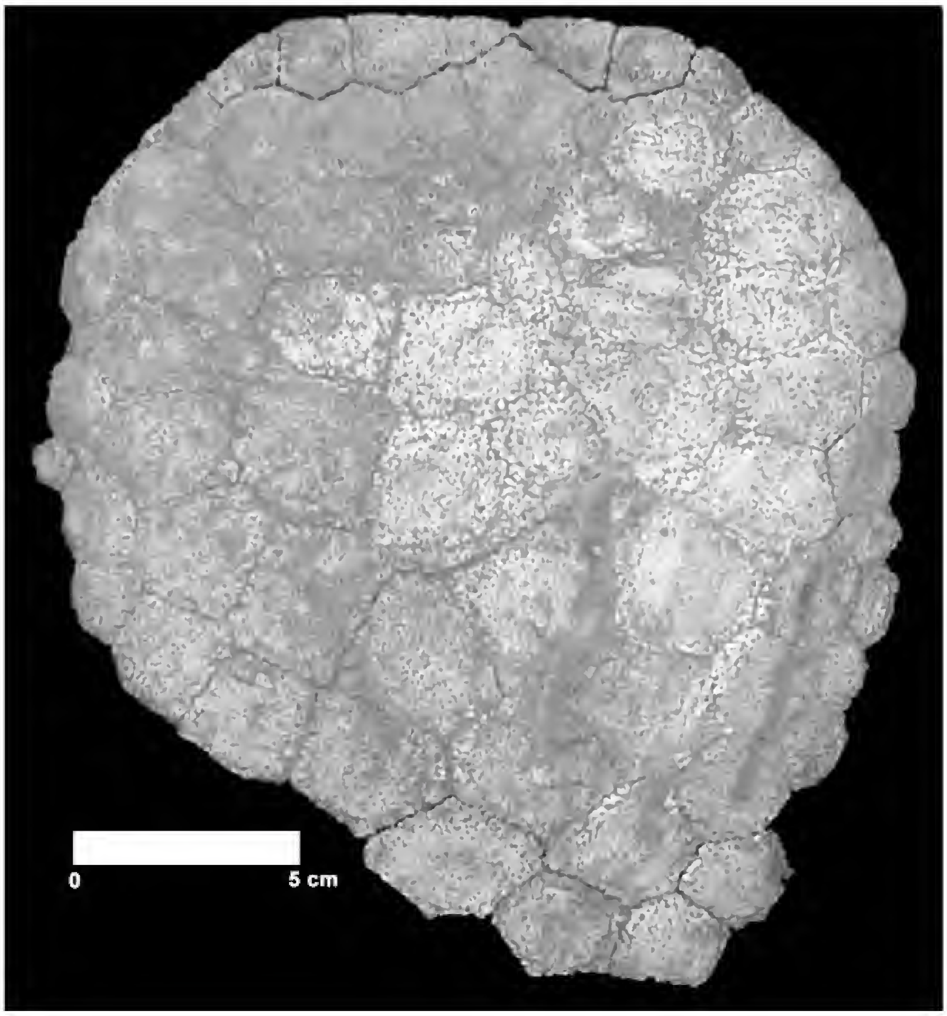

Fig. 4 – *Sclerocalyptus ornatus* - carapace fragment.

The finding in El Tala includes the complete shell, the skull, and the lower maxillary with the dentition; the cephalic small shield, ribs, and vertebrae belonging to different segments included the tail, articulate zone of the pelvic waist, extremities and plates of the movable rings of the tail. The shell is oval and low, with a fractured cupule and well-preserved anterior-lateral projections. The thin dorsal plates are hexagonally to subquadrangulary-shaped with well-defined sutures and piliferous pores. The central figure is oval and a little depressed, surrounded by peripheral polygonal figures with variable numbers (predominantly 8 to 9) with pronounced, narrow, and barely deep wrinkles. The ventral plates are smaller with rectangular shapes stretched in an anterior-posterior sense; the central figure occupies nearly all the space surrounded by small peripheral or absent figures. With regard to the extremities it can be mentioned as to have been conserved: femurs, tibiae, fibulae, right scapula, humeri, ulna, right radius, carpal, metacarpal, tarsal, and metatarsal bones. The shells assigned to Glyptodontidae recognized by the author in Arroyo Mundo Nuevo (high pampa of Sierra de San Luis) and Cerro El Morro have not been studied.

Stratigraphic and geographic distribution – It was frequently found in the deposits of the Pleistocene (Ensenadense and Lujanense Mammalian Ages) of Buenos Aires, Córdoba, Corrientes and Entre Ríos Provinces, in Argentina and in Uruguay.

Habitat – According to FIDALGO & TONNI (1983), this species lived in open areas of pastures and steppes.

Pasos Malos – MHN-UNSL-V 198.

El Tala – MHN-UNSL-V 487 to MHN-UNSL-V 500.

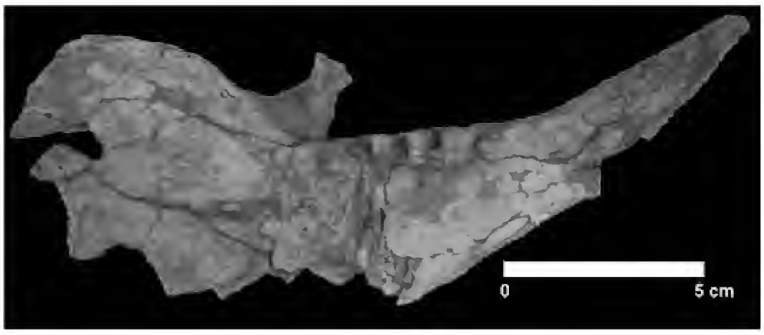

Fig. 5 – *Scelidotherium leptocephalum* – mandible fragment.

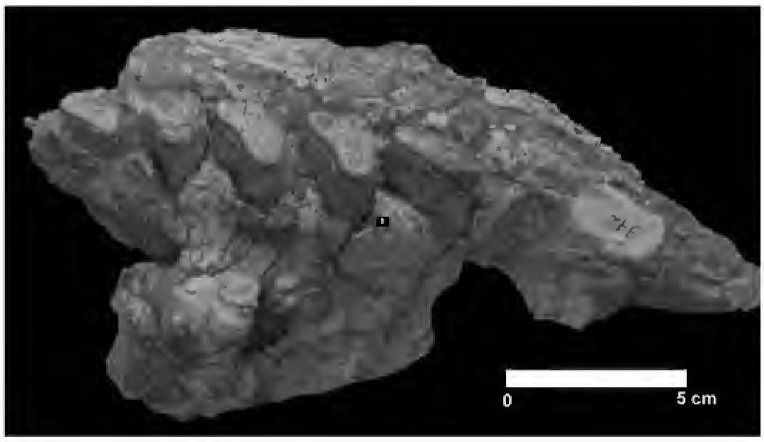

Fig. 6 – *Scelidotherium leptocephalum* – skull fragment 342.

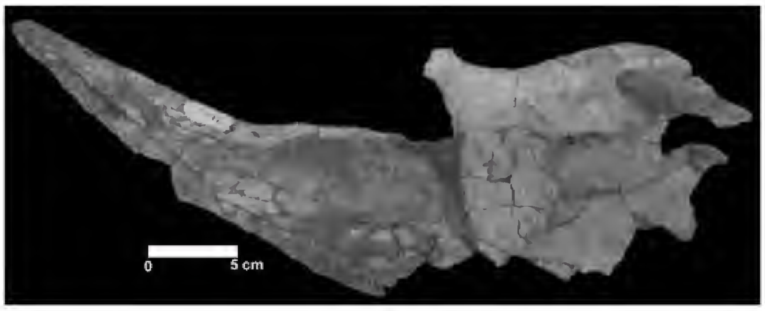

Fig. 7 - *Scelidotherium leptocephalum* – skull fragment 342.

Order TARDIGRADA Latham & Davies, 1795
Family Mylodontidae Gill, 1872
Subfamily Scelidotheriinae Ameghino, 1889
Genus *Scelidotherium* Owen, 1840
Scelidotherium leptocephalum Owen, 1840

Localities and descriptive aspects – Pasos Malos (Merlo), Villa Larca, and Valle de Pancanta. A complete skull was found in Pasos Malos. Upper and lower maxillaries with molars were found in Villa Larca. In Valle de Pancanta were found an isolated tooth; right and left femur without proximal portions; right humerus; proximal end of the left humerus; left tibia; right tibia without the proximal portion; right and left astragali; left calcaneus; four caudal vertebrae and an incomplete pelvic waist. The remains of Villa Larca correspond to the mandibular branch (without the 4th molar), the left zygomatic arch, and fragments belonging to the base of the skull with the complete left dentition and the right dentition without crown. In the horizontal mandibular branch, the part that stretches ahead of the molars is slightly curved, narrow, and extended twice the toothed region. They are molariform, prismatic, sub-triangular or sub-elliptical; the disposition is highly oblique except for the anterior-posterior stretching of the 1st upper molar with sub-equal size except for the 5th upper molar that is smaller.

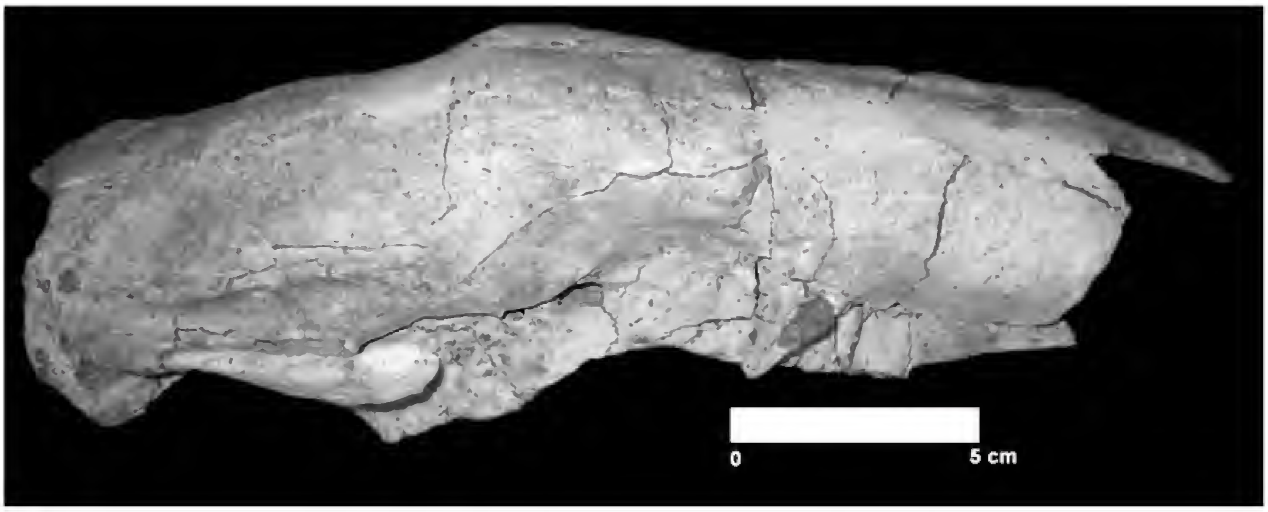

Fig. 8 – *Scelidotherium leptocephalum* – lateral view of the skull.

Fig. 9 – *Megatherium americanum* – fragment of a thoracic vertebra.

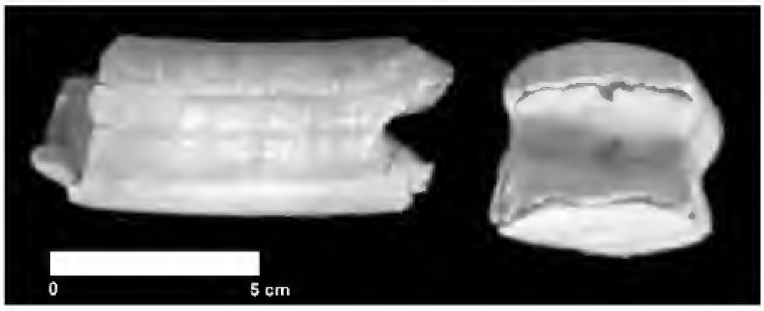

Fig. 10 – *Megatherium americanum* – molar tooth.

Fig. 11 – *Stegomastodon platensis* – first cervical vertebra (atlas).

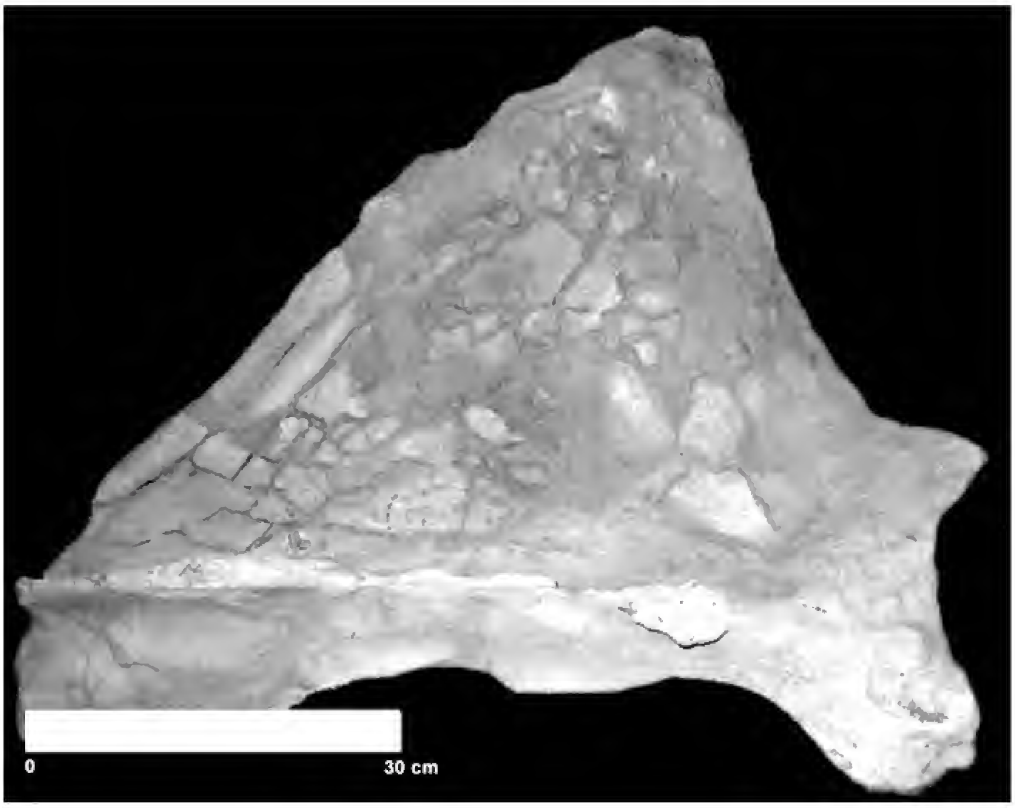

Fig. 12 – *Stegomastodon platensis* – scapula (?).

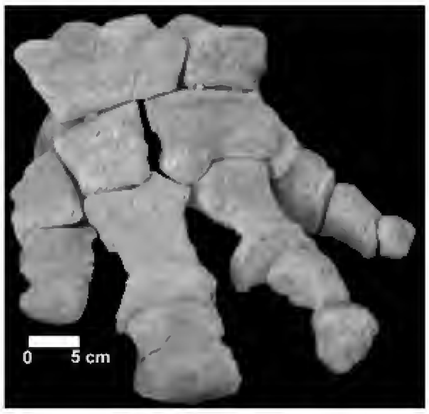

Fig. 13 – *Stegomastodon platensis* – manus.

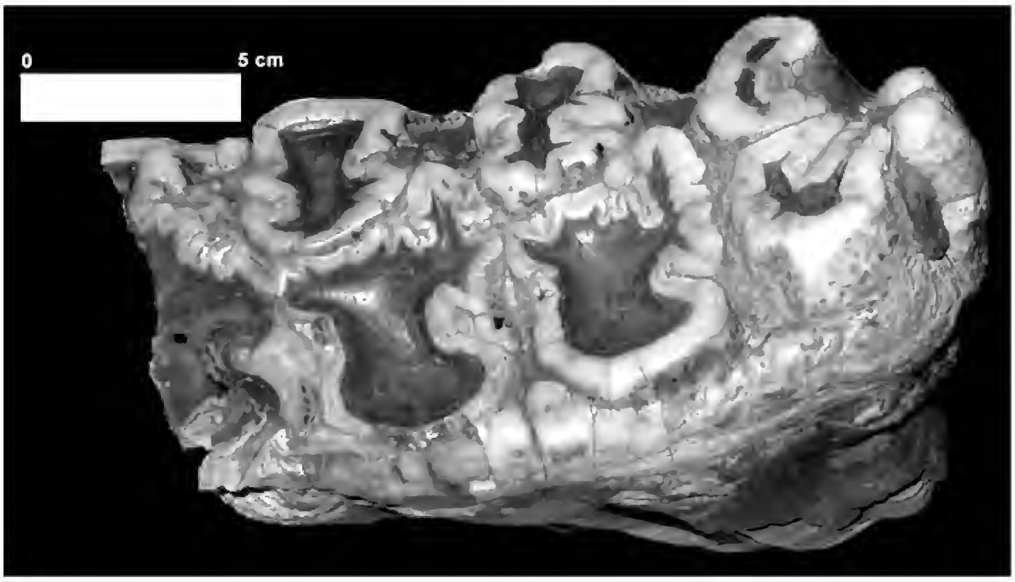

Fig. 14 - *Stegomastodon platensis* – molar tooth.

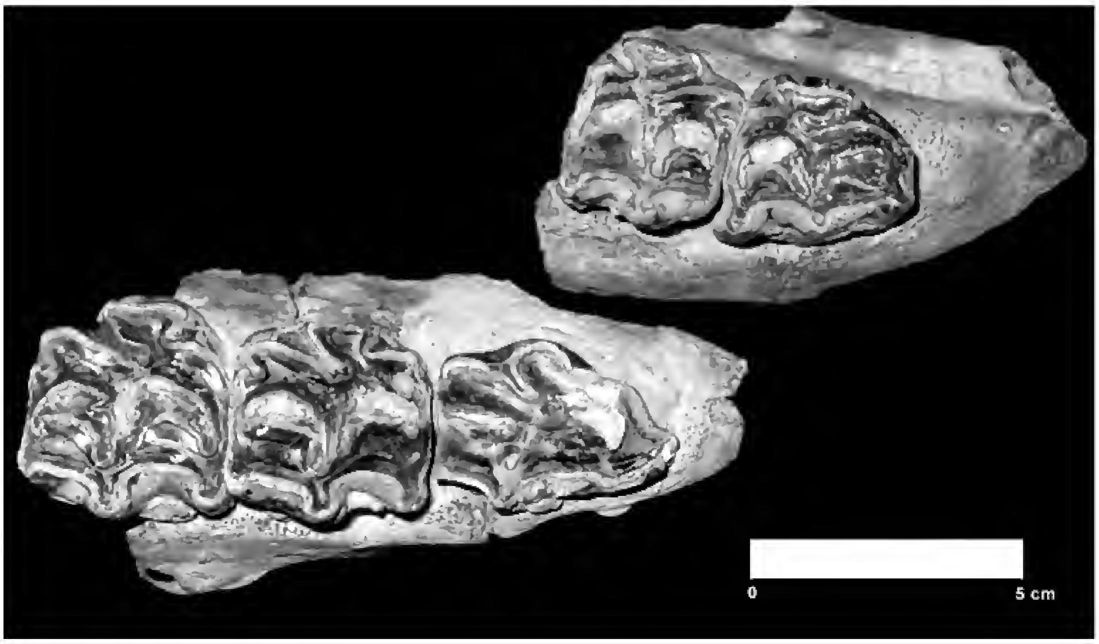

Fig. 15 – *Equus (Amerhippus) neogeus* - teeth.

Stratigraphic and geographic distribution – The gender is registered in the Pleistocene of Ecuador, Peru, Paraguay, and Uruguay, whereas in Argentina it is distributed in Córdoba, Santa Fe, Chaco, and Entre Ríos Provinces. It is frequent in the deposits of Buenos Aires Province; this species has been quoted for the Lujanense Mammalian Unit of the Late Pleistocene, in the following local faunas: Paso Otero, Luján, and Quequén-Indio Rico (SCILLATO-YANÉ *et al.* 1995; ALBERDI *et al.* 1989).

Habitat – This species is characteristic of open and sub-arboreous biomes of mild climates, and their nourishment probably consisted of high pastures, shrubs and arboreous vegetation (BOMBIN, 1976; DESCHAMPS & TONNI, 1992; SCILLATO-YANÉ *et al.* 1995).

Comments – In order to help with the identification, the remains of San Luis were compared to the complete skeleton that is exhibited in the hall VII of the Museo de La Plata (MLP 3-401). The species assigned to the subfamily Scelidotheriinae are of medium to large size but they are still smaller than the ones belonging to the family Mylodontidae. Among the diagnostic characters of this group we can mention the presence of the humerus with entepicondyloid hole, the calcaneus with a diagonal crest on its inferior-external face, the astragalus with internal odontoid condyle and with a very hollow articular surface for the cuboid (CATTOI, 1966). *Scelidotherium* is a middle-sized form similar to *Scelidodon* in its general structure but it has a considerable smaller size and in general it is more slender. The skull of this species is stretched, narrow, and low.

Pasos Malos (Merlo) – MHN-UNSL-V 199.

Villa Larca – MHN-UNSL-V 372, 373 y 374.

Valle de Pancarta – MHN-UNSL-V 200 to MHN-UNSL-V 211.

Family MEGATHERIIDAE Owen, 1843
Subfamily MIEGATHERIINAE Owen, 1842
Genus *Megatherium* Cuvier, 1796
Megatherium americanum Cuvier, 1796

Localities and descriptive aspects – Arroyo Barranquita, Río Quinto, Paso del Rey, Laguna Los Pocitos, and Laguna Sayape. The Arroyo Barranquita provided two isolated teeth of the right hemi-jaw (m_1 and m_4); an almost complete left radius without the distal end; a left cubitus without the distal end and with a detached proximal end; diaphysis of a right humerus with a fragment of a detached proximal end; a left humerus with both epiphysis detached; an atlas and two fragments of thoracic vertebrae; a fragment of scapula; a fragment of collarbone and fragments of ribs. PRADO *et al.* (1998) quoted the finding of a femur of *Megatherium* on the ravine of Río Quinto (Fraga). Plentiful and very fractured remains belonging to the maxillary and molars tentatively assigned to this order were gathered in the Planicie Austral (Laguna Sayape and Laguna Los Pocitos) as well as the anterior mandibular and in the high pampas of Paso del Rey.

Stratigraphic and geographic distribution – Late Pleistocene of Argentina (TONNI *et al.*, 1985; FIDALGO *et al.*, 1986; BARGO *et al.*, 1986; PRADO *et al.*, 1987; POLITIS & PRADO, 1990). It was also cited for the Pleistocene of Chile (CASAMIQUELA, 1969), Brazil (PAULA COUTO, 1970), Bolivia (ORTEGA HINOJOSA, 1970), and Peru (HOFFSTETTER, 1970). The last record near Cuzco is the northern and of higher altitude for the species and the genus.

Habitat – This species is associated to open biomes of mild climate, arboreous vegetation that was probably its main source of food together with tall pastures and shrubs.

Arroyo Barranquita – MHN-UNSL-V 212 to MHN-UNSL-V 220 and MHN-UNSL-V 511.

Comments – The material under study corresponds to a sub-adult individual that is smaller than the Pampean specimens with which it was compared (MLP 27-VII-1-1) and the sutures of the zone of growth can still be observed in the epiphyseal region of the long bones. The bones were *in situ* but without signs of being articulated. In most of them it can be verified that the opposite face on which they lied has been affected by meteors presenting deep fissures that vary from one osseous element to the other. On the other hand, an interesting fact is the observation of the signs of an incipient deforming arthritis in the atlas. These signs seem to have been frequent in several forms of pleistocenic mega-mammals especially in the terminal forms. This kind of pathology is extremely rare because it is usually produced by recessive alleles. Nevertheless, an alteration of this nature can become prevailing and can contribute to the extinction of these forms under conditions of nutritional stress especially in reduced populations. These kinds of alterations (petrifying osteomyelitis, periostitis, and myositis in the long bones, deforming and ankylotic spondylitis in the vertebrae and general rickets) have been cited as possible causes of extinction for some species in the Northern Hemisphere (MELÉNDEZ, 1970:106).

Order PROBOSCIDEA Illiger, 1811
Family Gomphotheriidae Cabrera, 1922
Genus *Stegomastodon* Pohlig, 1912
Stegomastodon platensis (Ameghino, 1888)

Localities and descriptive aspects – Río Conlara and Río Quinto. A complete and articulated anterior right limb, a right scapula, an atlas, cervical and dorsal vertebrae, and a molar were found in Punta del Agua (Río Conlara, Santa Rosa). Two molars with much eroded crowns were found in the ravines of Río Quinto (Fraga). Molars of anterior section or fractured trigon supposedly pentalophodont with an advanced state of erosion; relatively simple clovers provided with a few accessory conules, which are well identified only on the ends of transversal valleys and more globate in the pre-trite. The lingual and oral walls with normal inclination present the characteristic wrinkled and striated enamel along the base of the crown. The transversal valleys are narrow and it can be identified a thin cover of cementum in an even way but it is absent in the middle sulcus because of the close contact between the main conules of the post-trite and pre-trite. It is highlighted that the width of the valleys in the pre-trite section is several times smaller than the one corresponding to the post-trite that is subquadrangulary-shaped. In the occlusal area the post-trite conules present a relatively greater height than in the pre-trite; this situation is not preserved in the last lobe where the three accessory posterior conules also show a little erosion.

Stratigraphic and geographic distribution – This species is characteristic of the Middle and Late Pleistocene of Argentina especially in the Pampean Region. It is also found in Uruguay, Brazil, and Paraguay (ALBERDI & PRADO, 1995). This species is frequent in the Ensenadense deposits not surpassing the parallel 37° in the Pampean region in Buenos Aires Province. It is slightly frequent in the Lujanense deposits where colder and drier environmental conditions prevail. In Argentina it has been identified in Buenos Aires, Córdoba, Santa Fe, Entre Ríos, Corrientes, and Chaco Provinces (ZURITA *et al.*, 2004).

Habitat – It is adapted to a mild-warm climate predominantly with pastures or savannah.

Punta del Agua (Santa Rosa) – MHN-UNSL-V 221, 222, 223, 224, 225, 226, 376 and 510.

Fraga (Río Quinto) – MHN-UNSL-V 377 and 378.
Comments – The foundations of this species are well laid, especially on the basis of cranial characteristics and the morphology of the defenses (PAULA COUTO, 1979). Although we do not count with these characteristics, the proportions of the humerus, the cubitus, and the radius coincide with the rank of variability of the species (maximum length of the cubitus: 64cm). Nevertheless, the remains are assigned to *Stegomastodon platensis*, considering the complicated character of M^3/M_3 for the disposition of cusps accessory, partners to choerodonty and ptychoconty, with the rifling of the enamel and the coverage of the cement in the valleys as out-standing characters (TOBIEN, 1973).

Order PERISSODACTYLA Owen, 1848
Family Equidae Gray, 1821
Genus *Equus* Linnaeus, 1758
Sub-Genus *Equus (Amerhippus)* Hoffstetter, 1950
Equus (Amerhippus) neogeus Lund, 1840

Localities and descriptive aspects – Arroyo Barranquita, Pasos Malos, and Río Rosario. A proximal fragment of scapula was found in Arroyo Barranquita and M^{1-2} in Pasos Malos. In Río Rosario it was found: the identified molars correspond to the lower dentition, five to the right (P_2-P_3-P_4-M_1-M_2), and three to the left (P_4-M_1-M_3); they are moderately eroded but some diagnostic characteristics of *E.* (*A.*) *neogeus* can be clearly identified. The characteristics previously mentioned are the following: the edge of the rounded metaconid and the angular metastyle; the "*ectofléxido*" without contact with the "*linguafléxido*" and varying from penetrative with respect to the "*isthmus*" and an end slightly rounded to a very shallow one with a sharp end; in general the "*linguafléxido*" is open and V-shaped; the "*prefléxidos*" are asymmetrical, and the "*pósfléxidos*" with the anterior horn with variable forms and the posterior horn slightly rounded.

Stratigraphic and geographic distribution – Late Pleistocene of the south of Brazil, in the caves of Lagoa Santa corresponding to *Equus neogeus* Lund, 1840 and *Equus principales* Lund, 1846, and the Pampean Region in Argentina (ALBERDI & PRADO, 1992). In this last region, *Equus* (*Amerhippus*) *neogeus* (=*E.* (*A.*) *curvidens*) is registered in the Lujanense sediments in the cities of Río Luján, Quequén Salado, Paso Otero, Arroyo Camet, Tapalqué, Lobería, and Arroyo Seco among others (AMEGHINO, 1889; TONNI, 1985; TONNI *et al.*, 1985; PRADO *et al.* 1987, ALBERDI *et al.*, 1989). It is considered a leader fossil of Guerrero Member of the Late Pleistocene of the Luján Formation (ALBERDI & PRADO, 2004).

Habitat – *E.* (*A.*) *neogeus* is associated to open areas of xerophilous pastures in Argentina and Brazil.

Pasos Malos (Merlo) – MHN-UNSL-V 227.

Arroyo Barranquita – MHN-UNSL-V 228, 468 and 469.

Río Rosario – MHN-UNSL-V 469.

Comments – It is here referred to *E.* (*A.*) *neogeus* even when the material analyzed is scarcely diagnostic at a specific level, especially because the material is fragmentary, although it coincides with the proportions of the specimens coming from the Pampean Region.

PALEOENVIRONMENT AND STRATIGRAPHIC RELATIONS

The present-day environment of San Luis Province is characterized by presenting different physiographic units and climates. The center and northeast of the province, the most southern spurs of the Geological Province Sierras Pampeanas, is occupied by the western edge of the Sierra de Comechingones and the Sierra de San Luis with an inter-highland region known as the Depresión de Conlara. In this area the climate presents characteristics as those of a "mild Pampean"; this links it to Córdoba, Santa Fe, and Buenos Aires Provinces.

The northwest and southern regions are depressions with dry weather. The former presents a set of small hill countries that belongs to the "dry of sierras" type. This links it to the north of Mendoza, San Juan, La Rioja, and the south of Catamarca. Otherwise, in the latter – a sandy plain –, the weather is "dry of steppe" with conditions similar to the south of Mendoza, Neuquén, the center and the west of La Pampa, and Río Negro. Such conditions, probably with limits similar to the present-day ones, prevail during the Late Pleistocene and Early Holocene, what were affected to a bigger or smaller scale by the global weather changes, especially the Late Maximum Glacial Ice. The arguments of this hypothesis are the distribution and frequency of the fossil remains and the characteristics of the sedimentary successions especially if we consider the bearing levels of the interval under study in which sediments are assigned to deposits of different paleoenvironments such as aeolian, alluvial, fluvial-lacustrine, and in all of them the development of paleoedaphic horizons.

During the Late Pleistocene there prevailed conditions of wide environmental heterogeneity and a dry-semidry character probably linked to the pleniglacial (very dry and very cold) with winter temperatures biologically non-usable and below the present-day ones (below 10°C) (TONNI *et al.*, 1985; PRADO *et al.*, 1987; ALBERDI *et al.*, 1989).

Consequent with these weather conditions it is proposed a faunistic association planting open areas with pastures and steppes where the seasonal rains allowed the development of temporary, shallow body waters with low energy and high evaporation making evident the presence of Ostracoda (DESCHAMPS & TONNI, 1992). To this effect, the Late Pleistocene bird fauna of Patagonian affinity suggests an steppe and shrub-like vegetation in the south of Buenos Aires Province (TONNI & LAZA, 1980).

Such conditions prevailed from the middle Pleistocene to a certain point of the Holocene (TONNI, 1985) in which they alternate with phases of higher humidity characterized by the presence of paleosoils (TONNI *et al.*, 1988). The fragmentary character and the unarticulated bone remains (except the Sclerocalyptinae) generally on the base of the present-day fluvial courses and small tracks excavated by water generated in the loessoid plains of San Luis restrict us the access to more important information from the morphological and consequently paleoecological points of view. Nevertheless, the important association collected up to the present allows us to move forward in the paleoenvironmental characterization and linking with other bordering areas.

From the stratigraphic units assigned to the Late Quaternary of Buenos Aires Province, those characteristics gathered by Luján Formation (Guerrero Member and Río Salado Member) and La Postrera Formation, as well as the edaphic horizons Puesto Callejón Viejo and Puesto Berrondo, show strong similarities with the outcropping successions in San Luis Province. In the event of the actual contribution annotated to the Late Pleistocene, the Guerrero Member and the overlying paleosoil Puesto Callejón Viejo are tied to Barranquita Formation and the paleosoil Los Toldos.

Such relation can be regionally extended to consider the deposits of La Invernada Formation and the paleosoil Las Tapias (Cantú, 1992) in the plain of Río Cuarto (Córdoba) and the sediments assigned to La Estacada Formation and the paleosoil of the Holocene (Zárate, 2002) in the region of Tunuyán (Mendoza).

One of the problems about the current knowledge of the Quaternary in San Luis is the lack of association of the microflora and microfauna studies that would contribute to improve the interpretation about the paleoclimatic and paleoenvironmental history of the main depositional areas of the region.

To this effect, it is only available information about diatoms of a profile in the fluvial-lake environment of Salinas del Bebedero (Maidana, 1994), ravines of Río Desaguadero (Strasser *et al.*, 2000), and ravines of Río Conlara (Cappannini, 1955; Chiesa *et al.*, 1997). Likewise the only studies about pollinic evidences correspond to González *et al.* (1998) and Rojo (2003), referred to perforations in the depositional center of Salinas del Bebedero.

CONCLUSIONS

The faunistic association described is referred to the Lujanense Mammalian Age assigning the deposit of the sediments to the temporal interval Late Pleistocene-Early Holocene. The presence of *E.* (*A.*) *neogeus* and the dates of absolute dating (^{14}carbon) available for the region enclose it between ca. 22 and 8 ka. B.P.

Considering the habitat proposed for the most subjects of the faunistic set in the Pampean and Chaco region and the Aeolian (loess) character prevailing in the depositational paleoenvironmental of the bearing sediments, it can be inferred semidry paleoclimatic conditions for the region. The shortage of fossil remains in the southern and western zone is associated to a very poor availability of resources linked to a climatic situation of extreme dryness for this paleofauna characterized by sand deposits and negative hydric balances.

At the same time, in the central and northeastern zone, occupied by the sierras of San Luis and Comechingones and the inter-highland unity to them, the Depresión del Río Conlara, the paleoecological situation has been relatively different especially considering the water resource coming from the above-mentioned elevations. Likewise, the presence of an edaphic horizon also suggests some climatic stability optimum for the development of vegetation and favorable for the presence of these megaherbivora. The findings mainly come from ravines produced by the fluvial erosion of the last millennium in the area of influence of the piedmont of the highlands and linked to the basins of the rivers Quinto and Conlara; the loessoid plain developed on the east of the latter bed constitutes the area most potentially important to be explored considering the last findings of shells of *Sclerocalyptus ornatus*. A particular situation corresponds to the environment of the “high pampas” on the basement of Sierra de San Luis; there the presence of fossil remains is linked to loessoid deposits. An important development of the paleosoil, the weather conditions and especially the availability of hydric resources in such areas generated optimum paleoenvironmental conditions documented by the appearance of isolated and fragmentary remains, except the *Scelidotherium leptocephalum* of Valle de Pancanta.

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A CONCISE HISTORY OF MEXICAN PALEOMAMMALOGY [1]

(With 6 figures)

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ABSTRACT: A brief historical account is given about the development of Mexican paleontological research. Although some knowledge existed from Prehispanic cultures, the main development occurs in three periods: colonial, 19th century, and Recent in accordance with the geographic boundaries for exploration. Also, the birth of academic paleontology is shown through scientific publications and the type specimens described at the end of the 19th and early 20th centuries.

Key words: Paleontology. Vertebrates. Mammals. Mexico. History of Biology.

RESUMEN: Una breve historia de la paleontología de mamíferos de México.

En este trabajo se hace una breve recapitulación cronológica acerca de los orígenes de la investigación paleontológica en mamíferos de México. Se muestran algunos conocimientos de las culturas prehispánicas, pero de manera principal el conocimiento obtenido en tres períodos: el colonial, el decimonónico y el actual, observado mediante el alcance geográfico de la exploración. Se muestra también el surgimiento de la paleontología profesional mediante la cantidad de publicaciones y los tipos descritos entre fines del siglo XIX y principios del XX.

Palabras Clave: Paleontología. Vertebrados. Mamíferos. México. Historia de la biología.

INTRODUCTION

Currently, paleontology is an important scientific discipline focused on understanding a series of biological processes, among which are geographic distribution, taxonomic characters determination, and primarily the establishing of evolutionary relationships of organisms. All of those topics have produced deep discussion between specialists. Bowler (1996) has synthesized the most important controversies. However, little analysis of the development of this scientific field in most geographic regions has been undertaken. For Latin America, some efforts have occurred in Brazil and Argentina (Lopes, 2000; Podorgny, 2005). For Mexico, historical research in the development of paleomammalogy is warranted as an explicative tool for the present state of the art. Nevertheless, it has been considered only in passing in a few papers (Miller & Carranza-Castañeda, 1984; Castillo-Cerón *et al.*, 1997), or as general accounts that can be used as a reference framework (Montellano-Ballesteros, 1999; Corona-M., 2002a; González & García, 2002; Gío Argáez, 2004; Carreño & Montellano-Ballesteros, 2005).

MATERIAL AND METHODS

In order to contribute to the historical analysis of the development of mammal paleontology in Mexico, a chronological perspective is proposed, highlighting the main outcomes at each stage and how those support, increase, and enhance the field development. The study uses information collected in regard to the main novohispanic chronicles produced between the 16th and 18th centuries by army personnel, priests, settlers, and scientists, noting geographic data and, if possible, the tentative identification of the specimen. Additionally, a synthesis of the literature has been produced for the mid-19th century to the first two decades of the 20th century (Corona-M., 2002a, b). Those data are the source of maps and graphic.

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RESULTS AND DISCUSSION

FROM PREHISPANIC TO COLONIAL STAGES

Many examples abound in Mexico of knowledge concerning rocks and minerals among the prehispanic native groups. Fossils were only known as ornaments by the Olmecs and the Maya, although other uses may have occurred (GONZÁLEZ & GARCÍA, 2002).

In accordance with the main novohispanic chronicles (*e.g.*, Francisco Hernández [HERNÁNDEZ, 1959] and Fray Bernardino de Sahagún [SAHAGÚN, 1989]), the ancient Mexicans believed that the fossil bones of megafauna were remains of giants named *quinametzin*, antique people that inhabited the Earth. From those remains, native belief was that the grinded bone had medical properties (SAHAGÚN, 1989).

The conquers, priests, and scientists that visited New Spain found these activities a point of meeting with the components of their own naturalist research. Researchers fed both on the native legends and European myths as well as on the knowledge from Aristoteles and Plinius. They explained the fossil remains of big vertebrates as giants that lived before the biblical flood, an explanation now known as the giant hypothesis of mankind (PELAYO, 1996).

With the conquers, a country-wide monitoring is started with the main focus on the findings of precious metals and natural resources to exploit, as it can be found in the writings of Hernán Cortés, Francisco Hernández, Fray Bernardino de Sahagún, Bernal Díaz del Castillo, Jerónimo de Mendieta, José Torrubia, Antonio Pineda, and Antonio de Herrera, among others (CORONA-M., 2002b). During the overall process, animal remains were reported as large bones but without further analysis. From this period, animal fossils were known from eight country states and were characterized as a very large fauna (megafauna) (Fig.1).

Fig.1- Map showing the current political division of Mexico and the localities of mammal fossil in Colonial Mexico (based on data from CORONA, 2002a).

The states of Campeche and Querétaro are outstanding because currently few megafaunal records exist, since less than 10 localities for each are known for the Quaternary (Arroyo-Cabrales *et al.*, 2002). Those from the chronicles may be the oldest ones known. Also for this first period, only written documentation of the fossils exists, since the specimens were lost for a variety of reasons (*e.g.*, they were not completely fossilized; they were not preserved; or collectors did not care enough for them).

A second period started when the Spanish crown, in order to improve the mining of the country's natural resources that had turn into a very dynamic economic area, funded in 1792 the *Real Seminario de Minería* in Mexico City. This institution supported scientific development, trained specialists in mining, and developed the mining industry, while also encouraging exchange of knowledge between Europe and the Americas (Argueta Villamar, 2003; Flores Clair, 1999). This institution had outstanding personnel, like Fausto de Elhuyar, who discovered tungstene and was the Head of the Seminar. His stature and the influence of the well-known mineralogist Abraham Werner, who was the founder of the Neptunist school, helped the institution to be acknowledged in the European schools (Laudan, 1987).

This institution's role was most important in two areas within the scientific community, that of enhancement of a library and the edition of books. For the first issue, the institution had a policy to purchase the recent specialized scientific books, including personal libraries, like those from Joaquín Velásquez de León and Juan Eugenio Santelices, and several of the recent European editions. The library held over 3,000 volumes, most of them focused on basic and assaying sciences. The second issue was accomplished by publication policies that supported the edition of books by its own scientists, like that by Andrés del Río who, based on the notes for a mineralogy course, prepared a draft of the well-known book *Elementos de Orictognosia* (Flores Clair, 2001). This book was one of the first in the Americas to be published on this field of science, and also a discussion departure point for Neptunist theory, current at the time (Fig.2).

ELEMENTOS

DE

CTOGNOSIA,

CONOCIMIENTO DE LOS FOSILES,

SEGUN EL SISTEMA DE BERCELIO,

PRINCIPIOS DE ABRAHAM GÖTTLOB WERNER

SINONIMIA

SEMINARIO NACIONAL DE MINERIA

ANDRES DEL RIO,

PARTE PRÁCTICA—SEGUNDA EDICION.

FILADELFIA.

Fig.2- Cover of the book from Andrés del Río, and a picture of the *Colegio de Minería* made in 1864 by Casimiro Castro (both images taken from <www.palaciominería.unam.mx>).

The last decade of the 18th century was also outstanding for the advertisement of the sciences by other means, like the establishment of the first Cabinet of Natural History, due to the activity of the surgeon and naturalist José Longinos Martínez Garrido. Without any official support, José Longinos was able to create a place to exhibit natural resources with the aim to reach a similar fame as the Madrid Cabinet. Specimens were provided from the Botanical Expedition by Miguel Sessé, as well as from amateur naturalists.

The Cabinet had a small library focused on natural history and other important sciences for the period, like physics, chemistry, mathematics, and medicine, as well as anatomy replicas and research equipment. The specimens were arranged as a systematic collection based on the *Systema Naturae* from Linnaeus, and had samples of minerals, plants, and animals (Maldonado Polo, 1999; Lozoya, 1984). Among those materials there were 17 proboscidean bones. Their importance was in denying the presence of giant humans, and in showing a modern characterization of fossils as organic beings. This exhibit was one of the first denials for the giantology theory presented at the time among the Spaniard naturalists and chronicles. This new tendency was also found in the notes of other vertebrate fossils finders, like those by Antonio Pineda and José Torrubia (Maldonado Polo, 1999; Corona-M., 2002a).

New items were brought to the public by the *Gaceta de México*, established in the mid-18th century. It was one of the first weekly journals and had regular space for scientific discoveries. It can be cited among these new items the opening of the Cabinet of Natural History that was noted due to the discoveries of several fossil vertebrates in the period from 1790 to 1799 and the first formal publications on fossil vertebrates for Mexico (Miller & Carranza-Castañeda, 1984; Montellano-Ballesteros, 1999; Corona-M., 2002a). They also demonstrated that naturalist endeavours were to create local academic institutions.

Beginning of Modern Paleontology

Changes were brought about by the Independence from the Spanish Crown in 1821, and by the visit to the country and publications on America's nature of Alejandro de Humboldt. Great interest now prevailed to survey the country lands that previously were forbidden. That interest brought into the country a large group of foreign geographers and naturalists for research all over Mexico (Maldonado-Koerdell, 1952).

In 1825, the first national museum in Mexico was founded. It was more formal than practical due to the deep economical and political crises at the time. Such issues also affected other academic institutions, like the *Real Seminario de Minas*, that was extinguished and turned, first, into the *Colegio de Minería*, and later split into several small educational institutions that could not maintain the academic research endeavours (Gortari, 1980; Trabulse, 1983). Paleontological research was supported primarily by individual efforts. The museum (Museo Nacional) re-opened, however, between 1866 and 1867 and started a systematic increase of collections.

The analysis of the scientific publication record, including literature focused on fossil mammals and in the naming of new biological types furnished an overview of the development on the field at the time (Fig.3).

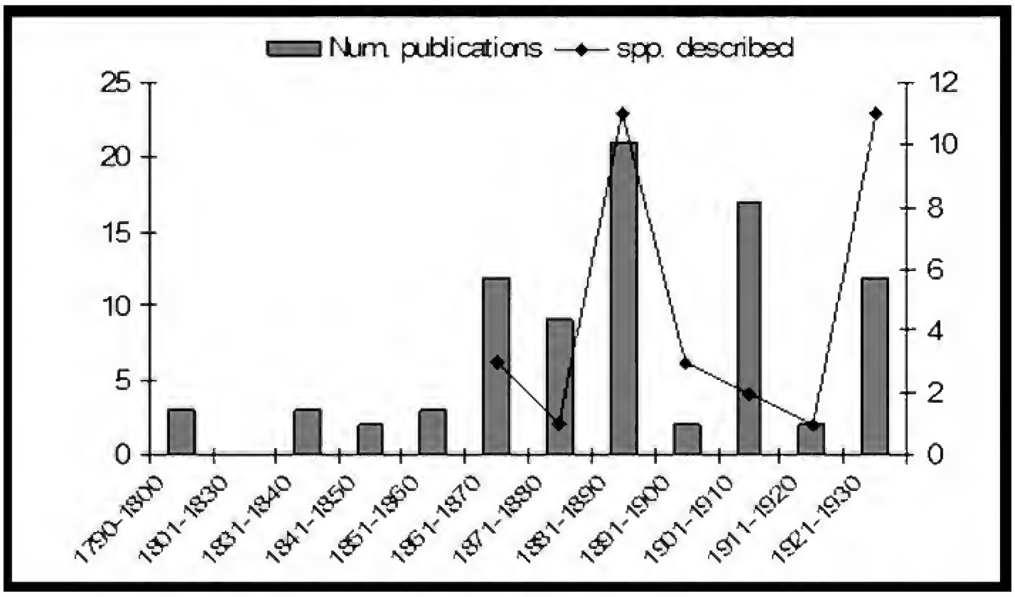


Fig.3- Double graph showing the mammal paleontological production from 1790 to 1930. The bars indicate number of publications, and line show the number of mammal-types described. More details in text.

Between 1838 and 1840, studies on mammoths and mastodonts by the well-recognized German scientists Christian Ehrenberg Ignaz von Olfers (CORONA-M., 2002a), and Herbert von Meyer (MEYER, 1840), were published. It was von Meyer who conducted the most important systematic research on Mexican paleontological materials at the time.

In the middle of the 19th century, a group of Mexican researchers started systematic studies of fossil mammals collected in the country. This endeavour was supported by the foundation of the *Sociedad Mexicana de Historia Natural*, constituted by most of the naturalists working at the Museo Nacional, and who established strong ties to the main American and European museums.

From 1860 to 1930, a systematic increment occurred in the scientific documentation in mammal paleontology. Three main issues were related to that: the visit and collaboration of foreign scientists; the opening of the first institutions focused on natural history studies; and the foundation of scientific societies. In the first issue, outstanding scientists were the Americans Joseph Leidy and Edward D. Cope, as well as the German naturalists, such as Roemer, Pohlig, Herbert von Meyer and Freudenberg. Most of them collaborated with local scientists, such as Antonio del Castillo, Mariano Bárcena, and Alfredo Dugès. Other important contributions came between 1901 and 1910 due to the research of other prominent American scientists, such as Henry F. Osborn as well as Gidley, Merriam, and Eaton.

Important publications for the period were: the synthesis on the discoveries in the Mexico Basin by Antonio del Castillo (CASTILLO, 1869); the *Catálogo de Fósiles del Museo Nacional* (VILLADA, 1897); and the outstanding report by FELIX & LENK (1889-1899), containing the findings on geology, volcanism, and fossils in the Mexico Basin, Oaxaca, Puebla, and the State of Mexico. Among the first documents written in Spanish, besides Villada's catalog, it can be cited: the publication by CUATÁPARO & RAMÍREZ (1875) describing a new species of *Glyptodon* from the Mexico Basin; and those by DUGÈS (1882, 1891), who recorded the fossil vertebrates from Guanajuato, and in particular described an extinct javelina (*Platygonus alemanii*), as well as other fossil remains associated with South America (Tab.1).

The foundation of important institutions for paleontological research occurred during this period. They were, as cited before, the *Museo Nacional* (1825) and the *Sociedad Mexicana de Historia Natural* (1868), including its official outlet *La Naturaleza*; and the *Sociedad Científica "Manuel Alzate"* (1884), later becoming the *Academia Nacional de Ciencias*.

Geographic coverage of the studies encompassed 14 states (Fig.4). The most important locality was at Tequixquiac, State of Mexico and nearby Mexico City. This locality was found, as was the case for several other localities at the time, during enhancement and increase of the sewer system of Mexico City. This excavation allowed the investigation into the sediments from one of the paleolakes from the Mexico Basin and procurement of a large number of specimens that enhanced the Mexican scientific collections. Camels, horses, proboscideans, glyptodonts, felines, bears, and ground sloths were among the studied fauna. Some of those taxa were quite similar to those discovered in North American sites at the end of the Pleistocene.

One of the discoveries that brought a wide interest by naturalists, and could be considered as the origin of both prehistory studies as well as archaeozoological studies in Mexico, is the bone known as "*sacro de Tequixquiac*" and its study. A camel sacrum, the bone is worked as representing an animal head. It is the first evidence of animal use by early people in the Mexico Basin. Although a recent view of the sacrum points to the evidence of a late work on the bone rather than while it was still fresh (O.J.Polaco, pers. comm., 2002), the bone has a historical importance for setting new trails for Mexican archaeological and paleontological studies (CORONA-M., 2002a).

CURRENT STAGE

During most of the 20th century, several foreign expeditions occurred, mainly by American professionals. One of the most important for the Pleistocene reconstruction was the search conducted in the 1940s by Chester Stock and personnel of the California Institute of Technology in San Josecito Cave, Nuevo León (ARROYO-CABRALES & JOHNSON, 1998; STOCK, 1943). Also in that decade, a synthetic study on the Quaternary Mexican mammals by MALDONADO-KOERDELL (1948) was published (Fig.5).

TABLE 1. Types described with Mexican specimens from the middle of 19th Century to early 20th Century.

Order	Taxon	Author	Locality	State	Relative age
Perissodactyla	*Equus conversidens*	Owen, 1869	Villa de Guadalupe	D.F.	Pleistocene
Artiodactyla	*Palauchenia magna*	Del Castillo, 1869	Tacubaya	D.F.	Pleistocene
Perissodactyla	*Equus tau*	Owen, 1869	Valle de México	Mexico	Pleistocene
Edentata	*Glyptodon mexicanus*	Cuatáparo & Ramírez, 1875	Tequixquiac	Mexico	Pleistocene
Edentata	*Scelidotherium guanajuatense*	Dugés, 1882	Rancho de Arperos	Guanajuato	Pliocene?
Perissodactyla	*Hippotherium montezuma*	Leidy, 1882	Tehuichila	Hidalgo	Pliocene?
Proboscidea	*Dibelodon tropicus*	Cope, 1884	Tequixquiac	Mexico	Pleistocene
Perissodactyla	*Equus barcenoi*	Cope, 1884	Tequixquiac	Mexico	Pleistocene
Perissodactyla	*Equus crenidens*	Cope, 1884	Tequixquiac	Mexico	Pleistocene
Artiodactyla	*Eschatius conidens*	Cope, 1884	Tequixquiac	Mexico	Pleistocene
Artiodactyla	*Eschatius longirostris*	Cope, 1884	Tequixquiac	Mexico	Pleistocene
Artiodactyla	*Holomeniscus vitakerianus*	Cope, 1884	Tequixquiac	Mexico	Pleistocene
Perissodactyla	*Hippotherium peninsulatum*	Cope, 1886a	Tehuichila	Hidalgo	Pliocene?
Perissodactyla	*Hippotherium rectidens*	Cope, 1886b	Tehuichila	Hidalgo	Pliocene?
Perissodactyla	*Protohippus castilli*	Cope, 1886a	Tehuichila	Hidalgo	Pliocene?
Artiodactyla	*Platygonus alemani*	Dugés, 1891	Moroleón?	Guanajuato	Quaternary
Proboscidea	*Mastodon oligobunis*	Cope, 1893	Tequixquiac	Mexico	Pleistocene
Edentata	*Glytodon nathorsti*	Felix & Nathorst, 1893	Valle de Ejutla	Oaxaca	Pliocene?
Carnivora	*Felis hyaenoides*	Freudenberg, 1910	Tequixquiac	Mexico	Pleistocene
Carnivora	*Hyaenognathus* (*Porthocyon*) *mathewi*	Freudenberg, 1910	Tequixquiac	Mexico	Pleistocene
Edentata	*Brachyostracon cylindricus*	Brown, 1912	Ameca	Jalisco	Pleistocene
Edentata	*Nothotherium mexicanum*	Freudenberg, 1921	Tequixquiac	Mexico	Pleistocene
Proboscidea	*Rhynchotherium tlascalae*	Osborn, 1921	nd	Tlaxacla	Pliocene?
Proboscidea	*Mastodon oligobunis* var. *antiquissima*	Freudenberg, 1922	Valle de Amajac	Hidalgo	Pliocene?
Proboscidea	*Elephas columbi* var. *falconeri*	Freudenberg, 1922	Tequixquiac	Mexico	Pleistocene
Proboscidea	*Mastodon oligobunis* var. *intermedia*	Freudenberg, 1922	Valle de México	Mexico	Pliocene
Perissodactyla	*Teloceras* (*Aphelops*) *felici*	Freudenberg, 1922	Tequixquiac	Mexico	Pleistocene
Proboscidea	*Elephas columbi* var. *felicis*	Freudenberg, 1922	Ejutla	Oaxaca	Pleistocene
Proboscidea	*Elephas columbi* var. *silvestris*	Freudenberg, 1922	Ejutla	Oaxaca	Pleistocene
Proboscidea	*Mastodon oligobunis* var. *felicis*	Freudenberg, 1922	nd	Puebla	Pliocene
Proboscidea	*Mastodon oligobunis* var. *progressa*	Freudenberg, 1922	Cañada de Acultzingo	Puebla	Pliocene-Pleistocene
Artiodactyla	*Capromeryx mexicana*	Furlong, 1925	Tequixquiac	Mexico	Pleistocene

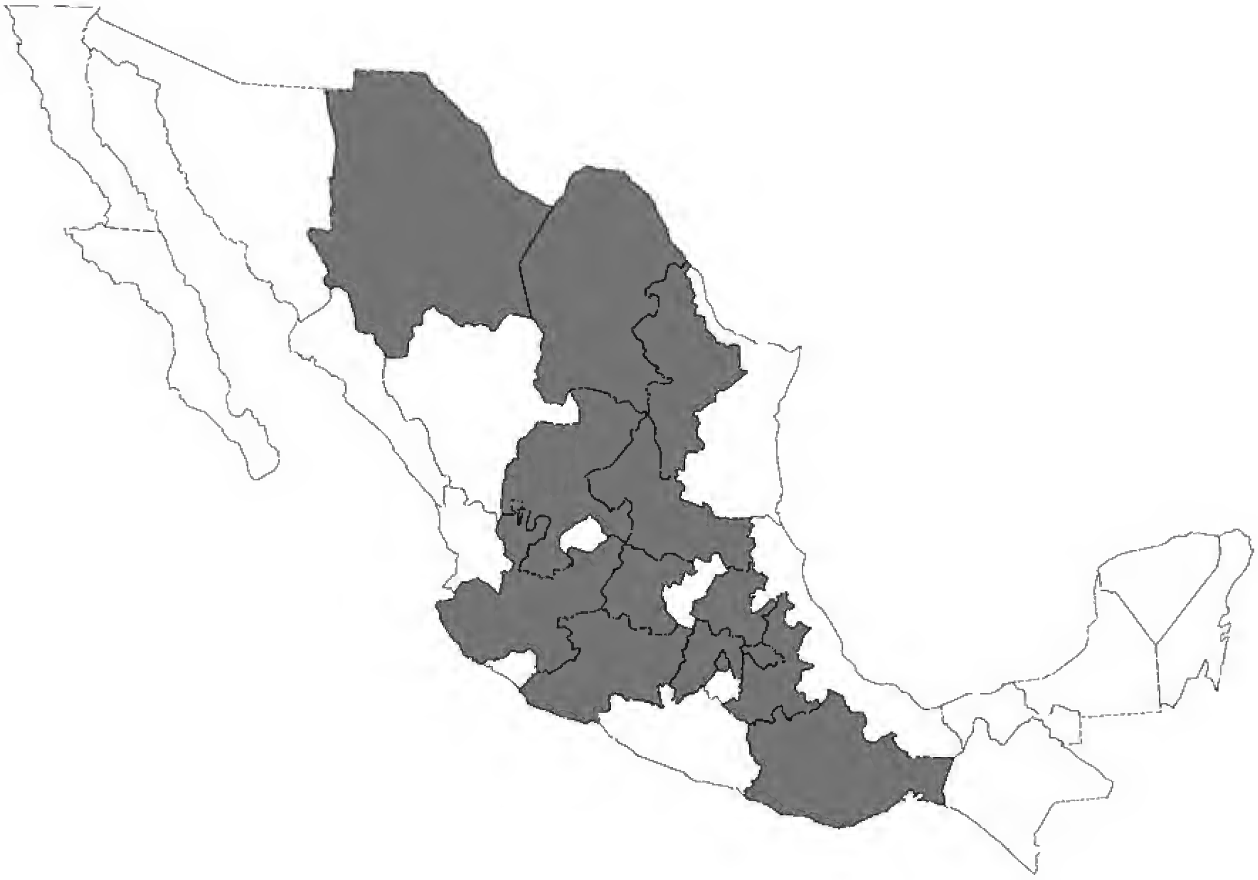


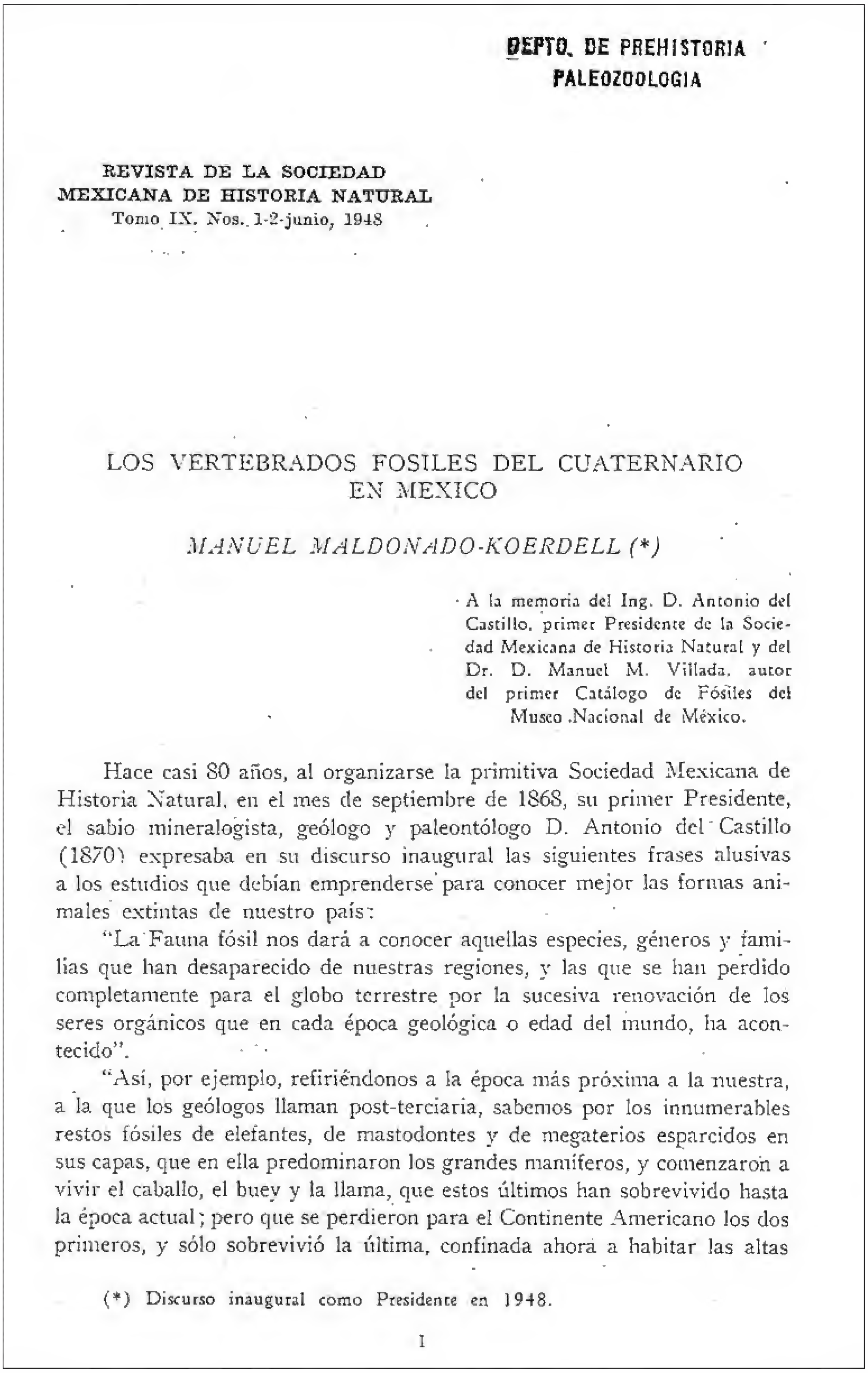
Fig.4- Map showing in the current political division of Mexico the findings of mammal fossil in the 19th century.

By the 1960s, courses on paleontology were started at the *Instituto Politécnico Nacional* (IPN) and the *Universidad Nacional Autónoma de México* (UNAM). Being the main teaching institutions, they also supported and provided an enhanced trained force for other institutions conducting field research. That cooperation is the case with the Geology Institute from UNAM, and the *Instituto Nacional de Antropología e Historia*, as well as departments from several state universities.

Several important publications were produced during the 1960s. Among these are the *Catálogo Paleomastozoológico Mexicano* by Álvarez (1965) and *Localidades de Vertebrados Fósiles en la República Mexicana* by Silva-Bárcenas (1969). The first correlations with US faunas were undertaken and rised the interest in the tempo and mode of the faunal exchange with South America, mainly by horses, gomphotheres, edentates, and camelids, and also focusing the interest in the man animal relationships by the early hunters-gatherers. Currently, for the Mexican Quaternary, localities are known all over Mexico, while Tertiary localities are known from 11 states and only three for the Mesozoic (Fig.6).

In the mid-1990s, a substantial change occurs in the diffusion of knowledge, with many papers appearing in peer-reviewed foreign journals. Furthermore, a broadening transpires on the researched topics, adding to the basic systematic studies. Contributions are included from other disciplines, like paleomagnetism and isotope theory. Also, a major emphasis is placed on integrative paleobiological studies that include evolutionary patterns and paleoenvironment reconstruction. This activity produces a continuous data updating the fossil mammals and localities, *i.e.*, the synthesis compiled by Montellano-Ballesteros & Arroyo-Cabrales (2002).

In this new 21st century, paleontology in Mexico is represented by a large number of researchers and institutions, including its professional society (*Sociedad Mexicana de Paleontología*, SOMEXPAL).



REVISTA DE LA SOCIEDAD
MEXICANA DE HISTORIA NATURAL
Tomo IX, Nos. 1-2-junio, 1948

LOS VERTEBRADOS FOSILES DEL CUATERNARIO EN MEXICO

MANUEL MALDONADO-KOERDELL (*)

A la memoria del Ing. D. Antonio del Castillo, primer Presidente de la Sociedad Mexicana de Historia Natural y del Dr. D. Manuel M. Villada, autor del primer Catálogo de Fósiles del Museo Nacional de México.

Hace casi 80 años, al organizarse la primitiva Sociedad Mexicana de Historia Natural, en el mes de septiembre de 1868, su primer Presidente, el sabio mineralogista, geólogo y paleontólogo D. Antonio del Castillo (1870) expresaba en su discurso inaugural las siguientes frases alusivas a los estudios que debían emprenderse para conocer mejor las formas animales extintas de nuestro país:

"La Fauna fósil nos dará a conocer aquellas especies, géneros y familias que han desaparecido de nuestras regiones, y las que se han perdido completamente para el globo terrestre por la sucesiva renovación de los seres orgánicos que en cada época geológica o edad del mundo, ha acontecido".

"Así, por ejemplo, refiriéndonos a la época más próxima a la nuestra, a la que los geólogos llaman post-terciaria, sabemos por los innumerables restos fósiles de elefantes, de mastodontes y de megaterios esparcidos en sus capas, que en ella predominaron los grandes mamíferos, y comenzaron a vivir el caballo, el buey y la llama, que estos últimos han sobrevivido hasta la época actual; pero que se perdieron para el Continente Americano los dos primeros, y sólo sobrevivió la última, confinada ahora a habitar las altas

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(*) Discurso inaugural como Presidente en 1948.

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Fig.5- Cover from one of the main publications of the current period.

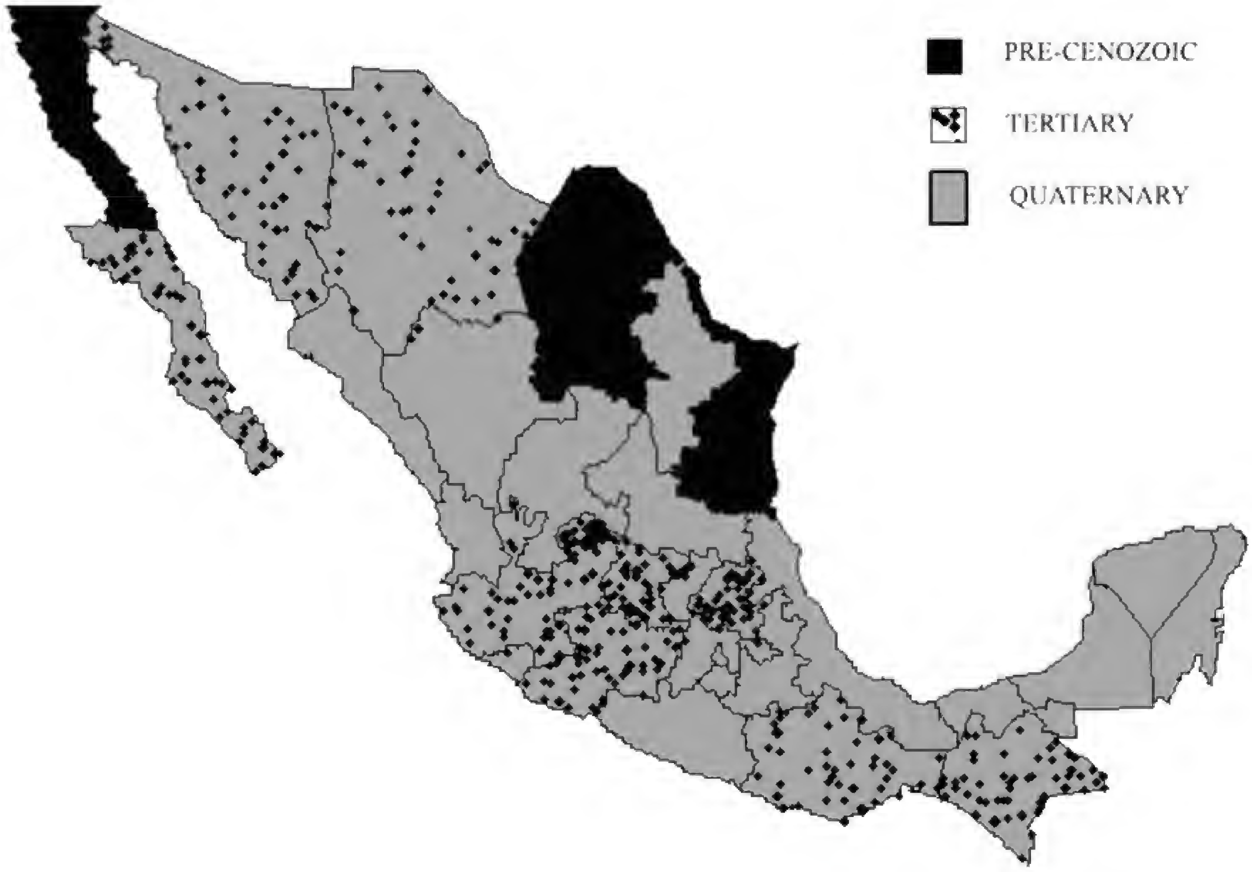

Fig.6- Map showing the chronological covering of the current studies in paleomammalogy, data from Montellano-Ballesteros & Arroyo-Cabrales (2002).

An increase in the social impact of paleontology is also occurring, as shown by the building of several local museums. Among the more important ones are in Guadalajara, Saltillo, Ciudad Victoria, Sabinas, and Cuernavaca. Another important issue has been the joint endeavour of the federal government, the academic institutions, and the SOMEXPAL to establish a legal framework to define and protect the paleontological heritage. Lastly, a third area that is being increased is the production of educational materials.

CONCLUSION

In approximately 200 years, the paleontological endeavour in Mexico has moved from naturalist conceptions based on the European knowledge to the diffusion of important geological theories to evolutionary concerns, where it is currently located. Theoretically, scholars have moved from giantology to Neptunism to Darwinian evolution. Such a slow but constant development is proving important for the creation of strong research teams with up-to-date infrastructure and well-prepared personnel. Equally important is the impact on society with new museums and travelling exhibits.

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THE TINGUIRIRICA FAUNA OF CHILE AND THE EARLY STAGES OF "MODERNIZATION" OF SOUTH AMERICAN MAMMAL FAUNAS[1]

(With 7 figures)

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ABSTRACT: The evolution of South American Cenozoic mammal communities is generally seen as encompassing three distinct "faunal strata". The recently formalized Tinguirirican South American Land Mammal "Age" (SALMA) represents the earliest interval within Simpson's second faunal stratum and presents an exceptional opportunity to investigate a remarkable period of faunal "modernization" in South America. Of the 25 species currently recognized from the Tinguiririca Fauna, 17 are notoungulates, illustrating the group's diversity and abundance during this interval. Two-thirds of notoungulate species are hypsodont, in marked contrast with earlier faunas, indicating the nearly simultaneous convergent appearance of this feature in several notoungulate clades. The most diverse and abundant notoungulates at Tinguiririca are archaeohyracids (six species, the highest diversity for any locality known to date), notohippids (four species), and interatheriids (two species). Large, brachydont notoungulates are scarce. In addition to the fauna from the type locality in central Chile, several Patagonian faunas of Tinguirirican age provide important complementary taxonomic and biogeographic data. Hegetotheriids are absent from the Tinguiririca Fauna but are reported from Tinguirirican faunules in Patagonia. Trachytheriine mesotheriids are uncommon during the Tinguirirican; they have previously been reported only from Rocas Bayas in Rio Negro, though a recently prepared Chilean specimen indicates presence of the group just north of Tinguiririca during this SALMA. Faunal hypsodonty, cenograms, and rainfall estimates have previously been used to suggest that the Tinguiririca Fauna is the earliest open-habitat community in South America. This conclusion is corroborated herein through an ecological diversity analysis (EDA) that consolidates browsers and grazers into a single dietary category, to counter potential errors in hypsodonty-based dietary interpretations of extinct taxa. The statistically significant results of a multivariate discriminant model based on this EDA confirm the resemblance of the Tinguiririca Fauna to modern open habitat communities, further supporting the presence of open habitats in high latitude South America by earliest Oligocene time, despite the apparent lack of a substantial regional climatic shift across the Eocene-Oligocene Transition in Argentine Patagonia.

Key words: South American Land Mammal "Age". Notoungulate. Ecological diversity analysis. Tinguiririca Fauna. Chile.

RESUMO: A Fauna de Tinguiririca do Chile e os primeiros estágios de "modernização" das faunas de mamíferos sul-americanos.

A evolução das comunidades de mamíferos cenozóicos sul-americanos é geralmente vista como abrangendo três "estratos faunísticos" distintos. A recentemente formalizada "Idade" Tinguiririquense de Mamíferos Terrestres Sul-americanos representa o intervalo mais antigo do segundo estrato faunístico de Simpson e fornece uma oportunidade excepcional para se investigar um período notável de "modernização" faunística na América do Sul. Das 25 espécies atualmente reconhecidas para a Fauna de Tinguiririca, 17 são de notoungulados, ilustrando a diversidade e a abundância do grupo durante este intervalo. Dois terços das espécies de notoungulados são hipsodontes, em contraste marcante com as faunas mais antigas, indicando um surgimento convergente quase simultâneo desta característica em vários clados de notoungulados. Os mais diversos e abundantes notoungulados em Tinguiririca são os representantes de Archaeohyracidae (seis espécies, a mais alta diversidade para qualquer localidade conhecida), de Notohippidae (quatro espécies), e de Interatheriidae (duas espécies). Notoungulados de grande porte braquiodontes são raros. Além da fauna da localidade tipo no centro Chile, várias faunas da Patagônia, de idade Tinguiririquense, fornecem importantes dados taxonômicos e biogeográficos complementares. Os representantes de Hegetotheriidae estão ausentes

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da Fauna de Tinguiririca, mas são reportados para a fáunula Tinguiririquense na Patagônia. Os Trachytheriinae, representantes dos Mesotheriidae, não são comuns no Tinguiririquense; eles foram previamente registrados apenas para Rocas Bayas em Rio Negro, embora um espécime recentemente preparado indique a presença do grupo apenas ao norte de Tinguiririca durante a "Idade" de Mamíferos Terrestres Sul-americanos. A hipsodontia faunística, os cenogramas e as chuvas estimadas foram previamente utilizados para sugerir que a Fauna de Tinguiririca é a mais antiga comunidade de habitat aberto na América do Sul. Esta conclusão é aqui corroborada através de uma análise de diversidade ecológica (ADE), que consolida pastadores e ramoneadores em uma única categoria de dieta alimentar, indo contra erros potenciais de interpretação de uma dieta com base na hipsodontia de táxons extintos. Os resultados estatisticamente significantes de um modelo discriminante multivariado nesta ADE confirmam a semelhança da Fauna de Tinguiririca com as comunidades de habitat aberto, suportando, além disso, a existência de habitats abertos em altas latitudes na América do Sul durante o início do Oligoceno, apesar da aparente ausência de mudanças climáticas regionais substanciais durante a transição Eoceno-Oligoceno na Patagônia Argentina.

Palavras-chave: "Idade" Mamíferos Terrestres Sul-americanos. Notoungulados. Análise de diversidade ecológica. Fauna de Tinguiririca. Chile.

INTRODUCTION

The evolution of South American Cenozoic mammal communities is generally described as a succession of three "faunal strata" (Simpson, 1980; Flynn & Wyss, 1998; Fig.1). The oldest of these – spanning roughly the Paleocene-Eocene –, consists of communities dominated by the continent's "original inhabitants" (*e.g.*, endemic ungulates, marsupials, xenarthrans) (Marshall & Muizon, 1988). The second stratum is marked by the arrival of rodents (Wyss *et al.*, 1993) and primates (Hoffstetter, 1969) and the appearance of notable morphological advances within many of the original endemic clades. The final stratum is marked by extensive late Cenozoic interchange with North America and the extinction of many of the last remaining endemic clades (Webb, 1976; Marshall *et al.*, 1982). The recently formalized Tinguiririцan South American Land Mammal "Age" (SALMA) represents the earliest interval within Simpson's second faunal stratum (Wyss *et al.*, 1994; Flynn *et al.*, 2003). As such, the Tinguiririca Fauna of central Chile (the best-sampled and most diverse fauna of Tinguiririцan age) presents an exceptional opportunity to investigate the transition from Stratum 1 to 2, a remarkable period of faunal "modernization" in South America (Pascual *et al.*, 1985; Flynn & Wyss, 1998; Flynn *et al.*, 2007).

In addition to the fauna from the type locality in central Chile, a handful of Tinguiririцan SALMA faunas occur in Patagonia (see Flynn *et al.*, 2003); although most of these faunas remain poorly sampled, they provide important, complementary taxonomic and biogeographic data. One of these, Cañadón Blanco in Chubut, Argentina, discovered by Santiago Roth (Roth, 1901, 1903), was long mistakenly considered a temporally mixed fauna (*e.g.*, Simpson, 1967). In light of our findings in Chile, most of the fossils from Cañadón Blanco are now seen as pertaining to the Tinguiririцan (Wyss *et al.*, 1994; Flynn *et al.*, 2003), but the locality has yet to be relocated. Ameghino (Ameghino, 1901, 1902a) designated a faunally distinctive interval at the Gran Barranca south of Lago Colhué Huapí in Chubut as the "Astraponotéen plus supérieure" (APS) level; he later subsumed the APS within the Mustersan SALMA, but this post-Mustersan/pre-Deseadan faunal interval is now recognized as pertaining to the Tinguiririцan as well (Wyss *et al.*, 1994; Bond *et al.*, 1996; Flynn *et al.*, 2003; see also Kay *et al.*, 1999; Carlini *et al.*, 2005). Other smaller Argentine faunules of Tinguiririцan age include Rocas Bayas in Río Negro province and a variety of others in Chubut (*e.g.*, Laguna La Bombilla, Lomas Blancas/La Curandera, Campo de Velázquez/Paso de Indios, and Laguna Seca) (Bond *et al.*, 1997; Hitz *et al.*, 2000; Flynn *et al.*, 2003). The new Chilean locality of Cachapoal may also be of Tinguiririцan age (Flynn & Wyss, 2004; Hitz *et al.*, 2006) as might other recently discovered central Chilean localities yielding characteristic Tinguiririцan taxa (*e.g.*, various archaeohyracid and interatheriid species).

The purpose of the present brief report is twofold: to provide an overview of Tinguiririцan ungulates in a biogeographic context and to apply a new ecomorphological method of paleohabitat reconstruction to the Tinguiririca Fauna. We recognize that the names Notohippidae, Notopithecinae, Trachytheriinae, Archaeohyracidae, and Hegetotheriinae likely refer to paraphyletic groups, but we continue to use them in their traditional sense until phylogenetically based names of the relevant clades are formally defined.

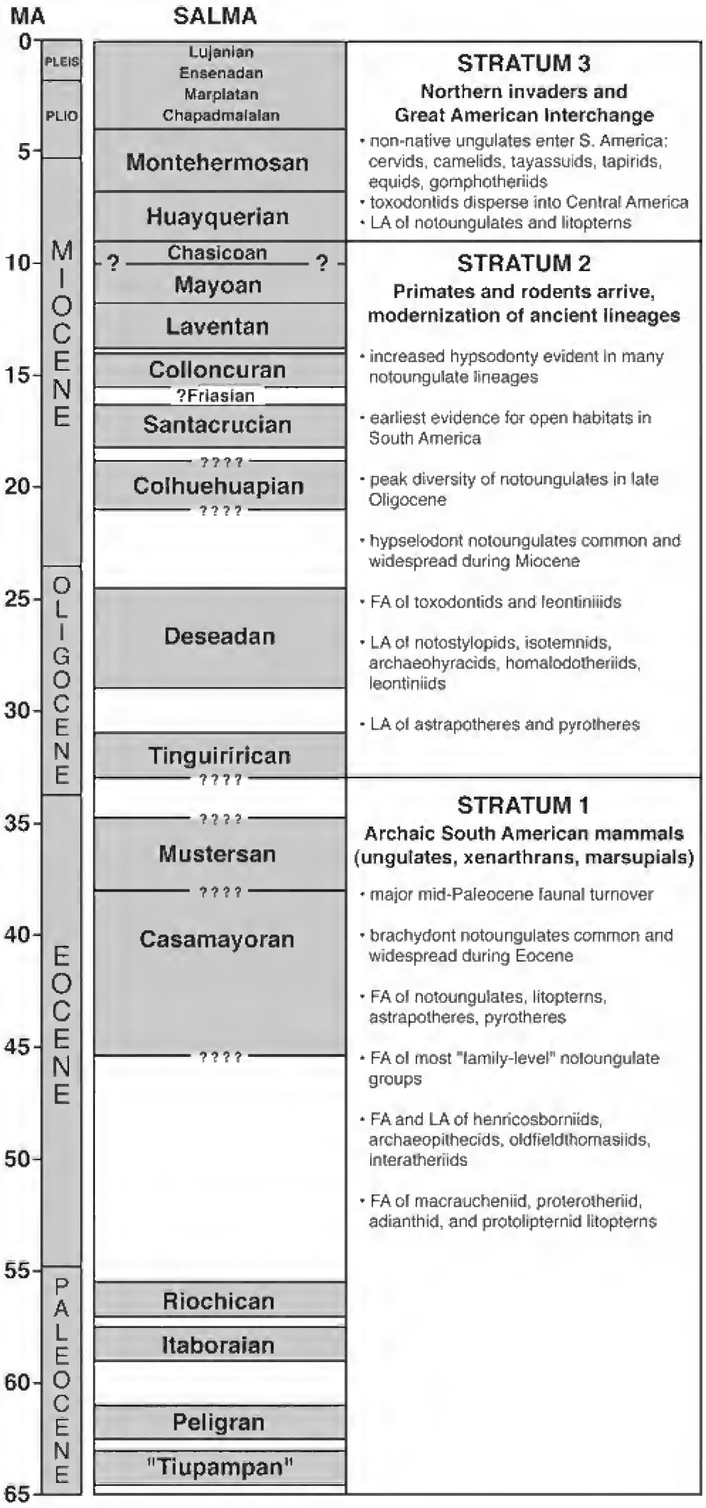

Fig.1- "Three stratum" model of mammalian faunal succession in South America highlighting major events in ungulate evolution. The three strata are calibrated to the timescale on the left, but the events listed for each stratum are not. FA and LA represent First Appearance and Last Appearance, respectively. The SALMA sequence is based primarily on Flynn & Swisher (1995) and Flynn *et al.* (2003); the four youngest SALMAs have been consolidated to increase legibility.

RESULTS AND DISCUSSION

Ungulate Diversity and Biogeography

Ungulates are the most conspicuous component of the Tinguiririca Fauna, accounting for more than two-thirds of alpha diversity (Tab.1). Nearly all of these are notoungulates (Fig.2), a group whose diversity peaked in the Oligocene (Cifelli, 1985b; Marshall & Cifelli, 1989; Croft, 1999). Many of these ungulates are present in other Tinguirirican faunas and are important biochronologically, permitting the recognition of Tinguirirican faunas in other parts of the continent (Hitz *et al.*, 2000, 2006; Croft *et al.*, 2003a; Reguero *et al.*, 2003a).

The following section provides an overview of the major groups of Tinguirirican ungulates in their biogeographic and temporal contexts. Figure 3 provides a map of the main Tinguirirican localities and other localities discussed in the text. Recent studies suggest that the peculiar "Divisadero Largo Fauna" of west-central Argentina – generally considered to be late Eocene (Bond, 1991; Flynn & Swisher, 1995; Flynn *et al.*, 2003) – is a mixed fauna including both ?early-middle Eocene specimens (from the Divisadero Largo Formation) and ?early Miocene specimens (from the overlying Mariño Formation) (Cerdeño *et al.*, 2005; López & Manassero, 2006). We therefore follow these authors in rejecting the "Divisaderan" SALMA, and below we treat specimens from this locality as either Eocene or Miocene in age.

Notostylopidae

A single specimen from the type locality of the Tinguiririca Fauna marks the last appearance of the Notostylopidae (Wyss *et al.*, 1994; Flynn *et al.*, 2003) but additional unprepared notostylopid specimens may be present in the Chilean collections. The Tinguiririca notostylopid most closely resembles *Otronia muehlbergi* from the Mustersan of Chubut (Simpson, 1967) and *Boreastylops lumbrerensis* from the Casamayoran of Salta Province (Vucetich, 1980), but likely represents a new species (Wyss *et al.*, 1994).

Notostylopids are first recorded from the Itaboraian and Riochican of Chubut (Bond, 1986). They are abundant and characteristic components of Patagonian Casamayoran faunas (Simpson, 1948, 1984; Bond, 1986) and are present in both subdivisions of that SALMA, the Vacan and Barrancan (Cifelli, 1985a).

TABLE 1. Tinguiririca faunal list and corresponding ecomorphological variables for each taxon.

Taxon	Order	Family	Diet	Locomotion	Mass
Klohnia charrieri	Marsupialia	Groeberiidae	FR	A	I
Polydolops abanicoi	Marsupialia	Polydolopidae	FR	A	IV
Pascualdelphys fierroensis	Marsupialia	(Didelphimorphia)	I	A	I
gen. et sp. indet.	Xenarthra	Dasypodidae	O	T	V
Pseudoglyptodon chilensis	Xenarthra	Phyllophaga (i.s.)	FO	T	VI
Indaleciinae gen. et sp. nov.	*Incertae sedis*	*incertae sedis*	FO	T	III
gen. et sp. nov.	Rodentia	?Dasyproctidae	FR	T	IV
?Prolagostomus sp.	Rodentia	Chinchillidae	FO	T	III
gen. et sp. nov.	Notoungulata	Notostylopidae	FO	T	VI
Notopithecinae gen. et sp. nov.	Notoungulata	Interatheriidae	FO	T	I
Santiagorothia chiliensis	Notoungulata	Interatheriidae	FO	T	IV
Archaeotypotherium tinguiriricaense	Notoungulata	Archaeohyracidae	FO	T	V
Archaeotypotherium pattersoni	Notoungulata	Archaeohyracidae	FO	T	VI
Protarchaeohyrax gracilis	Notoungulata	Archaeohyracidae	FO	T	IV
Protarchaeohyrax intermedium	Notoungulata	Archaeohyracidae	FO	T	II
Pseudhyrax strangulatus	Notoungulata	Archaeohyracidae	FO	T	V
Pseudhyrax eutrachytheroides	Notoungulata	Archaeohyracidae	FO	T	V
cf. *Rhyphodon* sp.	Notoungulata	Isotemnidae	FO	T	XI
Trigonolophodon cf. *elegans*	Notoungulata	Homalodotheriidae	FO	T	IX
Periphragnis sp.	Notoungulata	Homalodotheriidae	FO	T	IX
Eomorphippus sp. nov.	Notoungulata	Notohippidae	FO	T	VIII
"Eomorphippus" cf. *pascuali*	Notoungulata	Notohippidae	FO	T	VII
gen. et sp. nov. A (large)	Notoungulata	Notohippidae	FO	T	VIII
gen. et sp. nov. B (small)	Notoungulata	Notohippidae	FO	T	VI
incertae sedis	Notoungulata	Leontiniidae	FO	T	X

Dietary abbreviations: FR, frugivore; FO, folivore; I, insectivore; O, omnivore. Locomotor abbreviations: A, arboreal; T, terrestrial. Body mass categories: I, 1-200 g; II, 201-400 g; III, 401-800 g; IV, 801-1600 g; V, 1.6-3.2 kg; VI, 3.2-6.4 kg; VII, 6.4-12.8 kg; VIII, 12.8-25.6 kg; IX, 25.6-51.2 kg; X, 51.2-102.4 kg; XI, 102.4-204.8 kg; XII, 204.8+ kg.

Notostylops itself is especially well-represented in Casamayoran assemblages (*e.g.*, Simpson, 1932a, 1948; Riggs & Patterson, 1935), forming the basis for Ameghino's original designation for these faunas, the "*Notostylops* beds" (Simpson, 1984). *Otronia* is the only described Mustersan notostylopid (Simpson, 1948; Bond, 1986), although López (1997) has noted a new notostylopid species from Antofagasta de la Sierra, an Eocene fauna of uncertain SALMA assignation.

The Tapado Fauna documents the presence of notostylopids in central Chile during the late Eocene, probably during the Casamayoran (Wyss *et al.*, 1996; Flynn *et al.*, 2005a). Notostylopids have not been recorded from the Divisadero Largo Fauna of Mendoza province (Simpson *et al.*, 1962). This absence is likely an artifact of sampling given that notostylopids were present throughout Patagonia, northwest Argentina, and central Chile during this interval.

Interatheriidae

The Tinguiririean is unique among SALMAs in documenting the co-occurrence of both traditional subfamilies of interatheriids: low-crowned notopithecines and higher crowned interatheriines (Wyss *et al.*, 1994; Hitz *et al.*, 2000, 2006; Flynn *et al.*, 2003). In this regard, the interatheriids mimic the Tinguiririean SALMA as a whole, in that various "archaic" taxa co-occur with members of clades marked by more derived morphologies (Wyss *et al.*, 1993, 1994; Flynn *et al.*, 2003).

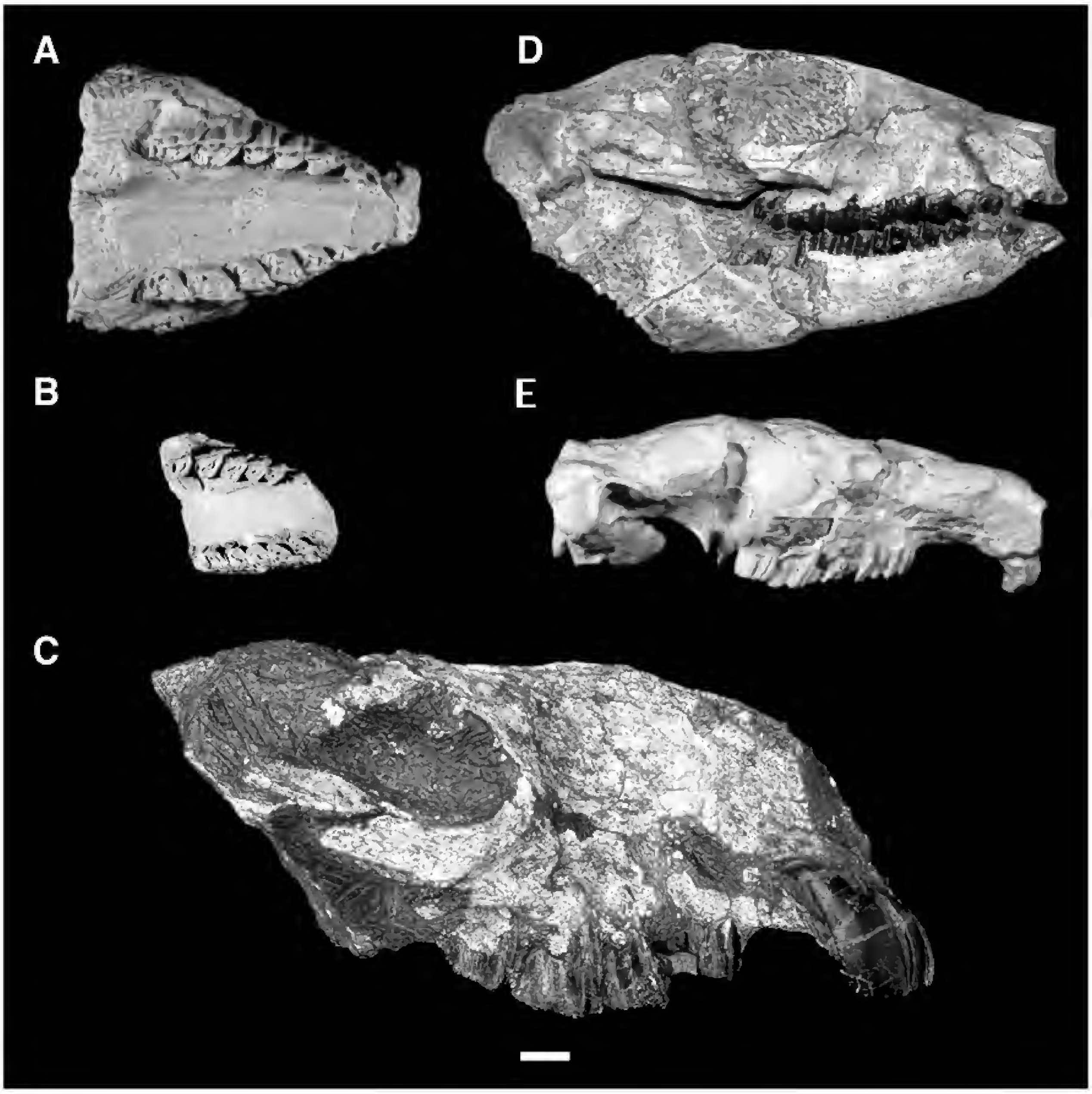

Fig.2- Representative notoungulate specimens from the Tinguiririca Fauna of central Chile. A, SGO PV 2923, holotype palate of *Archaeotypotherium tinguiriricaense*, occlusal view (cast); B, SGO PV 2998, palate referred to *Protarchaeohyrax intermedium*, occlusal view (cast); C, SGO PV 3046, skull of *Eomorphippus* sp. nov.; D, SGO PV 2914, holotype skull and mandibles of *Santiagorothia chiliensis* (left lateral view, reversed); E, SGO PV 2900, skull referred to *Archaeotypotherium tinguiriricaense*, right lateral view. Scale bar = 1cm.

The Tinguiririca Fauna itself includes two interatheriids: *Santiagorothia* (a basal interatheriine; Fig.2D) and a new species of basal interatheriid (Hitz *et al.*, 2000, 2006; Flynn *et al.*, 2003). Besides in the Tinguiririca Valley, *Santiagorothia* occurs at virtually every Tinguirirican locality in Patagonia with the exception of Cañadón Blanco (Hitz *et al.*, 2000), whereas the new basal interatheriid appears to be endemic to central Chile (Hitz *et al.*, 2006). The interatheriine *Eopachyrucos* occurs in the Tinguirirican APS level of Gran Barranca, Cañadón Blanco, and Rocas Bayas; the interatheriine *Proargyrohyrax* has been reported from the Gran Barranca (López *et al.*, 2005) and Lomas Blancas (Hitz *et al.*, 2000). Outside of Chile, basal interatheriids of Tinguirirican age have only been reported from the Gran Barranca (*e.g.*, La Cancha; López *et al.*, 2005). Interestingly, a basal interatheriid distinct from that of the Tinguiririca Fauna occurs at the more recently discovered locality of Cachapoal (Hitz *et al.*, 2006); at least one currently unidentified species of interatheriine is also present in that fauna.

The only interatheriids present prior to the Tinguirirican are basal members of the clade (*i.e.*, notopithecines or non-interatheriines), the earliest occurrence of which is in the Riochican of Patagonia (Simpson, 1935b, 1967; Bond, 1986). *Notopithecus* and similar forms are abundant and characteristic of Casamayoran faunas (Simpson, 1967), although they are apparently restricted to the Barrancan (younger) subdivision in Patagonia (Cifelli, 1985a). *Guilielmoscottia* occurs in the Mustersan of Patagonia (Simpson, 1967; Marshall *et al.*, 1983), and may also occur in the Tinguiririan (López *et al.*, 2005). A diminutive basal interatheriid, *Punapithecus*, has been described from the indeterminate Eocene fauna of Antofagasta de la Sierra (López & Bond, 1995; López, 1997). Two other small basal interatheriids are now known from Eocene deposits in Chile, a new diminutive taxon from the Tapado Fauna and *Antepithecus* from the Azufre Fauna (Hitz *et al.*, 2006). As is the case for notostylopids, interatheriids are absent from Divisadero Largo, probably due to small sample sizes.

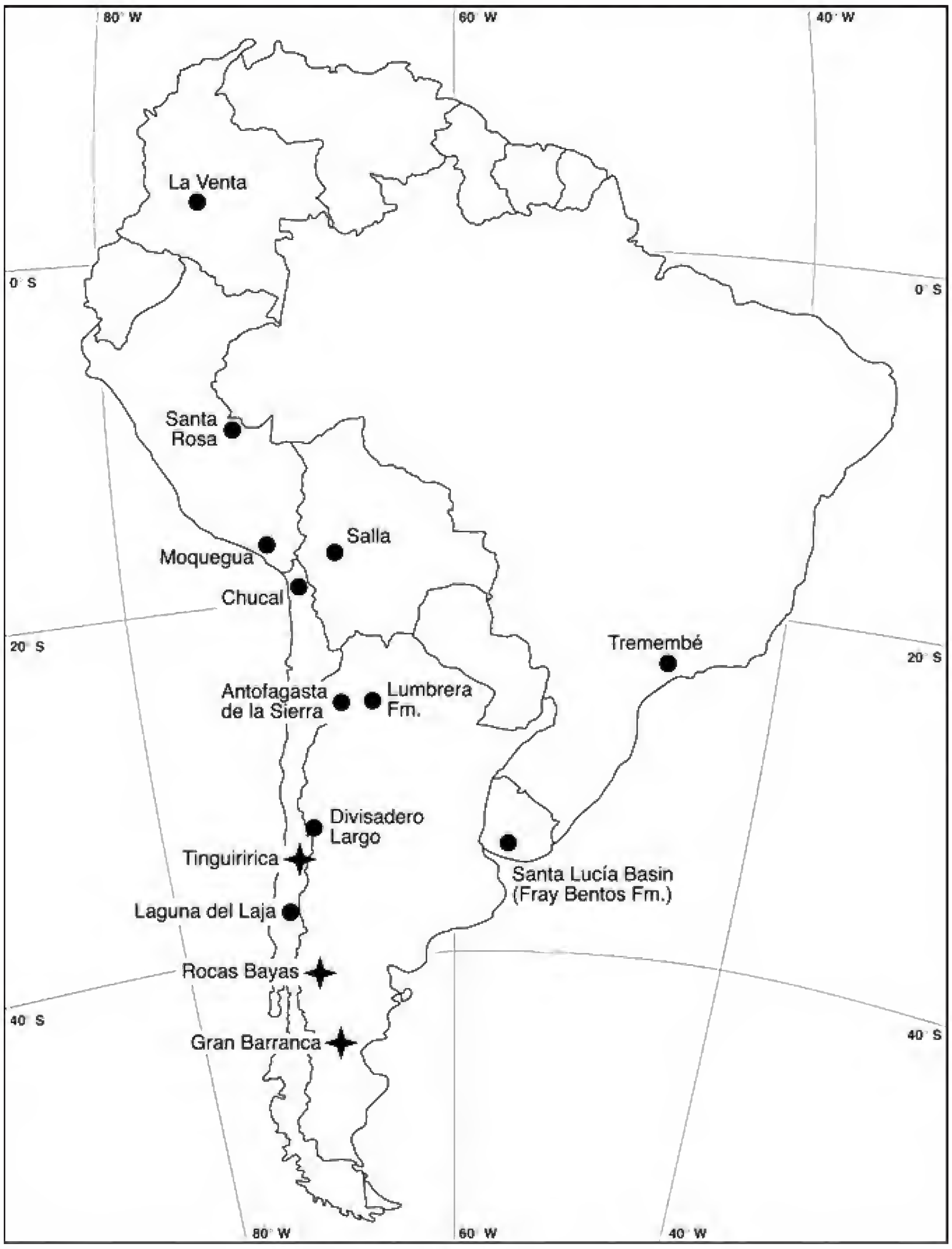

Fig.3- Map of primary localities discussed in the text; localities with Tinguiririican-aged intervals are designated by a star.

Shockey *et al.* (2004) reported a small, indeterminate interatheriine from the Paleogene fauna of Santa Rosa in the lowland Peruvian Amazon. That locality has been considered late Eocene (possibly Mustersan) in age (Campbell *et al.*, 1996, 2004; Campbell, 2004), which would make this taxon the earliest known interatheriine. The interatheriine and the other notoungulates from Santa Rosa are more indicative of an Oligocene age for the fauna, however (Shockey *et al.*, 2004), and given the general reliability of notoungulates for biochronologic correlation, this age assignment seems more likely. Regardless, Santa Rosa is the northernmost record of interatheriids in South America prior to the middle Miocene.

MESOTHERIIDAE

Mesotheriids are rare in Tinguiririca faunas; no specimens have been collected from the type locality in Chile, nor have any been reported from the APS level at Gran Barranca or Cañadón Blanco (Flynn *et al.*, 2003). A trachytheriine specimen from Rocas Bayas in Río Negro, Argentina does record the presence of the clade in western Argentina during this interval, however (Bond *et al.*, 1997). Additionally, we have identified a trachytheriine upper molar from the Cachapoal Fauna of central Chile. Cachapoal may correlate with or predate a level preliminarily dated at 29.3 ± 0.1 Ma (*i.e.*, early Deseadan SALMA or older) and thus may be of Tinguiririca age (Flynn & Wyss, 2004). This chronological assessment is supported by the occurrence of *Protarchaeohyrax* and *Archaeotypotherium* at Cachapoal, both typical Tinguiririca archaeohyracids (Croft *et al.*, 2003a; Flynn *et al.*, 2003; Reguero *et al.*, 2003a; see also below). A relatively large mesotheriid (?trachytheriine) mandible from a third central Chilean fauna of potential Tinguiririca age further documents the presence of mesotheriids in central Chile at this time. The clade has long been reported from Divisadero Largo of Mendoza, Argentina (Simpson & Minoprio, 1949) and this was thought to be the oldest occurrence of mesotheriids (Reguero & Castro, 2004). It appears these specimens more likely derive from the overlying Mariño Formation, however, and are therefore Miocene in age (Cerdeño *et al.*, 2005).

Mesotheriids apparently increased in abundance after the Tinguiririca; *Trachytherus* is a characteristic component of Deseadan faunas and is arguably the best known late Oligocene typothere (Marshall *et al.*, 1986; Reguero & Escribano, 1996). Specimens of *Trachytherus* (or closely related forms) have been collected from Deseadan faunas in Patagonia (Patterson, 1934; Marshall *et al.*, 1986; Reguero & Escribano, 1996), Bolivia (MacFadden *et al.*, 1985; Sydow, 1988; Shockey, 1997a, b; Shockey *et al.*, 2007), Perú (Shockey *et al.*, 2006), and Uruguay (Bond *et al.*, 1998) – essentially from all reasonably well-sampled Deseadan faunas. The absence of mesotheriids in the Tremembé Formation of Brazil (Bergqvist & Ribeiro, 1998; Vucetich & Ribeiro, 2003) and the Paleogene Santa Rosa Fauna of lowland Perú (Campbell *et al.*, 2004; Shockey *et al.*, 2004), if not attributable to small sample sizes, may reflect true absence (see below).

Until recently, mesotheriids were unknown from the earliest Miocene Colhuehuapian SALMA (Marshall *et al.*, 1983; Croft *et al.*, 2003b, 2004; Flynn *et al.*, 2005b; Kramarz *et al.*, 2004). Trachytheriines therefore became extinct between the Deseadan and Colhuehuapian SALMAs, and mesotheriines evidently originated. Based on the geographic and temporal distributions of the earliest diverging mesotheriines (Fig.4), it seems that this clade differentiated in the middle latitudes of South America (Flynn *et al.*, 2002; Croft *et al.*, 2003b, 2004). No mesotheriids are recorded from low latitudes (*i.e.*, north of 10° S; see Kay *et al.*, 1997; Linares, 2004), however, suggesting the presence of a geographic or ecological barrier to their dispersal during much of the Cenozoic.

ARCHAEOHYRACIDAE

The Tinguiririca is the "Age of Archaeohyracids"; this assemblage – paraphyletic though it may be – exhibited greater species richness during this period of time than at any other point in its relatively short history (Croft, 1999; Croft *et al.*, 2003a). Not only did it achieve its own peak diversity during this period, archaeohyracid alpha diversity at Tinguiririca is among the highest exhibited by any "family-level" notoungulate group for any SALMA. The reasons for this short-lived species richness are unknown but may relate to the group's early acquisition of hypsodont cheek teeth (Simpson, 1967; Croft *et al.*, 2003a). Archaeohyracids are quite abundant at Tinguiririca; in this regard, Tinguiririca is more similar to Salla, Bolivia than typical Patagonian faunas.

At least six archaeohyracids are known from Tinguiririca, two species each of *Archaeotypotherium* (Fig.2A, E), *Protarchaeohyrax* (Fig.2B), and *Pseudhyrax* (Croft *et al.*, 2003a; Flynn *et al.*, 2003, Reguero *et al.*, 2003a). *Archaeotypotherium* and

Protarchaeohyrax are recorded from the APS level at Gran Barranca and from Cañadón Blanco (Roth, 1903; Simpson, 1967; Croft *et al.*, 2003a; Reguero *et al.*, 2003a) and are characteristic of the Tinguiririrican SALMA (Flynn *et al.*, 2003). Tinguiririca is the only Tinguiririrican fauna yet known to record *Pseudhyrax*, a taxon otherwise typical of the Mustersan of Patagonia (Simpson, 1967).

Although Simpson (1967) viewed archaeohyracids as spanning the latest Riochican through Deseadan, he noted that their occurrence in the Riochican is doubtful. They are first definitively known from Casamayoran faunas, with all currently described species from this temporal interval being referred to *Eohyrax*. Of the dozen Casamayoran localities reviewed by Cifelli (1985a), *Eohyrax* occurs only in three (Gran Barranca, Río Chico oeste, and possibly in Cañadón Lobo), illustrating the scarcity of archaeohyracids at that time. Moreover, these three localities predominantly or exclusively represent the younger of Cifelli's (1985a) two subdivisions of the Casamayoran, the Barrancan, suggesting that the oldest securely identified archaeohyracids may be substantially younger than once thought. The northernmost report of *Eohyrax* is from the Cosquín Formation in Córdoba, Argentina (Linares *et al.*, 1960). Archaeohyracids have also been reported from Antofagasta de la Sierra in northwest Argentina, a locality of uncertain age that may pertain to the

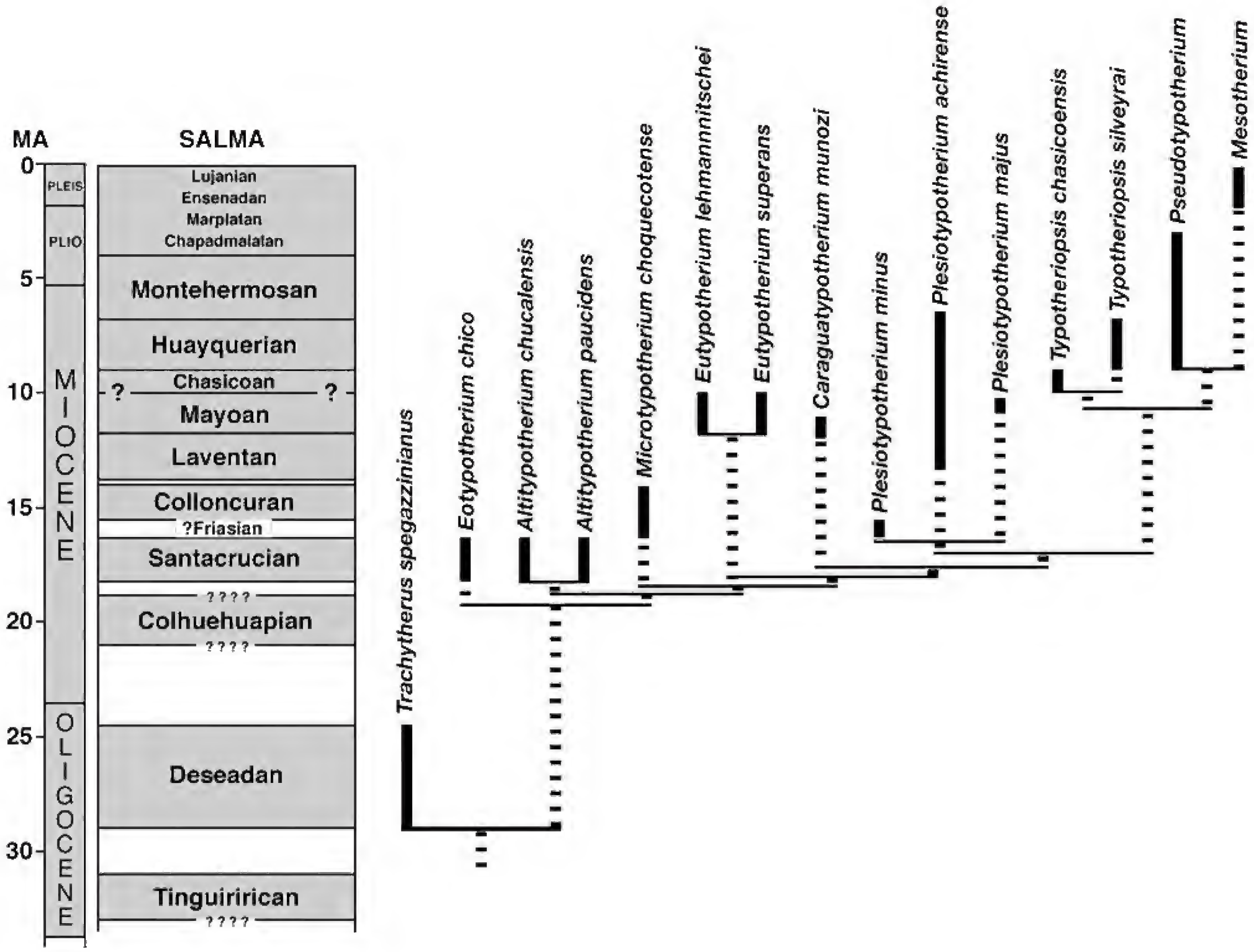

Fig.4- Time-calibrated phylogeny of mesotheriids based on the analysis of Croft *et al.* (2004). Solid bars represent fossil occurrences, dashed lines represent inferred phylogenetic lineages. The four youngest SALMAs have been consolidated to increase legibility.

middle or even early Eocene (López, 1997; Reguero & López, 1999; Reguero *et al.*, in press). If this age assignment proves correct, it could represent the earliest occurrence of the group. A time calibrated phylogeny of archaeohyracids suggests that a major diversification took place at or just prior to the Tinguiririican, potentially coincident with the Eocene-Oligocene Transition (Fig.5).

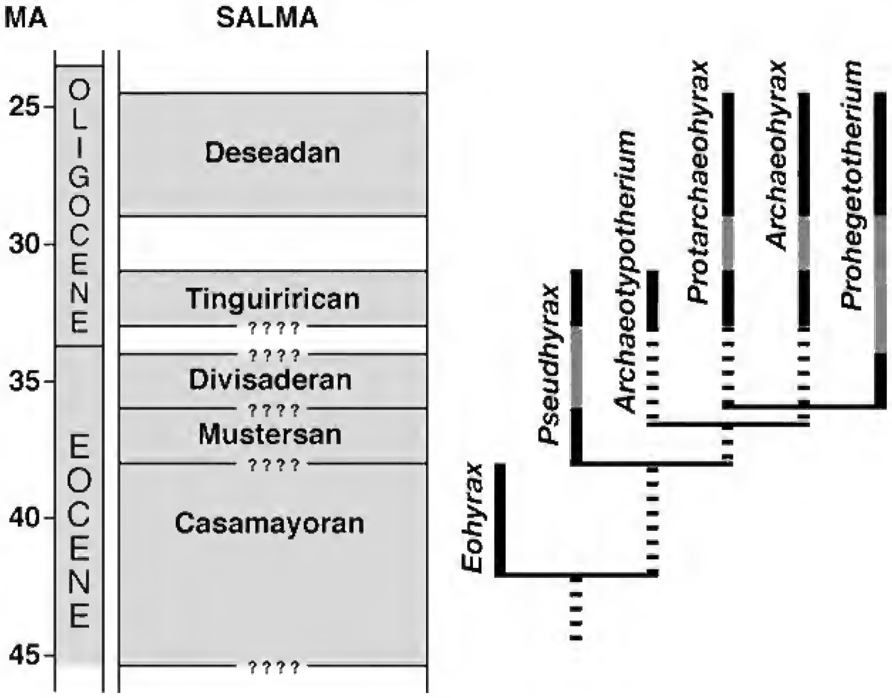

Fig.5- Time-calibrated phylogeny of archaeohyracids based on the analysis of Croft *et al.* (2003a). Solid bars represent fossil occurrences; gray bars represent interpolated occurrences; dashed lines represent inferred phylogenetic lineages.

Archaeohyracids are last recorded in the Deseadan where they are represented by species of *Archaeohyrax* (a primarily Deseadan taxon) and *Protarchaeohyrax* (known also from the Tinguiririican). Only *Archaeohyrax* occurs in Deseadan faunas of Patagonia (*e.g.*, Chaffee, 1952; Marshall *et al.*, 1986) and only *Protarchaeohyrax* occurs in the Fray Bentos Formation of Uruguay and northeastern Argentina (Reguero *et al.*, 1995; Bond *et al.*, 1998; Reguero *et al.*, 2003b). Both taxa occur in the Deseadan at Salla, Bolivia, but *Archaeohyrax* is much more abundant than *Protarchaeohyrax* there (Reguero & Cifelli, 1997). *Archaeohyrax* has also been reported preliminarily from the Tinguiririican Rocas Bayas locality (Bond *et al.*, 1997), which would be its oldest occurrence. Archaeohyracids have not yet been recorded from the late Oligocene Tremembé Formation of southeastern Brazil (Bergqvist & Ribeiro, 1998; Vucetich & Ribeiro, 2003) nor from the recently described Deseadan Moquegua Fauna of Perú (Shockey *et al.*, 2006); neither have they been recorded from the Santa Rosa Fauna from the Amazonian lowlands of eastern Perú (Campbell *et al.*, 2004; Shockey *et al.*, 2004) nor Divisadero Largo in western Argentina (Simpson *et al.*, 1962). Given the sparse sampling at most of these localities and the scarcity of archaeohyracids in many faunas, these absences likely have little biogeographic significance.

Hegetotheriidae

Hegetotheriids are absent from the Tinguiririca Fauna and the APS level at Gran Barranca; their only Tinguiririican occurrence is at Cañadón Blanco (Bond, 1991; Reguero, 1993; Flynn *et al.*, 2003), although several hegetotheriids specimens are now known from Cachapoal in central Chile, potentially also of Tinguiririican age. A skull and mandibles of a hegetotheriid from Divisadero Largo were previously thought to record the earliest Hegetotheriidae (Simpson & Minoprio, 1949; Simpson *et al.*, 1962), but this specimen likely comes from the Miocene Mariño Formation (López & Manassero, 2006).

Two hegetotheriid sub-groups are generally recognized (Simpson, 1945a; McKenna & Bell, 1997): Hegetotheriinae and Pachyrukhinae. Pachyrukhinae is universally considered monophyletic (Cerdeño & Bond, 1998) and the clade is certainly recognizable as early as the Deseadan (Loomis, 1914; Simpson, 1945b; Dozo *et al.*, 2000) and potentially as early as the Tinguiririican (Reguero, 1993). In contrast, Hegetotheriinae is likely paraphyletic, though it may include a monophyletic subset of Miocene taxa (Cifelli, 1993; Croft, 2000; Croft *et al.*, 2004; Croft & Anaya, 2006). All Paleogene non-pachyrukhine hegetotheriids have been referred to *Prohegetotherium*, a taxon that occurs at Divisadero Largo, La Cantera, and various Deseadan localities in Patagonia (Reguero & Cerdeño, 2001, 2005; López *et al.*, 2005; but see López, 2002), and possibly in Oligocene faunas in Chile (*e.g.*, Cachapoal).

Isotemnidae

Large, low-crowned notoungulates are poorly represented at Tinguiririca, where only a single species of isotemnid, cf. *Rhyphodon*, has been identified. If this tentative identification is substantiated, it would represent a temporal and geographic range extension for the taxon, otherwise known only from the Mustersan of Lago Musters/ Cerro del Humo in Chubut (Simpson, 1967). *Anisotemnus*, *Periphragnis*, *Pleurostylodon*, and *Rhyphodon* are known from the Tinguirirican APS level of Gran Barranca (Flynn *et al.*, 2003; López *et al.*, 2005), and an indeterminate isotemnid with affinities to *Periphragnis* has been reported from Rocas Bayas (Bond *et al.*, 1997). Both *Anisotemnus* and *Pleurostylodon* are known from the Casamayoran of Patagonia, with *Anisotemnus* previously restricted to the Barrancan (Simpson, 1967; Cifelli, 1985a); *Pleurostylodon* has also recently been identified from the ?Casamayoran Tapado Fauna of central Chile (Flynn *et al.*, 2005a). Besides various Tinguirirican localities, *Periphragnis* is known only from the Mustersan of Patagonia (Wyss *et al.*, 1994; Flynn *et al.*, 2003; López *et al.*, 2005). Although isotemnids appear to be fairly diverse during the Tinguirirican, precise comparisons and identifications are hampered by the relatively poor material presently known.

The Tinguirirican isotemnids are the youngest representatives of the group; the oldest are Riochican in age (Simpson, 1935a, 1967; Marshall *et al.*, 1983). Within this time interval, isotemnids are recorded at most Eocene localities from Patagonia and as far north as Jujuy (Bond & López, 1995).

Homalodotheriidae

Homalodotheriids are relatively large, vaguely chalicothere-like notoungulates that were never very diverse or abundant (Patterson & Pascual, 1968; Simpson, 1980; Coombs, 1983; Cifelli, 1985b; Croft, 1999). Simpson (1967) did not regard Mustersan *Periphragnis* as a homalodotheriid, but this may very well be the earliest member of the group (Bond, pers. comm.). During the Tinguirirican, *Trigonolophodon* is present at Tinguiririca, Cañadón Blanco, and the APS level at Gran Barranca (Wyss *et al.*, 1994; Flynn *et al.*, 2003). The group persisted through the late Miocene (Ringuelet, 1957).

Notohippidae

The phylogenetic relationships among notohippids are only beginning to be resolved (Shockey, 1997a, b), but the group's name (as traditionally conceived) almost certainly does not refer to a monophyletic entity. Cifelli (1993) found support for a monophyletic subgroup of Deseadan and later notohippids, but his analysis positioned *Eomorphippus* as the outgroup to a clade formed by these later notohippids plus toxodontids. In contrast, Shockey (1997a, b) found no such support for a monophyletic subclade, and in fact obtained very little resolution among notohippids; most notohippids were part of a six-way polytomy that included a clade formed by *Pascualihippus* plus toxodontids (Fig.6).

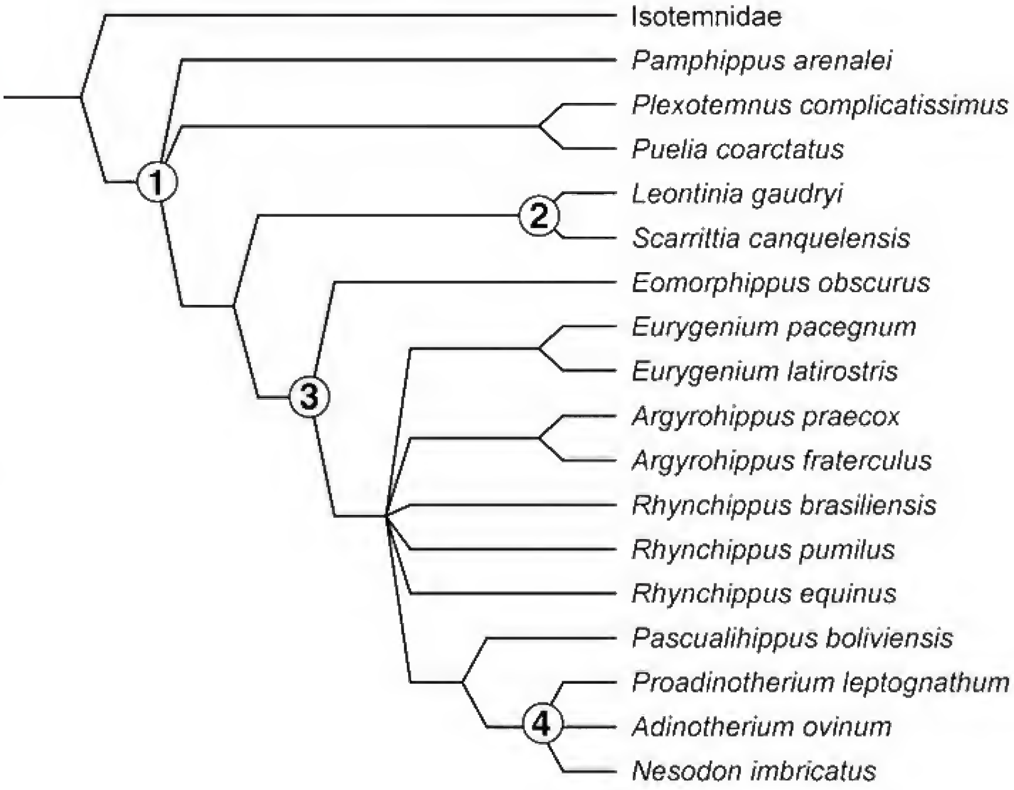

Fig.6- Notohippid relationships based on the analyses of Shockey (1997a, b). The following named nodes are indicated: 1, Notohippidae *sensu* Bond & López (1993); 2, Leontiniidae; 3, Notohippidae *sensu* Simpson (1967); 4, Toxodontidae.

The cladogram resembled Cifelli's (1993), however, in that *Eomorphippus* (*E. obscurus*) was the nearest outgroup to this larger clade including some notohippids plus toxodontids. If taxa such as *Plexotemnus*, *Pampahippus*, and *Puelia* are included in the Notohippidae, as advocated by Bond & López (1993), these taxa are positioned as outgroups to a clade formed by leontiniids plus traditionally recognized notohippids and toxodontids (Shockey, 1997a, b). In other words, notohippids are distributed across a variety of anatomically advanced toxodontian groups (Fig.6). Our research group is working to clarify relationships among these later diverging toxodontians, but for the purposes of the current discussion we employ Bond & López's (1993) broader conception of Notohippidae.

After archaeohyracids, notohippids are the most diverse group at Tinguiririca, with at least four species present (Wyss *et al.*, 1994, 2005; Flynn *et al.*, 2003). These include two relatively basal notohippids (an undescribed species (Fig.2C) and cf. "*Eomorphippus*" *pascuali*) and two more advanced notohippids (both new species of *Eomorphippus*, one close to *E. obscurus*) (Wyss *et al.*, 1994, 2005). *E. obscurus* occurs at Cañadón Blanco (Simpson, 1967; Flynn *et al.*, 2003) and both "*E.*" *pascuali* and *E. obscurus* have been collected from the APS level at Gran Barranca (Bond *et al.*, 1996). *Puelia*, an otherwise Mustersan taxon, possibly occurs at Rocas Bayas along with another indeterminate notohippid (Bond *et al.*, 1997). Species of *Eomorphippus* share the derived presence of hypsodont molars and incisors and are useful taxa for recognition of Tinguiririican faunas (Wyss *et al.*, 1994, 2005; Flynn *et al.*, 2003).

The earliest notohippids are Casamayoran in age and include *Pampahippus* from the lower part of the Lumbrera Formation of Salta, Argentina (Bond & López, 1993) and *Plexotemnus* from the Gran Barranca (Simpson, 1967). More refined age estimates for these taxa are lacking since the Lumbrera Formation is poorly constrained (Babot *et al.*, 2002; Hongn *et al.*, 2007) and the stratigraphic position of *Plexotemnus* at the Gran Barranca is unknown (Cifelli, 1985a). According to Bond & López (1993), *Pampahippus*, *Plexotemnus*, and *Puelia* appear to represent a structural lineage between basal toxodontians and later-occurring notohippids such as *Eomorphippus*; accordingly, northwest Argentina has been proposed as the center of diversification for the group.

Notohippids are diverse and abundant in Deseadan faunas (Cifelli, 1985b); besides the classic localities in Patagonia, they also occur in the Fray Bentos Formation, Uruguay (Reguero *et al.*, 2003b); Salla, Bolivia (Shockey, 1997a, b); new sites in the Abanico Formation, central Chile; and the Tremembé Formation, southeast Brazil (Soria & Alvarenga, 1989). They have not been reported from Moquegua or Santa Rosa in Perú (Shockey *et al.*, 2004, 2006) but this may be attributable to sparse sampling.

Leontiniidae

Leontiniids are rare during the Tinguiririican; only a single specimen has been collected from the type locality, and it has not yet been identified more precisely (Flynn *et al.*, 2003). The Tinguiririican leontiniid represented the earliest record of the group until the recent report of a new species (*Coquenia bondi*) from the ?Mustersan upper part of the Lumbrera Formation of northwest Argentina (Powell & Deraco, 2003; Deraco *et al.*, in press). A specimen from a new pre-Tinguiririican Chilean locality may comparably extend the group's range in Chile. Leontiniids are more diverse and apparently much more abundant in the Deseadan, having been reported from Bolivia (Shockey, 1997a, 2005), southeast Brazil (Paula Couto, 1983), and Uruguay/northeast Argentina (Reguero *et al.*, 2003b), in addition to Patagonia (Loomis, 1914; Chaffee, 1952; Marshall *et al.*, 1986). Some of these Deseadan specimens even include complete skeletons (Simpson, 1934; Chaffee, 1952). Leontiniids also are diverse and abundant at the locality of La Cantera at Gran Barranca, but the precise age of this Oligocene fauna is unclear (López *et al.*, 2005). Fragmentary material from the Paleogene locality of Santa Rosa, Perú, may pertain to a leontiniid (Shockey *et al.*, 2004); as noted above, this likely represents an Oligocene occurrence.

In the Neogene, the record of leontiniids is much patchier. Although *Colpodon* is characteristic of the early Miocene Colhuehuapian SALMA (Ameghino, 1902b; Simpson, 1932b, 1935b; Bordas, 1939; Marshall *et al.*, 1983) the group is thereafter absent from the Patagonian record. The last occurrence is in the middle Miocene La Venta Fauna of Colombia (Villarroel & Colwell Danis, 1997). Based on this distribution, it appears that leontiniids experienced a significant contraction and/or shift in their geographic range by the late early Miocene. Testing this hypothesis will require additional low and middle latitude faunas, especially from the early and middle Miocene. Moderately well-sampled later Cenozoic faunas from the middle latitudes of Chile and Bolivia appear to lack evidence of leontiniids (Croft *et al.*, 2004, 2007; Croft, 2007). A recently identified leontiniid from the Miocene Laguna del Laja region of south-central Chile (Wyss *et al.*, 2003; Wertheim *et al.*, 2004, 2005; Flynn *et al.*, in press) may provide important information on the geographic and temporal distribution of leontiniids, depending on resolution of its precise age and stratigraphic position.

Other ungulate groups

In addition to the groups discussed above, the presence or absence of several less diverse groups from the Tinguirirican merit comment. Among notoungulates, no henricosborniids, archaeopithecids, or oldfieldthomasiids have been reported from this interval; all of these groups are restricted to Eocene and older localities (Simpson, 1948, 1967; Marshall *et al.*, 1983). Given the abundance and diversity of oldfieldthomasiids at Divisadero Largo and the number of Tinguirirican faunas that have been sampled, it seems likely that those from Divisadero Largo predate the Tinguirirican (Wyss *et al.*, 1994; Flynn *et al.*, 2003). No toxodontids occur in the Tinguirirican, apparently constraining their origin to the small interval of time between the Tinguirirican and the Deseadan.

Ungulates other than notoungulates constitute only a minor component of Tinguirirican faunas. Astrapotheres (including trigonostylopids) range from the Riochican through the middle Miocene (Simpson, 1935b, 1967; Cifelli, 1985b) and are only represented during the Tinguirirican by *Isolophodon* at Cañadón Blanco (Roth, 1903; Flynn *et al.*, 2003). Litopterns exhibit a pattern similar to that of astrapotheres; the sole representative of the clade during the Tinguirirican is the proterotheriid *Anisolambda* from Cañadón Blanco (Roth, 1903). *Anisolambda* is a particularly long-ranging taxon, occurring in Riochican through Deseadan faunas (Cifelli, 1983).

A single indaleciine has been reported from Tinguiririca (Wyss *et al.*, 1994; Flynn *et al.*, 2003); although traditionally allied with litopterns, several analyses have cast doubt on this taxonomic affiliation (Cifelli, 1983, 1993; Cifelli & Soria, 1983; Wyss *et al.*, 1994). Regardless of its proper higher-level relationships, the form from Tinguiririca is most similar to *Indalecia grandis* from the Casamayoran lower part of the Lumbrera Formation of Salta, Argentina (Bond & Vucetich, 1983; Wyss *et al.*, 1994). The close similarity of this taxon to a species from northwest Argentina parallels geographic patterns seen other Tinguirirican ungulate groups such as basal interatheriids and notostylopids (see above).

Tinguiririca Paleoenvironment

Multiple lines of evidence (faunal hypsodonty, cenograms, rainfall estimates via ecological diversity analysis) have previously been used to suggest that the Tinguiririca Fauna represents the earliest 'open' habitat (likely grassland/ wooded grassland) community in South America (Flynn *et al.*, 2003). Although these lines of evidence are not entirely independent (*e.g.*, diet and body mass factor into ecological diversity analyses), their congruence increases confidence in the resultant habitat reconstruction. An open question, however, is the degree to which unusual aspects of the Tinguiririca Fauna (and/or South American mammalian paleofaunas in general, relative to those on other continents) might be driving these patterns. For example, is it possible that the high proportion of hypsodont ungulates at Tinguiririca reflects not the consumption of siliceous phytolith-bearing open habitat vegetation (*i.e.*, grasses), but rather exogenous grit produced by nearby volcanoes, as suggested by Pascual & Ortiz Jaureguizar (1990)? Or might notoungulates have had some intrinsic tendency to increase the height of their cheek teeth regardless of the environment, as implied by Simpson (1980)? With these questions in mind, we undertook an even more conservative ecological diversity analysis (EDA) in which the influence of hypsodonty would be minimized.

As in our previous ecological diversity analysis, we coded each Tinguiririca taxon for three variables: diet, locomotor style, and body mass (Flynn *et al.*, 2003). For comparative purposes, we also coded mammals from sixteen modern Neotropical faunas (from Kay & Madden, 1997) for the same variables. In the present analysis, however, we coded these attributes differently. We used far broader, more conservative dietary categories than in our previous analysis, to minimize the chance of misinterpreting diet based on tooth crown height (hypsodonty); these five dietary categories included folivore (a combination of browser, grazer, and mixed feeder categories), frugivore, insectivore, omnivore, and carnivore. Our locomotor categories also were quite broad; species were classified as either terrestrial or arboreal, with the latter category including scansorial and semi-arboreal species. In contrast, we used narrower body mass categories (following Townsend, 2004) which permitted greater discrimination among taxa than the six categories used previously, but still buffered against small errors inherent in estimating body masses of extinct taxa (Damuth & MacFadden, 1990; Croft, 2001). For details of paleobiological inferences, see Flynn *et al.* (2003).

The proportion of taxa in each category noted above (*e.g.*, number of frugivores/total number of species) was calculated for Tinguiririca and each modern fauna. These proportions were then arcsine transformed to normalize the data (Sokal & Rohlf, 1995) and seven of the original nineteen categories were used in a discriminant function analysis (DFA); the seven categories employed were those demonstrated by Townsend (2004) to be statistically correlated with habitat type in her dataset of modern South American mammal faunas. The DFA was performed using SPSS (SPSS Inc.) on an Apple G4 computer; the prior probabilities for the three habitat types (open, mixed, closed) were considered equal. The resultant two functions correctly classified 15 of 16 modern faunas by habitat type and classified Tinguiririca as an open habitat fauna with 100% probability, thus strongly supporting previous habitat interpretations (Wyss *et al.*, 1994; Flynn *et al.*, 2003). The raw percentages used in our analysis are provided in table 2 and the structure matrix of the two functions is provided in table 3.

TABLE 2. Structure coefficients (pooled within-groups correlations between discriminating variables and standardized canonical discriminant functions) for DFA by habitat type.

	FUNCTION 1	FUNCTION 2
Frugivorous	-0.023	-0.256
Folivorous	0.106	0.252
Insectivorous	-0.148	0.423
Mass Class VII	0.332	-0.626
Mass Class VIII	-0.090	0.468
Arboreal	-0.147	-0.498

The proportion of terrestrial taxa was not used in either discriminant function.

TABLE 3. Percentages of mammal species in each of seven macroecological categories for Tinguiririca and sixteen modern Neotropical faunas from Kay & Madden (1997).

FAUNA	HABITAT	FRUGIVORES	FOLIVORES	INSECTIVORES	MASS CLASS VII	MASS CLASS VIII	ARBOREAL	TERRESTRIAL
Guatopo	Mixed	42.5	15.0	20.0	10.0	2.5	60.0	40.0
Masaguaral	Open	37.9	17.2	13.8	13.8	3.4	55.2	44.8
Puerto Páez	Open	45.8	20.8	4.2	12.5	0.0	45.8	54.2
Puerto Ayacuchi	Mixed	53.3	13.3	15.6	4.4	4.4	57.8	42.2
Esmeralda	Closed	60.6	9.1	13.6	6.1	3.0	69.7	30.3
Manaus	Closed	49.0	13.7	17.6	7.8	5.9	62.7	37.3
Belém	Closed	35.5	14.5	19.4	8.1	4.8	58.1	41.9
Caatingas	Mixed	19.0	23.8	28.6	4.8	4.8	38.1	61.9
Federal District	Mixed	39.4	19.7	19.7	3.0	4.5	37.9	62.1
Acurizal	Mixed	35.7	19.0	11.9	4.8	11.9	42.9	57.1
Chaco	Mixed	19.4	27.8	25.0	0.0	11.1	30.6	69.4
Transitional Forest	Closed	20.0	22.2	24.4	2.2	4.4	42.2	57.8
Low Montane	Closed	34.6	26.9	3.8	3.8	0.0	46.2	53.8
Cocha Cashu	Closed	52.9	14.3	14.3	8.6	5.7	67.1	32.9
Rio Cenapa	Closed	43.5	12.9	17.7	8.1	4.8	61.3	38.7
Ecuador Tropical	Closed	43.9	11.0	18.3	7.3	3.7	63.4	36.6
Tinguiririca	Unknown	12.0	80.0	4.0	4.0	8.0	12.0	88.0

Although the DFA unequivocally classifies Tinguiririca as an open habitat, the Mahalanobis distance between it and the open habitats centroid far exceeds that for any modern fauna (Fig.7). In other words, Tinguiririca is more similar to a modern savanna than a modern forest, but it still differs markedly from the sixteen modern faunas used in the DFA. This is best illustrated by the extremely high proportion of folivorous species at Tinguiririca (close to three times that of any modern fauna) and the equally low proportion of arboreal taxa (less than one third that of any modern fauna) (Tab.3). Given these numbers, it is obvious why the fauna is classified as open habitat, but the non-analog aspect of the fauna is also evident.

There are, of course, several potential explanations for the uniqueness of Tinguiririca. Given that Tinguiririca is a fossil fauna, the possibility of taphonomic bias cannot be ruled out. What such bias might include is unclear, however, since taxa of many sizes are present at Tinguiririca and the preservation of specimens is generally excellent. Moreover, the number of small arboreal frugivores missing from the fauna due to taphonomic bias would have to be quite large to result in a fauna similar to any existing today in South America. Perhaps most compelling is the great similarity between the results obtained in this study and those obtained by CROFT & TOWNSEND (2005) in their EDA of the late early Miocene Santa Cruz Fauna of Argentina; if taphonomic bias were at work, it would have to produce similar effects despite considerable temporal, geographic, and depositional differences between Santa Cruz and Tinguiririca. This seems implausible.

Errors in ecological interpretations of extinct taxa could also bias this type of analysis. Since we used very conservative ecomorphological categories, it is difficult to imagine systematic errors that would result in drastically different locomotor or dietary interpretations for the taxa under consideration. That is not to say that such errors are impossible; perhaps some of the smaller notoungulates (or even some of the larger ones) were less folivorous and more frugivorous. But as noted above, such misinterpretations would have to be prevalent to significantly alter habitat inferences.

The most reasonable conclusion is that middle Cenozoic South American faunas simply were structured very differently than modern South American communities (*e.g.*, CROFT, 2001). This should not be surprising given the great differences in taxonomic composition (at high taxonomic levels) between most fossil and modern faunas, and the dramatic changes in endemism and interchange through the Cenozoic in South America. Such differences have also been observed in North American fossil faunas (JANIS *et al.*, 2002), but not necessarily to the same degree. Even though the differences between modern and fossil faunas necessarily limit confidence in paleohabitat interpretations, the evidence presented here

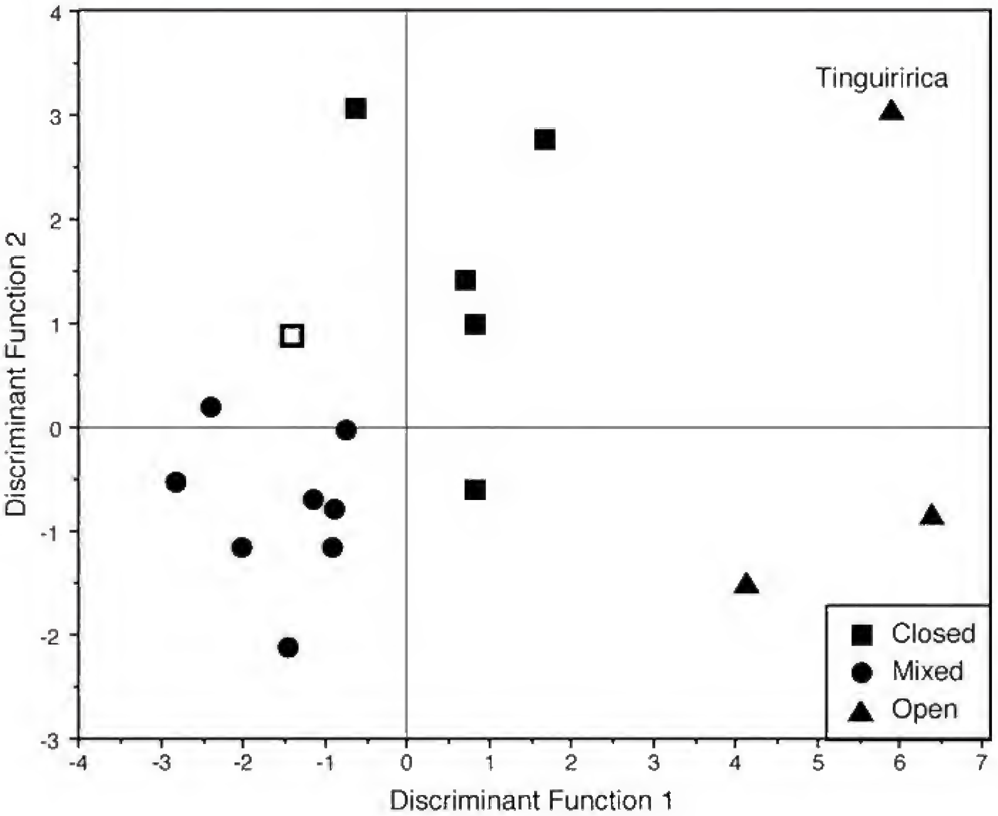

Fig.7- Bivariate plot of Tinguiririca and 16 modern Neotropical faunas based on the first two functions from the discriminant analysis described in the text. Habitats are plotted by predicted group membership (*i.e.*, habitat type), with Tinguiririca identified. The open box represents Puerto Ayacucho, a mixed habitat misidentified as a closed habitat; this was the only misidentified modern habitat.

combined with that of Flynn *et al.* (2003) provides compelling evidence for the presence of open habitats in South America by the earliest Oligocene.

CONCLUSIONS

Faunas dominated by hypsodont herbivores appear significantly earlier in South America than elsewhere in the world (Wyss *et al.*, 1994; Flynn & Wyss, 1998; Flynn *et al.*, 2003). This "precocious hypsodonty" has long been recognized for Deseadan faunas (*e.g.*, Patterson & Pascual, 1968) but has only recently been demonstrated to apply to the older Tinguirirican SALMA as well (Wyss *et al.*, 1990, 1993, 1994; Flynn *et al.*, 2003). The high degree of hypsodonty seen in many Tinguirirican species reflects a dramatic "modernization" of South American mammal communities compared to those immediately preceding this time, and may reflect environmental effects of the Eocene-Oligocene Transition (Wolfe, 1971; Prothero & Berggren, 1992). The results of EDA provide additional evidence that open habitats prevailed at these latitudes in South America by earliest Oligocene time, this despite the intriguing recent proposal that regional climate (*i.e.*, continental temperatures) in Patagonia did not change substantially across the Eocene-Oligocene Transition (Kohn *et al.*, 2004).

In addition to documenting important changes in hypsodonty on a faunal level, Tinguirirican faunas have clarified other aspects of dental evolution in various notoungulate clades. A dramatic jump in hypsodonty (without the attainment of hypselodonty) is synchronous across several lineages of notoungulates (viz., notohippids, interatheriids, archaeohyracids) by the Tinguirirican. Hypselodonty (*i.e.*, "euhypsodonty"), in contrast, appears to have originated among notoungulates in two pulses: by the Tinguirirican in hegetotheriids and mesotheriids, and by the Deseadan (late Oligocene) in interatheriids and toxodontids. Although hypselodont taxa dominate Neogene faunas, it is the very hypsodont taxa that predominate during the Tinguirirican; early mesotheriids and hegetotheriids are represented by very limited material, and toxodontids and hypselodont interatheriines are not recorded until the Deseadan. Such a pattern suggests that these dentally advanced members of "primitive" lineages (*e.g.*, archaeohyracids, notohippids) enjoyed some type of competitive superiority and/or ecological incumbency during the early Oligocene and that the later success of hypselodont taxa may be less attributable to tooth crown height than previously believed.

Biogeographic interpretations based on Tinguirirican faunas are limited by the lack of corresponding faunas from northern South America and by the uncertain age(s) of the species from Divisadero Largo. Still, some trends are worth noting. The ungulate fauna of Tinguiririca demonstrates affinities to both classical localities in Patagonia and more recently uncovered localities in northwest Argentina (Wyss *et al.*, 1994; Flynn *et al.*, 2003). This mixed pattern thus provides evidence for a mild degree of faunal provinciality during this interval, but not one reflecting dramatic ecological or geographic barriers. Absences of certain Tinguirirican-aged ungulates at Tinguiririca stem either from sampling or regional differences; study of additional new Tinguirirican faunas in central Chile (*e.g.*, Cachapoal) should help discriminate between these two alternatives. Given the small size of collections from most Patagonian localities, absences of various Tinguirirican ungulates at Cañadón Blanco and the APS level of the Gran Barranca should be accorded little biogeographic significance at this time. Increased sampling of these faunas promises to clarify biogeographic patterns during this important interval of mammal evolution.

In contrast to the overall resemblance among Chilean and Patagonian Tinguirirican faunas, the faunal differences between Tinguiririca and Divisadero Largo are striking, especially given their close geographic proximity (Fig.3). This disparity is evident in both ecomorphological and taxonomic contexts; Tinguiririca is dominated by hypsodont taxa such as archaeohyracids, interatheriids, and notohippids, whereas brachydont taxa such as oldfieldthomasiids predominate at Divisadero Largo (Simpson *et al.*, 1962). No taxon is shared at the specific or generic level between the two faunas, and none of the most abundant families (*i.e.*, the four noted above) is recorded at both. The marked disparity between Divisadero Largo and earliest Oligocene Tinguirirican localities from central Chile is consistent with the recent suggestion that the former is a temporally mixed assemblage (Cerdeño *et al.*, 2005; López & Manassero, 2006). Our review of Tinguirirican notoungulates suggests that Divisadero Largo does not sample the Tinguirirican, but rather includes many pre-Tinguirirican species and two likely post-Tinguirirican ones.

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TAPHONOMIC ANALYSIS ON FOSSILS OF PLEISTOCENE MAMMALS FROM DEPOSITS SUBMERGED ALONG SOUTHERN RIO GRANDE DO SUL COASTAL PLAIN, BRAZIL[1]

(With 15 figures)

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ABSTRACT: The taphonomic history of vertebrate remains is often complex, involving many different phases, which can be better understood by means of multivariate analyses of the taphonomic (biostratinomic and diagenetic) features on the remains. This paper describes the results of an analysis of biostratinomic features on 737 fossils of extinct terrestrial mammals (Pleistocene megafauna) from deposits submerged along the shoreline of Rio Grande do Sul State, southern Brazil. A taphonomic comparison with similar fossils from continental deposits of Chuí creek was also performed. Althought the fossils from deposits submerged along the coast of Rio Grande do Sul State exhibit some distinct physical features (*e.g.*, colour, hardness), as result of exposition of these remains to marine environment, the overall taphonomic similarities between these fossils and those from Chuí creek suggest that both fossil assemblages share a similar origin. The biostratinomic variations observed among the fossils from submarine deposits are result of differential preservation which allow to recognize at least three distinct taphofacies: a) In the foreshore, covered by sediment and subject to erosion and removal during winter storms; b) In biodethritic accumulations associated to topographic highs, also subject to erosion; and c) In deeper areas far from the coastline and not subject to wave action today.

Key words: Taphonomy. Taphofacies. Megafauna. Pleistocene.

RESUMO: Análise tafonômica em fósseis de mamíferos pleistocênicos provenientes de depósitos submersos ao longo do sul da planície costeira do Rio Grande do Sul, Brasil.

A história tafonômica de restos de vertebrados é freqüentemente complexa, envolvendo diversas fases diferentes, que podem ser compreendidas através da análise multivariada das feições tafonômicas (bioestratinômicas e diagenéticas) presentes nesses restos. Este artigo descreve os resultados da análise dos aspectos bioestratinômicos observados em 737 fósseis de mamíferos terrestres extintos (megafauna pleistocênica) provenientes de depósitos submersos o longo da costa do Rio Grande do Sul, Brasil. Foi feita também uma comparação com fósseis similares provenientes dos depósitos continentais do arroio Chuí. Embora os fósseis dos depósitos submersos ao longo da costa apresentem algumas características físicas distintas (e.g. coloração, dureza), resultantes da sua exposição ao ambiente marinho, os aspectos tafonômicos em geral são similares aos fósseis do arroio Chuí, sugerindo que ambas assembléias compartilham uma origem comum. Variações observadas nos aspectos bioestratinômicos dos fósseis dos depósitos submersos são resultado da preservação diferencial, que possibilitam reconhecer ao menos três tafofácies distintas: a) na antepraia, onde os restos estão recobertos por sedimento e sujeitos a erosão e remoção durante tempestades de inverno; b) em concentrações biodetríticas associadas a altos topográficos, também sujeitos a erosão; e c) em áreas mais profundas, longe da costa e atualmente fora da zona de ação das ondas.

Palavras-chave: Tafonomia. Tafofácies. Megafauna. Pleistoceno.

INTRODUCTION

The origin of Rio Grande do Sul coastal plain dates back to Late Pleistocene and was a result of glacio-eustatic sea level fluctuations (Tomazelli *et al.*, 2000). These fluctuations originated four extensive barrier-lagoon depositional systems parallell to the coastline (Villwock & Tomazelli, 1995).

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The third event, correlated to the maximum transgressive occurred 123 ky BP, according to oxygen isotopic curves (SCHACKLETON & OPDYKE, 1973; IMBRIE *et al.*, 1984), was responsible for the origin of Barrier-Lagoon System III, which is well preserved along the coastal plain. Lacustrine and fluvial deposits associated to this system are very important due to the presence of fossils of terrestrial mammals of Late Pleistocene age (Lujanian Land-Mammal Age, according to the biostratigraphic classification of PASCUAL *et al.*, 1966). Deposits containing these fossils are well known in two main areas along the coastal plain (LOPES, 2006): 1) on ancient fluvial deposits exposed along the banks of Chuí creek; and 2) on submarine deposits, along the foreshore and continental platform, associated to submarine topographic highs (parcels and banks). The distribution of fossiliferous deposits along the coast is uneven, with two areas of higher fossiliferous concentration (BUCHMANN, 1994): Cassino beach, near the estuary of Lagoa dos Patos lagoon, and along the 40km-long beach area known as "Concheiros", located 160km to the south (Fig.1). This uneven distribution seems to be determined by geomorphological features of the pre-Holocene substrate (BUCHMANN & TOMAZELLI, 2001). While these deposits have not yet been directly surveyed, its fossiliferous content is well-known, since many fossils are removed by winter storms and are thrown onto the beach by wave action (Fig.2). Besides fossils of terrestrial mammals, the submarine deposits also contain remains of marine invertebrates (crustaceans and echinoderms) and vertebrates (cetaceans, elasmobranchs and teleosts). Fossils of seabirds (LOPES *et al.*, 2006) and reptiles (HSIOU & FORTIER, 2007) have also been found associated to these deposits.

The fossiliferous deposits of Chuí creek are a result of the accumulation of vertebrate remains in lacustrine and fluvial environments (LOPES *et al.*, 2005a). Althought the exact origin of the submarine deposits found along the foreshore and continental platform is not yet known, the mammalian faunal content allow to establish biostratigraphic correlation with the deposits of Chuí creek, suggesting a similar age for both. The presence of fossils of terrestrial mammals suggest that the submarine deposits were originally continental deposits associated to Barrier-Lagoon System III which were subsequently drown by sea-level transgressions.

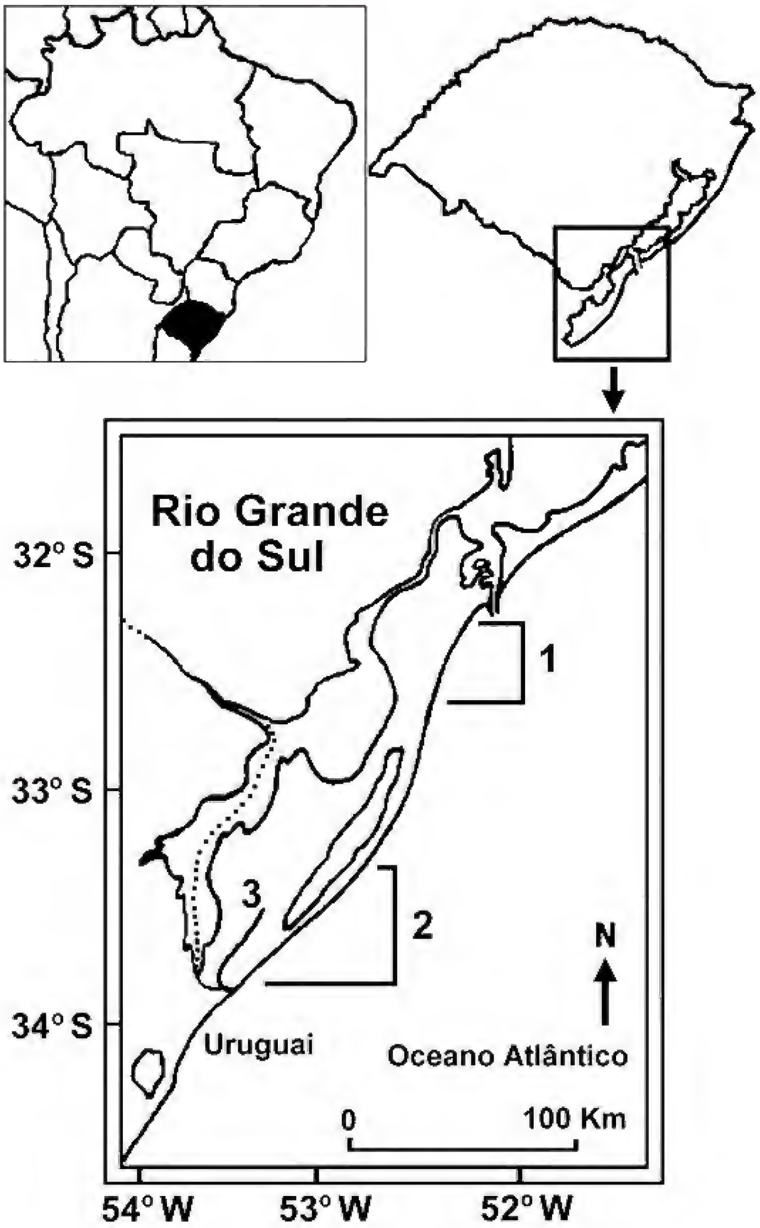

Fig.1- Map of the southern portion of Rio Grande do Sul Coastal Plain showing fossiliferous areas: 1) Cassino beach; 2) Concheiros and 3) Chuí creek.

OBJECTIVES

Since taphonomic features on fossils are determined by physical characteristics of the depositional environment in which were accumulated (Speyer & Brett, 1986), the analysis of these features on fossils from the deposits submerged along Rio Grande do Sul coast should provide information regarding the nature and characterisitcs of these deposits.

Fig.2- Fossil of an extinct mammal (in black) as found on the beach, thrown by storm waves.

The main scope of this work is to describe the biostratinomic features on fossils of Pleistocene mammals collected along the coastal plain of Rio Grande do Sul State, in order to evaluate the taphonomic context in which are preserved. Althought the ocurrence of these fossils have been known for decades, the origin of the deposits which contain it, as well as the taphonomic context of these remains are still unknown. The similar fossil content found on these deposits and in those from Chuí creek, suggest that both share a similar origin, thus some taphonomic similarities between these remains should be present. In order to test this hypothesis, a comparison between the biostratinomic features on the fossils from and those from Chuí creek was also performed. These analyses should not only provide information concerning the taphonomic context of the fossils from submerged deposits but should also improve our knowledge regarding the origin and physical characeristics of these deposits.

MATERIAL AND METHODS

The taphonomic analysis described here was carried out on 737 fossil samples from the paleontological collection of Fundação Universidade Federal do Rio Grande (FURG). Most of these fossils were collected between 1990 and 2004, on the coast section between Rio Grande and Chuí, by researchers from FURG and Universidade Federal do Rio Grande do Sul (UFRGS), while others have been donated by fishermen who accidentally collected it on bottom trawlers. Most of the fossils collected on the beach come from the area known as “Concheiros”, located about 160km south of Rio Grande, between Albardão lighthouse and Hermenegildo. The Concheiros are roughly 40km long and the beach in this area is characterized by coarser sand, steeper slope and great amount of bioclasts of marine origin (Fig.3).

Fig.3- Detail of the concentration of marine bioclasts at the Concheiros.

In this area, the marine bioclasts and fossils are accumulated by the same coastal physical processes that apparently were responsible for the origin of similar deposits in the past (Lima, 2004). The fossils collected by trawlers came from areas farther from the coast, at distances of 20km and depths between 50 and 100m.

Among the fossils subject to this analysis, all of those that could be positively identified are of Pleistocene herbivores (Tab.1), mainly medium- to large-bodied species, which are also found on deposits along Chuí creek. Small species, such as rodents (Rodrigues, 2003), are known only by teeth. For comparison with remains from Chuí creek, only those of larger species were considered (Tab.2), since small ones are either absent or scarce on this deposit.

According to Behrensmeyer (1991), taphonomic history of vertebrate remains is often complex, involving many different phases during the transition of the remains from biosphere to lithosphere. These phases can be better understood by analysing the taphonomic features on fossils, which allow to compare the remains with those from other deposits. That author proposed a quali-quantitative multivariate analysis method involving several taphonomic parameters observable on fossil remains. This method should provide information regarding biostratinomic processes these remains were subject to, therefore allow to reconstitute the taphonomic history of these remains, and is the same method employed on the analysis of fossils from Chuí creek (Lopes *et al.*, 2004), which should allow comparison between fossils from both assemblages.

The present analysis was based solely on physical characteristics of the fossils, since to date no chemical or isotopic analysis was performed on these remains. The analysis was based upon the following parameters:

1) Physical Integrity - For this analysis, the fossils were divided in three classes:
   - ➢ Complete,
   - ➢ Broken (when more than 50% of the original structure remains)
   - ➢ Fragments (when less than 50% of the structure remains).

2) Cracking - Three distinct stages were recognized:
   - ➢ Stage 0: There are no crackings.
   - ➢ Stage 1: There are only surface crackings.
   - ➢ Stage 2: There are deep crackings, which expose the internal structure of the fossil and may compromise its structural integrity.

3) Surface Abrasion - The fossils were classified either as Abraded or Unabraded.

4) Skeletal Parts - Divided according to Voorhies groups:
   - ➢ Group I - Bones easily removed by weak currents (vertebrae, ribs, etc.)
   - ➢ Group II - Bones that require higher energy to be removed (humerus, femur, tibia, etc.)
   - ➢ Group III - Bones removed only by very strong currents (skull bones, teeth, mandible, etc.).

5) Surface Markings - Present or Absent.

6) Cement - Present or Absent.

7) Colonization by Organisms - Present or Absent.

TABLE 1. Mammalian genera analyzed in this work

- Superordem Xenarthra
  - Ordem Cingulata
    - Família Dasypodidae
      - *Propraopus*
    - Família Pampatheriidae
      - *Holmesina*
      - *Pampatherium*
    - Família Glyptodontidae
      - *Doedicurus*
      - *Glyptodon*
      - *Hoplophorus*
      - *Lomaphorus*
      - *Neothoracophorus*
      - *Panochthus*
  - Ordem Tardigrada
    - Família Megatheriidae
      - *Megatherium*
    - Família Mylodontidae
      - *Glossotherium*
      - *Lestodon*
      - *Mylodon*
  - Ordem Litopterna
    - Família Macraucheniidae
      - *Macrauchenia*
  - Ordem Notoungulata
    - Família Toxodontidae
      - *Toxodon*
- Ordem Rodentia
  - Família Myocastoridae
    - *Myocastor*
  - Família Caviidae
    - *Cavia*
  - Família Hydrochoeriidae
    - *Hydrochoerus*
- Ordem Proboscidea
  - Família Gomphotheriidae
    - *Stegomastodon*
- Ordem Perissodactyla
  - Família Equidae
    - *Equus*
    - *Hippidion*
  - Família Tapiridae
    - *Tapirus*
- Ordem Artiodactyla
  - Família Camelidae
    - *Lama*
    - *Palaeolama*
    - *Hemiauchenia*
  - Família Cervidae
    - *Morenelaphus*
    - *Ozotocerus*

TABLE 2. Body mass estimations (from Fariña *et al.*, 1998) of the fossil mammalian taxa from submarine deposits which were compared with those fom Chuí creek.

Taxa		Body Mass(Kg)
Tardigrada: Megatheriidae Mylodontidae	*Megatherium* sp. *Lestodon* sp. *Scelidotherium* sp.	1300-4000
Cingulata: Glyptodontidae	*Glyptodon* sp. *Panochthus* sp.	1100-2000
Artiodactyla: Cervidae	*Blastoceros* sp. *Ozotoceros* sp. *Mazama* sp. *Morenelaphus* sp.	30-100
Perissodactyla: Equidae	*Hippidion* sp. *Equus* sp.	300-600
Notoungulata: Toxodontidae	*Toxodon* sp.	1100
Proboscidea: Gomphotheriidae	*Stegomastodon* sp.	4000

These taphonomic parameters were defined by preliminar observation of the physical aspects of the fossils, and are the same adopted by Lopes *et al.* (2004) on the analysis of fossils from Chuí creek, with the exception of the two last parameters (Cement and Colonization), which are specific of marine environment. The presence of those biostratinomic features is presumably result of the physical characteristics of the depositional environment in which these fossils were originally preserved, and subsequent alteration by re-working on marine environment. Therefore, the analysis of the taphonomic features on these fossils may provide not only information regarding their taphonomic history, but also on the depositional context in which these fossils are preserved today.

RESULTS AND DISCUSSION

The results of this analysis allowed to establish comparisons between the taphonomic features on the fossils from submerged deposits and on fossils from continental deposits exposed along the banks of Chuí creek (Lopes, 2006). The comparison between biostratinomic features on fossils from both assemblages was plotted on a taphogram (Fig.4). The most striking features on the fossils from submerged deposits are the dark colour, ranging from black to reddish, and their extreme hardness, while the fossils from Chuí creek are light-coloured (Fig.5) and more fragile. These physical differences between fossils from Chuí and from submarine deposits are presumably result of the re-working of the latter in marine environment due to sea-level transgressions. The analysis of the biostratinomic features on these fossils provided the following results:

Physical Integrity

Of the 737 fossils analyzed, 33% are fragments, 12% are broken, and 55% are complete.

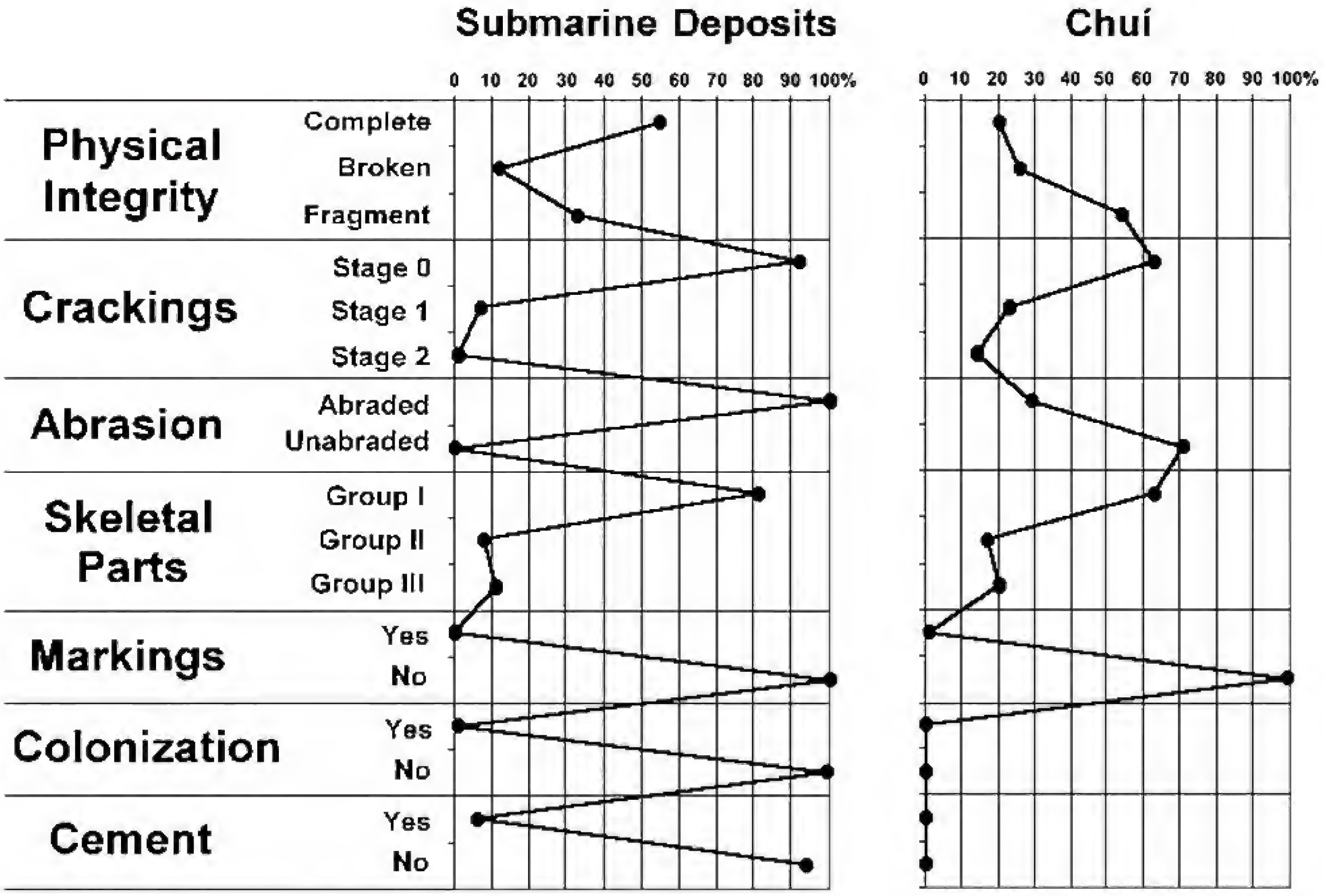

Fig.4- Taphograms comparing results of the analysis of biostratinomic features on fossils from Chuí creek and submarine deposits.

These latter are mainly small elements (about 5cm in length or diameter) such as osteoderms of armadillos (*Pampatherium* sp., *Holmesina* sp., and *Propraopus* sp.) and glyptodonts (*Glyptodon* sp., *Panochthus* sp., and *Doedicurus* sp.), as well as phalanges. Due to its shape and small size these fossils are easily removed and transported by mechanical action of water currents.

The fossils from Chuí creek are mainly small-sized, unidentifiable fragments, which exhibit plain breaking patterns characteristic of post-fossilization breaking (Holz & Simões, 2002), and still have the internal spongy structure preserved, suggesting that were subject to re-working after fossilization, otherwise the soft internal structure of the bones would not have been preserved; among these fossils there is only one conclusive example of pre-fossilization breaking. Among the fossils from submarine deposits, there is no conclusive evidence of breaking prior to fossilization, althought some fossils have lost the internal spongy structure (Fig.6). Most of the broken fossils still have the internal spongy structure preserved (Fig.7), indicating that they were broken after the fossilization.

⊀ Fig.5- Comparison between colour on a fossil from Chuí creek (left) and submarine deposits (right). Scale bar = 15cm.

Fig.6- Distal portion of a *Toxodon* femur, without internal spongy structure, probably result of re-working prior to fossilization. Scale bar = 10cm.

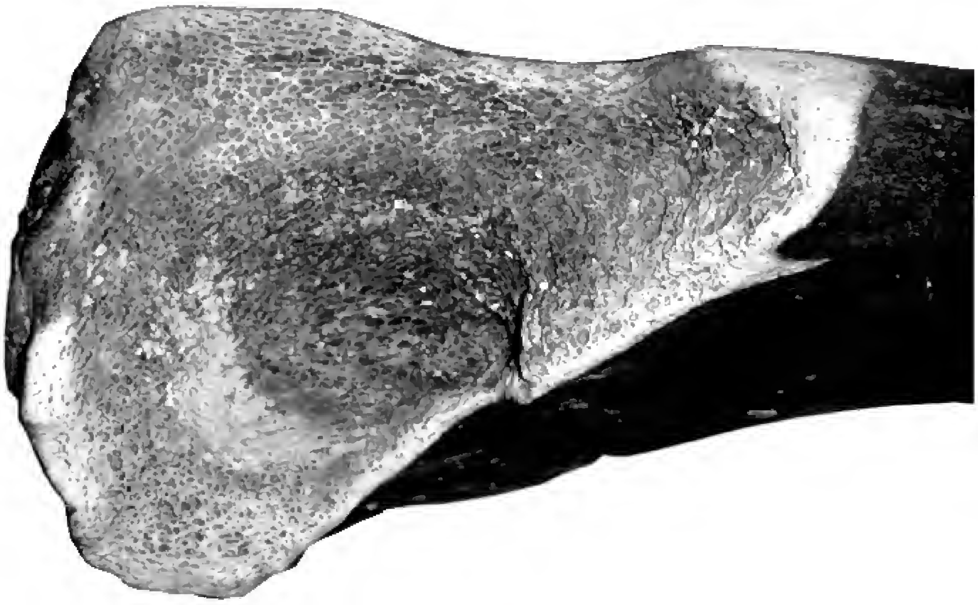

Fig.7- Fossil with preserved internal structure, indicating post-fossilization re-working.

CRACKINGS

Surface crackings on fresh bones are result of weathering and the extension and depth of these features allow to estimate how much time the remains were exposed under subaerial environment prior to deposition (BEHRENSMEYER, 1978). This author recognized six weathering stages according to the surface crackings observed on fossils. Among the fossils from Chuí creek and submarine deposits, only three cracking stages were recognized.

Only 7.3% of the fossils from submerged deposits exhibit crackings; of these, 88% exhibit Stage 1 crackings, and 12% Stage 2 (Fig.8). The crackings are more evident parallel to the longer axis of long bones, such as femora, humeri and tibiae. Althought crackings on vertebrate bones are result of weathering under subaerial conditions (BEHRENSMEYER, 1978), in the case of the fossils from submerged deposits these crackings may be result of recrystallization and expansion of the elements permineralized in the bone's structure during the diagenesis in marine environment.

Few fossils from Chuí creek exhibit surface crackings, a pattern similar to those observed among fossils from the submerged deposits. According to BEHRENSMEYER (1978) bones develop crackings within months of exposure to subaerial environment, thus the relative absence of crackings on fossils from both deposits suggest that the remains were covered by water and/or sediment shortly after death, which prevented weathering.

SURFACE ABRASION

The degree of surface abrasion on the fossils was measured by the wearing and rounding of the surfaces. The extent and degree of abrasion allowed to classify the fossils either as abraded or unabraded. Among fossils from Chuí creek, only 29% are abraded. The lack of abrasion on these fossils is probably due to their fragility that causes them to break more easily, so cannot withstand the mechanical action of water currents that would cause abrasion. All fossils from submarine deposits show signs of abrasion, and small elements such as phalanges and osteoderms (Fig.9) are more abraded. These elements are lighter and easily removed by waves, thus remaining longer time under the abrasive action of suspended sediments and friction with the bottom in the surf zone. This abrasive action is responsible for the great amount of small (<1cm) and rounded, unidentifiable fossil fragments found along the beach.

Bigger and heavier fossils (*e.g.*, tibiae, femora) exhibit fewer signs of abrasion, and these, when present, are more conspicuous on processes and articular surfaces (Fig.10). This lack of abrasion indicates that bigger fossils are subject to abrasive action of suspended sediment and friction with the bottom for a short time. This, plus the size and weight of these remains, which make their removal possible only under high wave energy conditions (during winter storms), suggest that the source area is not far from the beach, which make the time interval between removal and deposition of these fossils onto the beach relatively short. On the other hand, many small fossils exhibit very abraded and polished surfaces, and there is also a great amount of very rounded centimeter-sized fossil fragments.

Comparisons between fossils from Cassino beach and Concheiros performed by CARON (2004) revealed that those from Cassino are much more rounded and spherical than those from Concheiros, indicating greater re-working probably due to greater distance from source area.

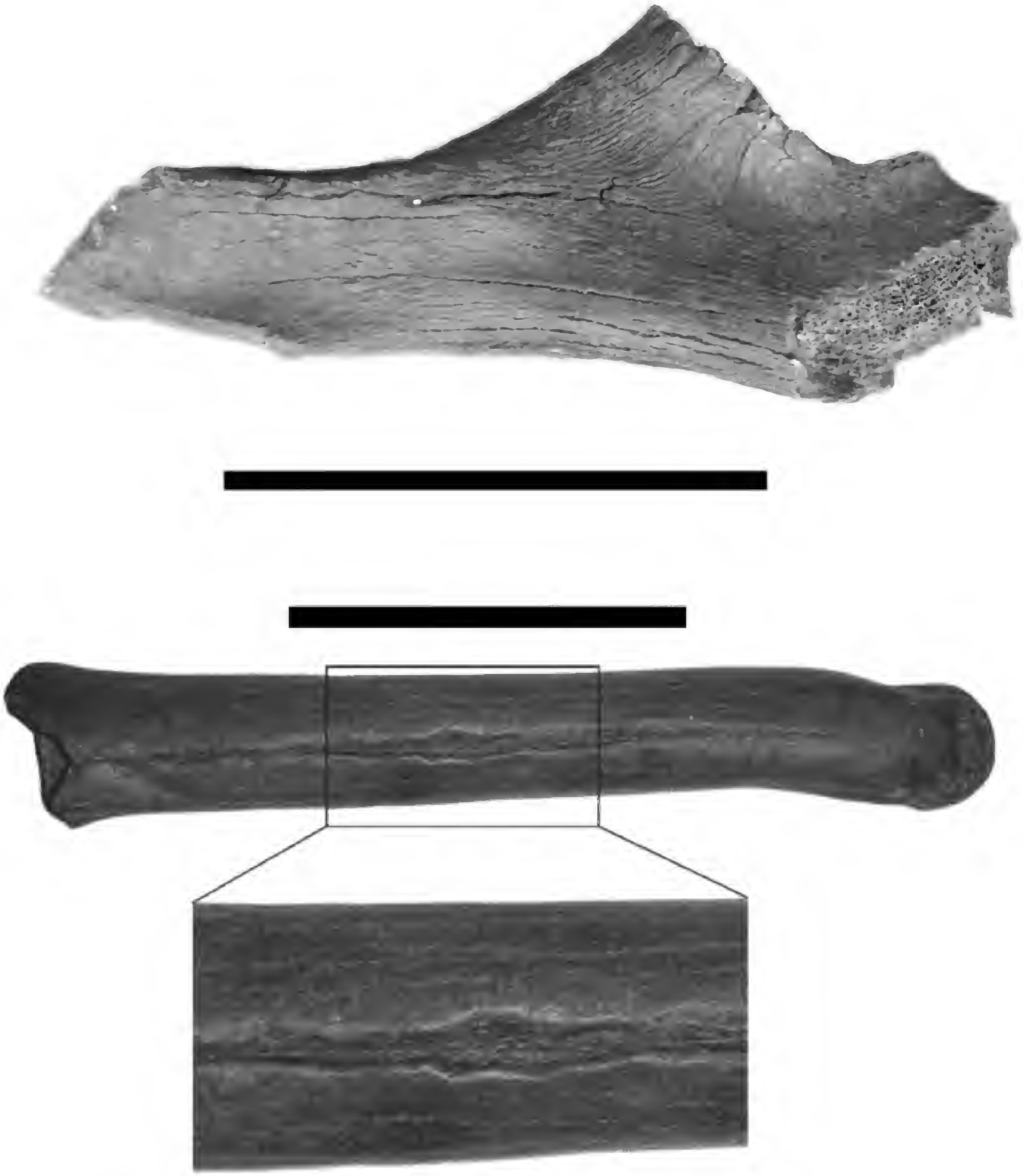

Fig.8- Differences between cracking stages: Stage 1 (top) and Stage 2 (bottom). Scale bars = (a) 20cm; (b) 10cm.

The fossils from Cassino also exhibit a normal size distribution, with modal size between 32 and 64mm. On the other hand, fossils from Concheiros exhibit a bi-modal distribution, with modes comprising fossils of 8 to 16mm and 32 to 64mm (Fig.11). These features allow to divide the fossils from Concheiros in two groups: 1) small (<2cm) fossils that are continuously being abraded, and 2) bigger fossils that are not under constant abrasive action of suspended sediment and/or friction with the bottom.

SKELETAL PARTS

For the analysis of this parameter, only fossils that could be assigned to Voorhies Groups were considered. The analysis revealed the presence of skeletal parts of the three Groups, being 81% of Group I, 8% of Group II, and 11% of Group III. These proportions are comparable to those observed among the fossils from Chuí creek. This similar pattern suggests that both deposits originated in the same sedimentary context, on fluvial environments in which vertebrate remains were accumulated and re-worked. The presence of articulated skeletal parts (Lopes *et al.*, 2001) among fossils from Chuí creek indicate that some remains were deposited and fossilized in place, while other fossils were removed and transported from source areas located at varying distances.

Surface Markings

None of the fossils analyzed exhibit any surface markings that could conclusively be attributed to biogenic processes such as scavenging, predation or use as human tools. It is possible that these markings, if present, were masked by the re-working of these fossils on marine environment. On the other hand, only three fossils from Chuí creek exhibit surface markings, in the form of thin, parallel grooves, but the origin of these markings could not be conclusively attributed to biogenic processes. The lack of surface marking suggests that the vertebrate remains from these deposits were quickly covered by water and / or sediment soon after death.

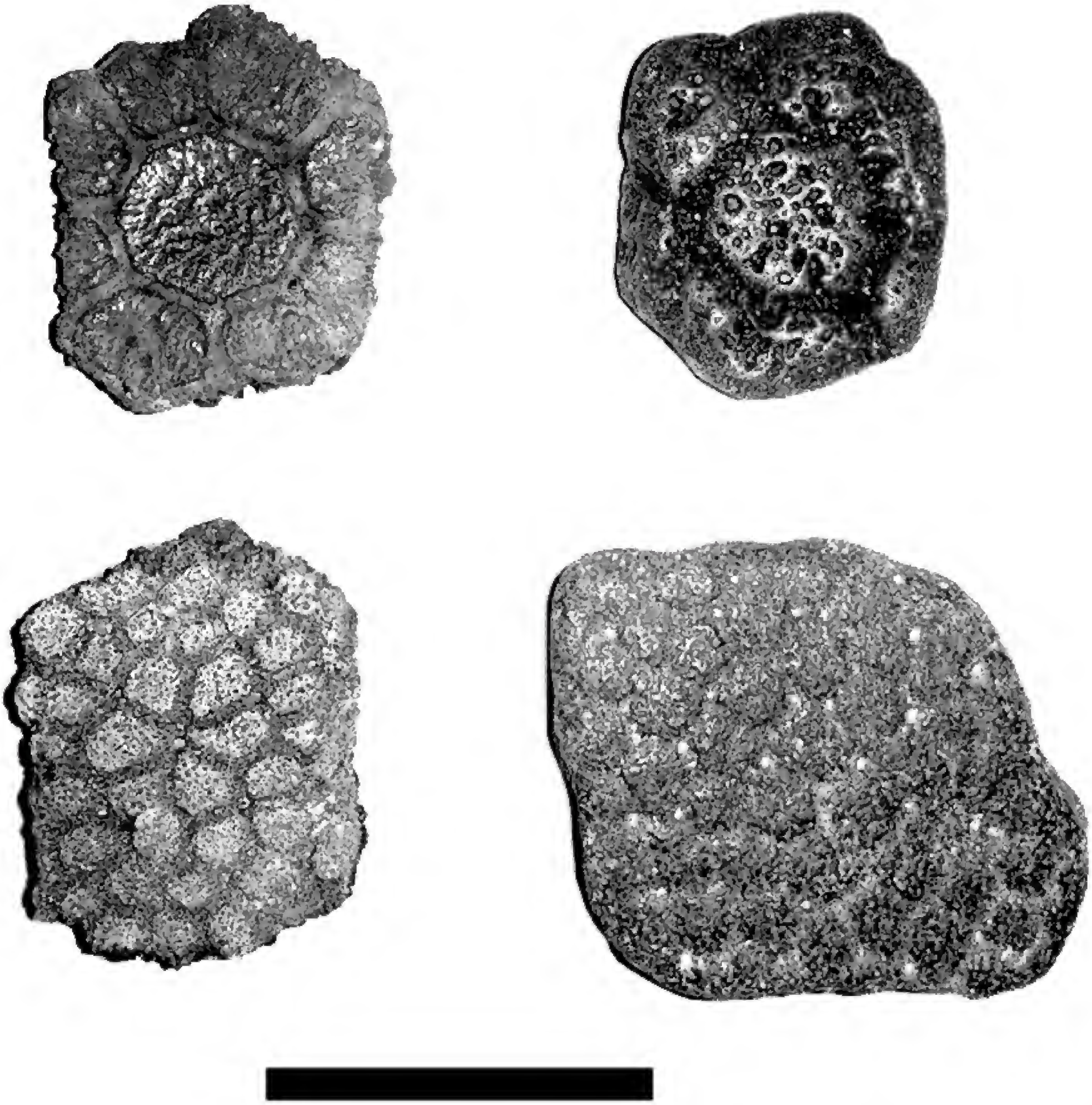

Fig.9- Comparison between fossils from Chuí creek (left) and submarine deposits (right), showing the significant abrasion on the latter. The fossils are osteoderms of *Glyptodon* sp. (top) and *Panochthus* sp. (bottom). Scale bar = 5cm.

CEMENT

Among the fossils analysed, 45 samples are associated to cement, either embedded in beach rock blocks (Fig.12) or with cavities filled with cement (Fig.13). The cement is carbonatic in origin, precipitated under beach environment warmer climate regime and exhibits recrystallization, which indicates subsequent exposition to freshwater (BUCHMANN, 2002). In one of the fossils, the recrystallization and subsequent expansion of the calcite crystals caused the fossil to fracture (Fig.14). The cementation of fossils of terrestrial mammals together with very fragmented marine bioclasts suggests that these remains were concentrated together in the past on high-energy beach environment.

The dissolved carbonate precipitation as cement would be possible only under tropical climate conditions (STODDART & CANN, 1965), a process that can be observed today in northeastern Brazil (BARROS *et al.*, 2003; GUERRA *et al.*, 2005). This implies that the climatic conditions at the time of precipitation of the carbonate cement associated to fossils were warmer than the present climate regime in southern Brazil.

The source of the beach rock blocks are rocky topographic highs (parcels and banks), located on the continental platform. These highs are disposed parallel to the coastline as narrow, linear ridges (FIGUEIREDO, 1975), separated from each other by depressions where bioclasts are accumulated. These deposits are regarded as ancient coastlines (ASP, 1999), cemented by carbonate precipitation during events of sea-level stabilization under warmer climate regime. The erosive action of storm waves, mainly during winter, removes blocks from the highs and transport it to the beach. The biofabric of the beach rocks ranges from matrix-supported to bioclasts-supported; the shells range from milimetric-sized, unidentifiable fragments, to bivalves in life position, with valves still closed. The granulometry of the matrix ranges from mud to medium-sized sand grains, and there is also colour variation, from black to reddish. These differences suggest several events of accumulation and cementation of bioclasts, under varying local conditions and episodic storm events.

COLONIZATION

Only eight fossils exhibit its surface colonized by marine organisms (Fig.15). These organisms are representative of diverse taxonomic groups, which have a wide bathymetric distribution. There are no conclusive evidences of the presence of boring organisms, only fouling organisms were observed, such as barnacles, corals, sponges, and bryozoans. The few colonized fossils come from great distance from the coast, at depths more than 50m, outside the influence of waves. None of these fossils ever come to the beach. All the samples were collected by fishing boats with trawls.

Fig.10- Abrasion on bigger fossils. Scale bar = 10cm.

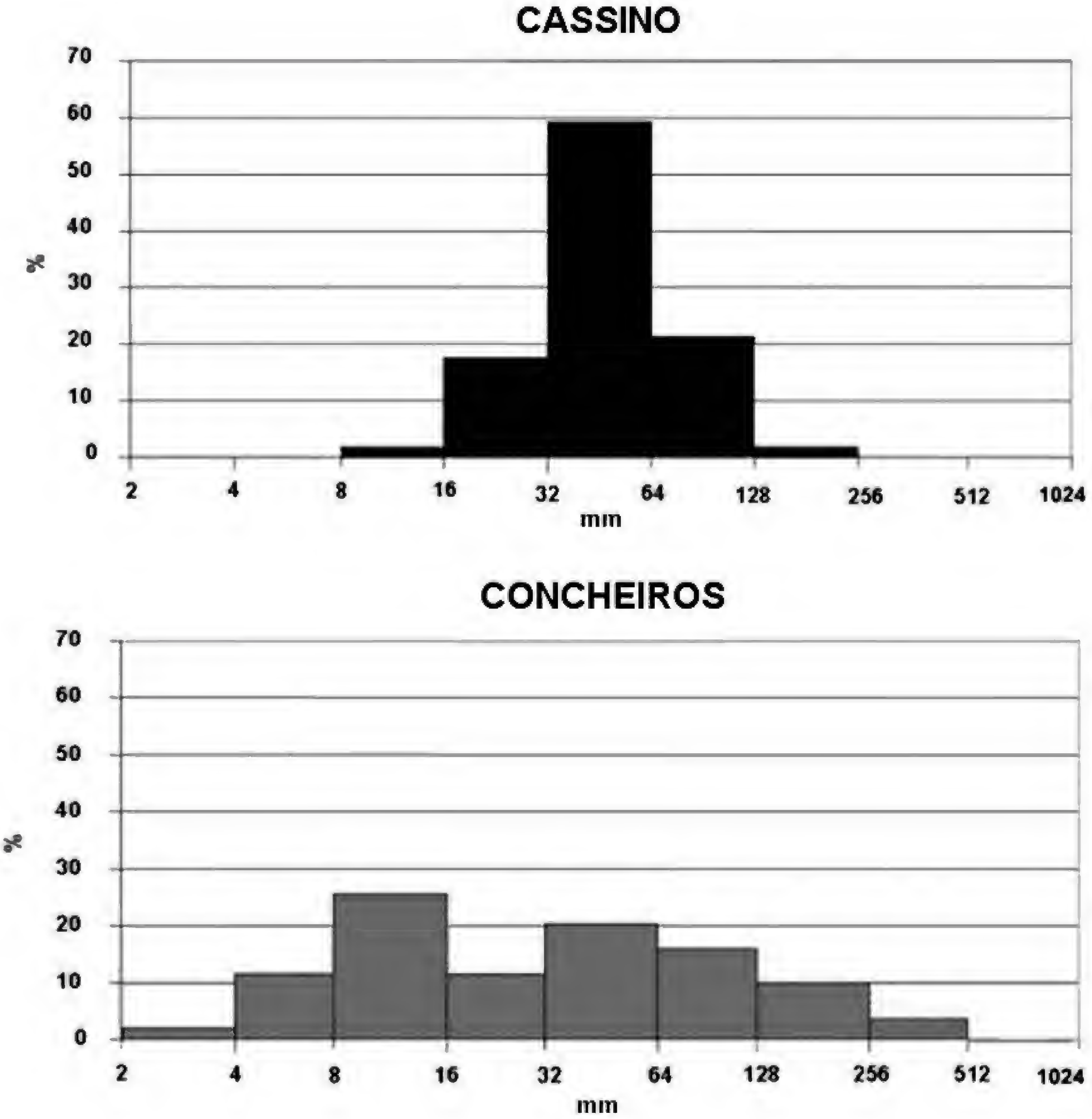

Fig.11- Comparison between sizes (in milimeters) of fossils from Cassino beach and Concheiros (modified from CARON, 2004)

The absence of colonizing organisms in bigger and well-preserved fossils indicate that these remains are covered by sediments in deposits that are only recently being exposed to erosion by marine dynamics; the smaller fossils are not colonized because they are constantly being transported and abraded by wave action in the surf zone.

Since taphonomic features on fossils are determined by physical characteristics of the depositional environment in which were accumulated, differences on preservation among fossils of the same taxonomic groups should reflect the influence of distinct environmental conditions (SPEYER & BRETT, 1986). The analysis of these features should allow the recognition of specific sedimentary environments, as well as reconstitute the taphonomic history of these remains. Althought re-worked and altered by exposition to marine environment, the fossils from submerged deposits along southern Rio Grande do Sul coast show taphonomic similarities with fossils from Chuí creek deposits. These similarities, as well as the presence of the same taxonomic groups in both deposits, suggest that they share a similar origin, on lacustrine environments in which the fossils were accumulated.

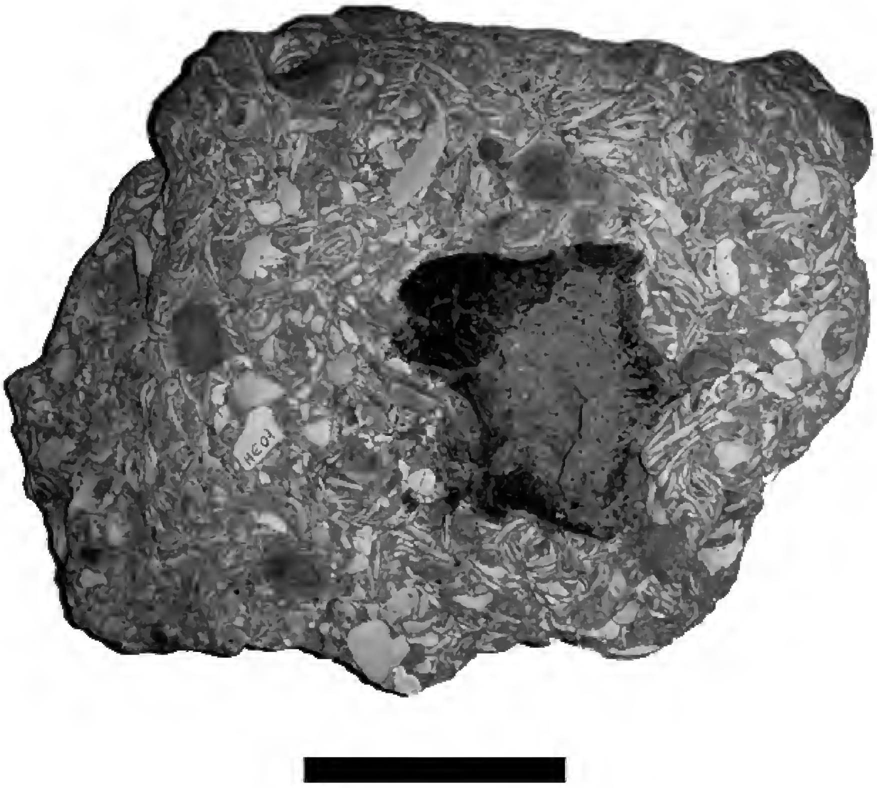

Fig.12- Beach rock with a fossil (in black) embedded on the matrix. Scale bar = 5cm.

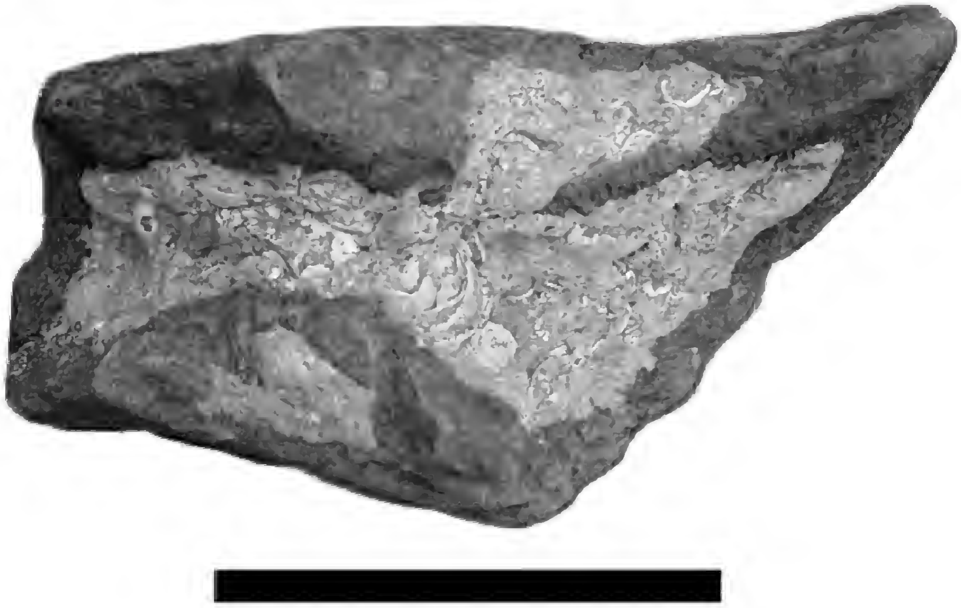

Fig.13- Fossil with cavity filled with carbonate cement. Scale bar = 10cm.

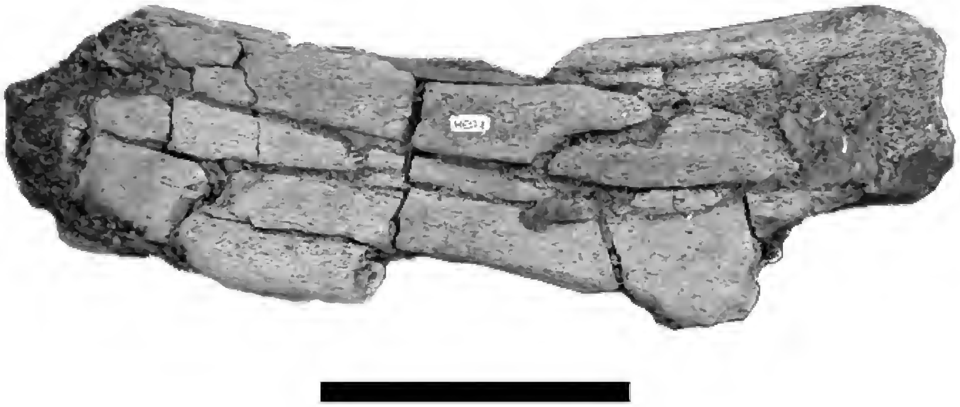

Fig.14- Fossil cracked due to recrystallization and expansion of carbonate cement. Scale bar = 10cm.

Fig.15- Fossil of a *Toxodon* sp. (occipital portion of skull, in dorsal view) with surface colonization. Scale bar = 20cm.

Subsequently, sea-level transgressions re-worked some of these deposits and its associated fossils. This re-working in marine environment exposed these fossils to new environmental conditions, which resulted in distinct taphonomic features, which allow to divide these remains in three groups:

Group 1: Fossils without cement and/or colonization by marine organisms – In general, the bigger fossils of this group are well-preserved, while the small ones are broken and so much abraded. These fossils can be found associated to shell fragments and fossils of marine organisms (crustaceans, fishes, echinoderms) on the beach, where are thrown by waves during winter storms.

Group 2: Fossils with cement, without colonization – These fossils are either embedded in beach rock blocks or with its cavities filled with cement. The cement is carbonatic and was subject to recrystallization due to subsequent exposition to freshwater. Fossils embedded in beach rock slabs are more rounded and exhibit significant abrasion, which suggest that were subject to intense re-working prior to cementation.

Group 3: Fossils colonized by marine organisms – These fossils have their surfaces colonized by fouling marine organisms such as sponges, corals, bryozoans, and barnacles. These fossils are relatively well-preserved, without abrasion or cement, like fossils from Group 1.

CONCLUSIONS

Althought the fossils from deposits submerged along the coast of Rio Grande do Sul State exhibit some remarkable physical differences (*e.g.*, colour, hardness) in comparison to those from Chuí creek, the overall taphonomic similarities between these remains suggest that both fossil assemblages share a similar origin. The main taphonomic differences are result of the exposition of the former to marine environment. These remains were probably deposited and fossilized in continental environments of Barrier-Lagoon System III, just like the fossils from Chuí creek. Subsequently, sea-level oscillations re-worked those deposits and made its fossil content subject to a new diagenetic process, which caused these remains to become darker and heavier than the fossils from Chuí creek.

The taphonomic variability among fossils from submarine deposits indicates that these remains are preserved in at least three distinct sub-environments along the foreshore and continental platform. In the fossils from Group 1, the absence of surface colonization suggests that these remains are covered by sediment until its removal and transport to the beach. The general good preservation of these remains indicates that they spend a short time under direct wave action, from the removal to transport to the beach. The presence of fragile seabird fossils from these deposits (Lopes *et al.*, 2006) seems to corroborate this. Therefore, the submerged deposits from where they come are biodethrithic concentrations located near the shoreline, which are being re-worked by erosive processes observed today along Rio Grande do Sul coast (Dillenburg *et al.*, 2004). The fossils from Group 2 come from rocky deposits that were originated by carbonate precipitation under warmer climate in paleo-beaches, where were re-worked and concentrated together with shell fragments and fossils of marine organisms, in an environment similar to Concheiros. Subsequent sea-level oscillations exposed these deposits to freshwater, which caused the carbonatic cement to recrystallize. The lack of surface colonization by marine boring organisms (*e.g.*, sponges, corals) suggests that these remains are being subject to direct and constant wave action today. Fossils from Group 3 are the most scarce among the samples, due to the fact that they are never thrown onto the beach by wave action, but are often brought to surface by trawlers from depths between 20 to 150m, in areas called "graveyards" by fishermen. The good preservation suggest that these fossils are not being subject to re-working by waves today, and the presence of fouling organisms indicate that they are not covered by sediment.

The concept of taphofacies can be defined as a sedimentary rock recognized by a specific set of preservation features on the fossils contained on it (Holz & Simões, 2002). Thus, the biostratinomic variations observed among fossils from submarine deposits can be interpreted as result of differential preservation of these remains, therefore allowing the recognition of at least three submarine taphofacies to which these fossils are associated: Taphofacies 1 – characterized by well-preserved fossils that have been recently exposed to marine environment, due to its removal from deposits near the present beach that are being subject to erosion; Taphofacies 2 – contains fossils with recrystallized carbonate cement and evident signs of abrasion and cracking, due to exposition and re-working on a beach environment in the past; and Taphofacies 3 – characterized by well-preserved fossils, similar to those of Taphofacies 1, but are colonized by fouling organisms such as barnacles, sponges and corals.

The association of fossils of terrestrial mammals to remains of marine organisms in the same depositional environment on the past (as evidenced by fossils cemented together with marine bioclasts in beach rocks) and at the present (at the Concheiros), and the varying degrees of preservation of these remains, suggest that sea-level oscillations have been cyclicaly re-working fossiliferous continental deposits of Barrier-Lagoon System III throughout the Pleistocene and Holocene.

The present work is the first detailed description of taphonomic features on fossils of terrestrial mammals from deposits submerged along Rio Grande do Sul coast. Additional and more detailed research, employing other methods such as hydroacoustic soundings, autonomous diving, and petrological and geochemical analyses on the fossils should provide information about the origin, extension, and geometry of the submerged fossiliferous deposits, their stratigraphical context, and the nature of the diagenetic modification on these fossils. The data presented here, together with stratigraphical, geochemical and sedimentological data, should allow the detailed reconstitution of the taphonomic history of the fossil remains fom these deposits. This will allow to assess the physical processes responsible for the origin of the fossiliferous deposits, which will improve our knowledge regarding the origin and evolution of Rio Grande do Sul coastal plain.

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THE PALAEOBIOGEOGRAPHY OF MESOZOIC MAMMALS: A REVIEW [1]

(With 21 figures)

THOMAS H. RICH [2]

ABSTRACT: The fossil record of Mesozoic mammals is much more meagre than that of Cainozoic ones. Despite this deficiency, it is possible to make some useful generalisations about the biogeographic history of this group during the Mesozoic Era. Compared with the Jurassic, where cosmopolitanism is frequent amongst the various mammalian families, regionalism is more commonly the case in the Cretaceous, particularly the Late Cretaceous. This reflects the progressive breakup on first Pangea and then Gondwana as the Mesozoic Era progressed. The conventional hypothesis that the therians arose on the northern continents and spread to the southern ones owes much of its strength to the poor Mesozoic mammalian record in the latter. Recent discoveries in the Southern Hemisphere suggest that caution is warranted in accepting the conventional hypothesis.

Key words: Palaeobiogeography. Fossil mammals. Mesozoic.

RESUMO: Paleobiogeografia dos mamíferos mesozóicos: uma revisão.

O registro fóssil de mamíferos do Mesozóico é bem mais escasso que o do Cenozóico. Apesar dessa deficiência, é possível fazer algumas generalizações sobre a história bioestratigráfica desse grupo durante a Era Mesozóica. Comparado com o Jurássico, onde o cosmopolitismo é freqüente entre as várias famílias de mamíferos, o regionalismo é mais comum no Cretáceo, particularmente no Cretáceo Superior. Isto reflete a separação progressiva do Pangea e do Gondwana, à medida que a Era Mesozóica progredia. A hipótese convencional de que os Theria se originaram dos continentes do norte e se dispersaram para os do sul se deve ao pobre registro de mamíferos do Mesozóico nestes últimos. Descobertas recentes no Hemisfério Sul sugerem que é necessário se ter maior cautela para se aceitar a hipótese convencional.

Palavras-chave: Palaeobiogeografia. Mamíferos fósseis. Mesozóico.

INTRODUCTION

In 1947, George Gaylord Simpson published a detailed analysis of the distribution of mammals in North America and Eurasia during the Cainozoic (SIMPSON, 1947) (Fig.1). In this paper, he pioneered quantitative methods for assessing the interchange between the two areas. This paper stands as a model of how mammalian biogeography should be done.

Ideally, Simpson's methodology should be extended into the Mesozoic. However, several factors make that impractical. In the first place, there are far fewer mammalian taxa in the Mesozoic than the Cainozoic. Were Simpson writing that paper today on a worldwide scale, in the Cainozoic there would be about 3,500 non-volant terrestrial mammalian genera available for analysis. This is in stark contrast to the 300 mammalian genera known from the Mesozoic. For the Cainozoic, there are 50 genera for every one million years while for the Mesozoic, only two.

Second, the Mesozoic mammalian fossil record is much more incomplete than the Cainozoic. There are large temporal gaps in the Mesozoic record (Fig.2) and the number of sites where Mesozoic mammals occur is quite uneven (Fig.3). North America in the Late Cretaceous, for example, has a number of sites comparable to the Palaeocene on that continent while Australia has only four sites in the late Early Cretaceous and none in all other parts of the Mesozoic. Generally, the Gondwanan continents have far fewer sites than Laurasia, making the recognition of biogeographic phenomena in the former quite tentative for the most part.

METHODS

Unless otherwise specified, the distribution data for Mesozoic mammals given in this paper is taken from KIELAN-JAWOROWSKA *et al.* (2004).

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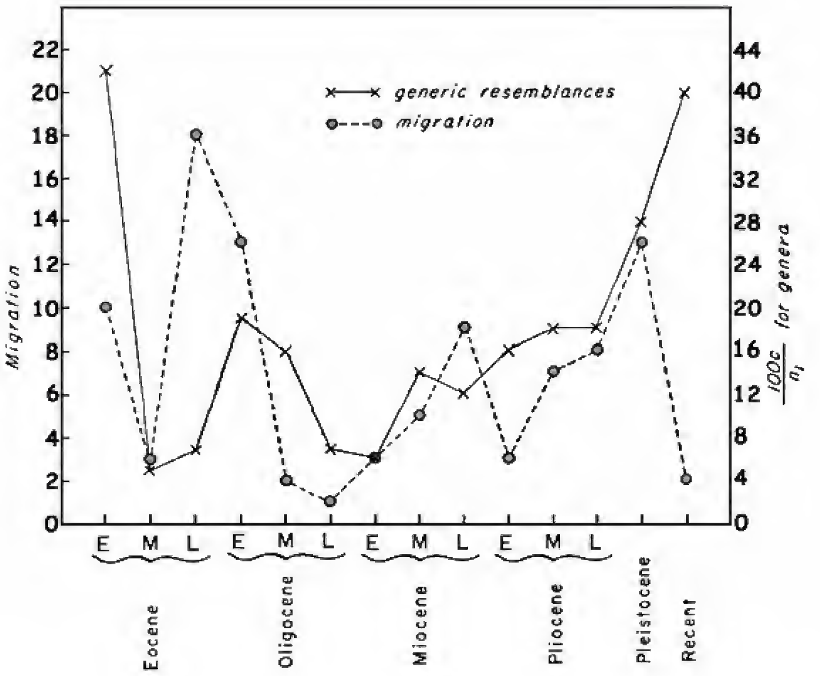


Fig.1- Figure 4 in Simpson (1947). Number of genera in common between North America and Eurasia during the Cainozoic (solid line) and amount of migration (dashed line) between the two land masses. From Simpson (1947).

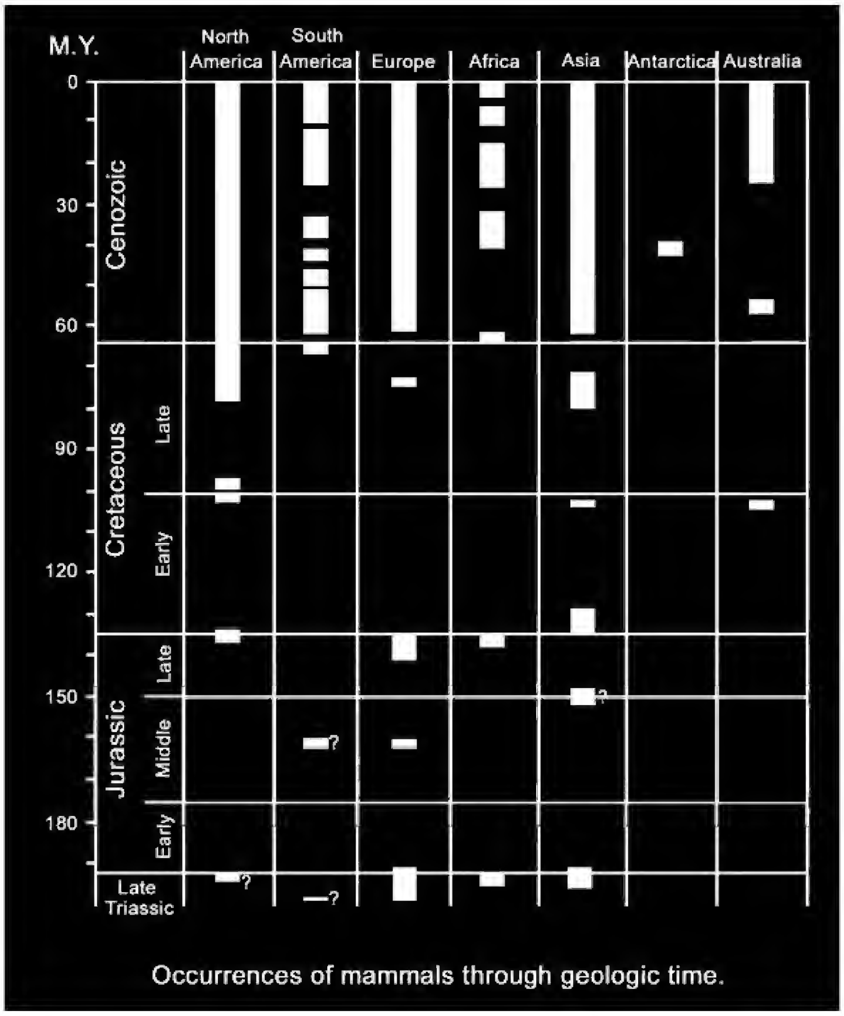


Fig.2- Periods of time in the Mesozoic and Cainozoic when fossil mammals are known on the various land masses (modified from Lillegraven *et al.*, 1979).

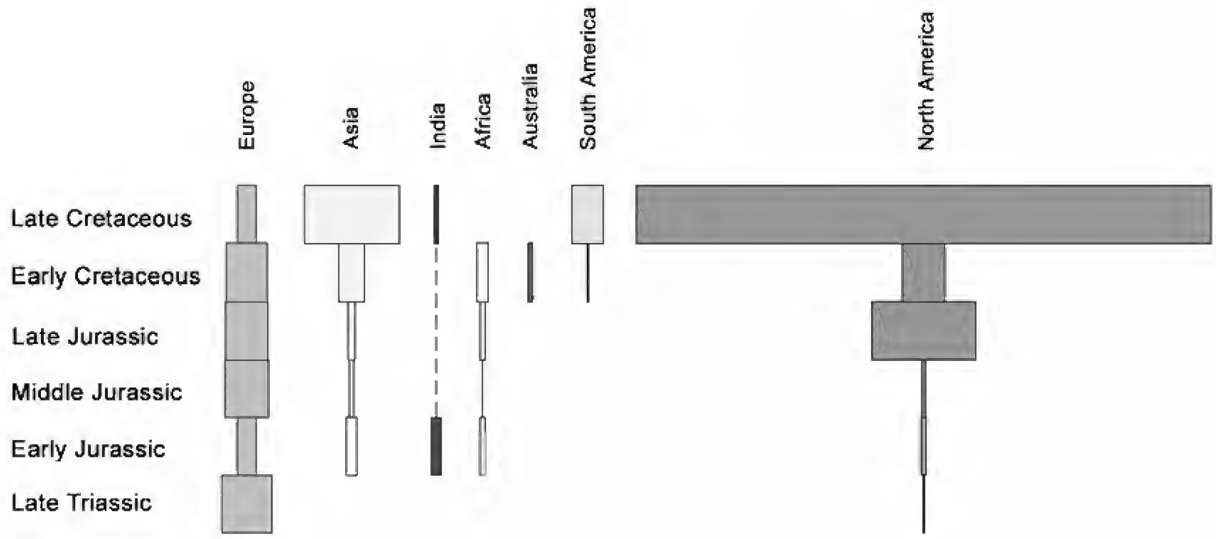


Fig.3- Relative numbers of Mesozoic mammals by continents and age. "For most pre-Late Cretaceous occurrences and virtually all occurrences outside of North America, the totals reflect all taxa from all known sites and in many cases reflect most known individual specimens. Lumping occurrences by local faunas results in under representation for the North American Late Cretaceous, which nonetheless includes a disproportionately large number of occurrences" (KIELAN-JAWOROWSKA *et al.*, 2004, p.108).

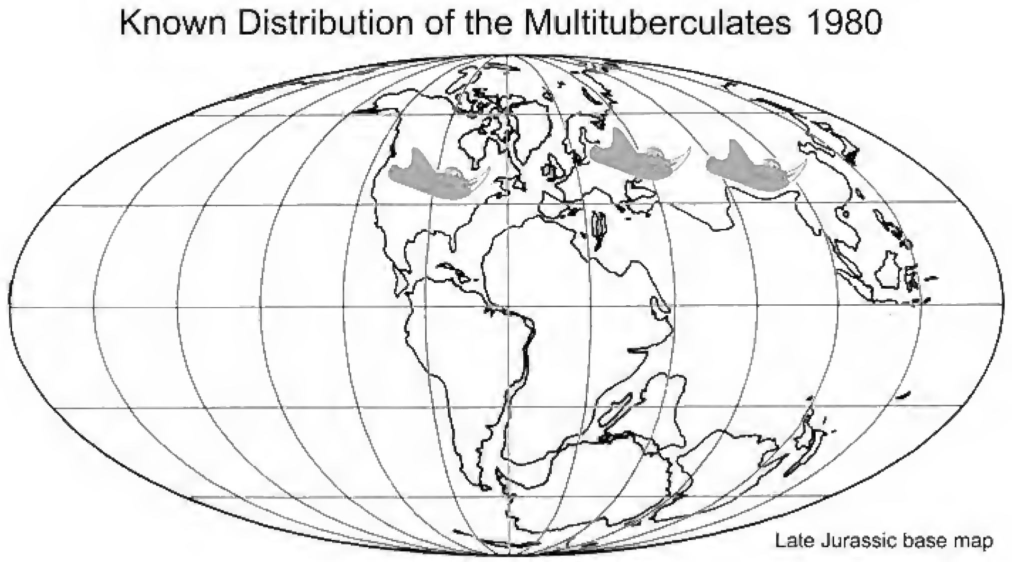
DISCUSSION

The depth of our ignorance about the distribution of Mesozoic mammals is well illustrated by the multituberculates. A distribution map of them drawn in 1980 would show the group confined to the Laurasian continents where their remains were quite abundant (Fig.4). At that time, it was quite reasonable to envision them as an exclusively Laurasian group. In the twenty-five years that have passed, records of them, some of them tentative, have been found in Africa and South America (Fig.5). These Gondwanan records are based on a handful of specimens. With this paucity of Gondwanan material, can we safely conclude that the multituberculates were primarily a Laurasian group with a few species in Gondwana? Given the few specimens of mammals of any kind that occur where these Gondwanan Mesozoic multituberculates have been found, that is an interpretation of the evidence that seems unwarranted. True, they are rare as fossils but as part of living communities, they may have been quite abundant. We simply cannot tell from the available specimens.

The Mesozoic palaeobiogeography of mammals can conveniently be divided into the Late Cretaceous and the pre-Late Cretaceous. This is owing to two factors. First, during the Late Cretaceous the number of productive fossil mammal sites and hence the record is much better. Second, the extant metatherians and eutherians are a significant part of the Late Cretaceous mammalian assemblage and hence molecular techniques can be applied to their living descendants to get additional insights about them.

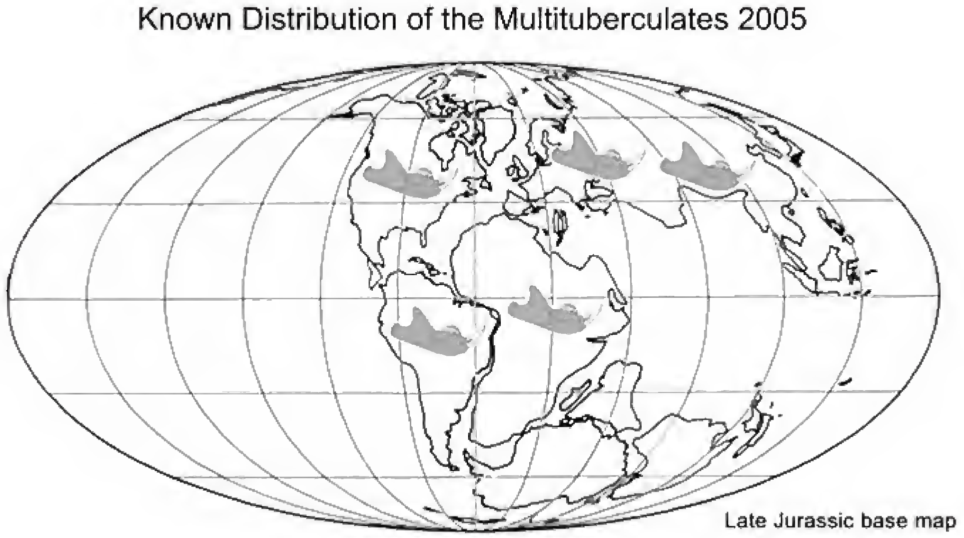
The Morganucodontidae are either regarded as amongst the most primitive mammals or mammaliformes close to the base of the Mammalia. Because of this, they provide a clue as to the place of origin of the Mammalia. In the late Triassic, except for Greenland, they occur on every landmass where any mammals or mammaliforms are known (Fig.6). From this, in the highly appropriate words of Jason Lillegraven in another context, the conclusion seems to be that mammals arose somewhere on the Earth's dry surface.

Because in the Mesozoic, there is only about 4% as much data concerning mammalian distributions per unit time as is available in the Cainozoic, only the broadest biogeographic generalisations are possible. Despite this drawback, a significant contrast can be seen in the distribution of mammalian families in the Jurassic as opposed to the Cretaceous (Figs.7-8). A greater percentage of the Jurassic families occur on two or more land masses than is the case in the Cretaceous. This is concordant with the closer proximity of the land masses during the Jurassic as compared with the Cretaceous when the break up of Pangea had proceeded much further.


Known Distribution of the Multituberculates 1980

Late Jurassic base map

Fig.4- Land masses where multituberculates were known to have been present in 1980.


Known Distribution of the Multituberculates 2005

Late Jurassic base map

Fig.5- Land masses where multituberculates were known to have been present in 2005.

Interestingly, in the both the Jurassic and Cretaceous, there are more links between individual Gondwanan land masses and Laurasian ones than there are between pairs of Gondwanan land masses. This is presumably due to the fact that many more families are known on the Laurasian land masses so, all else being equal; a match is more likely to be found there. Given the continental positions, particularly in the Jurassic, it seems unlikely that these greater frequencies of connections of the Gondwana land masses with those to the north rather than to each other was actually the case. What this broad brushstroke data cannot do is to provide evidence for the direction of movement between land masses. That would require far more information, particularly well dated sites.

Unquestioned docodontids are known only from Laurasia and range in age from Middle Jurassic to Early Cretaceous. Outside of this temporal and geographic range, there are two specimens that may be docodonts. First is a single Late Triassic tooth from France assigned to the genus *Delsatia* (SIGOGNEAU-RUSSELL & GODEFROIT, 1997).

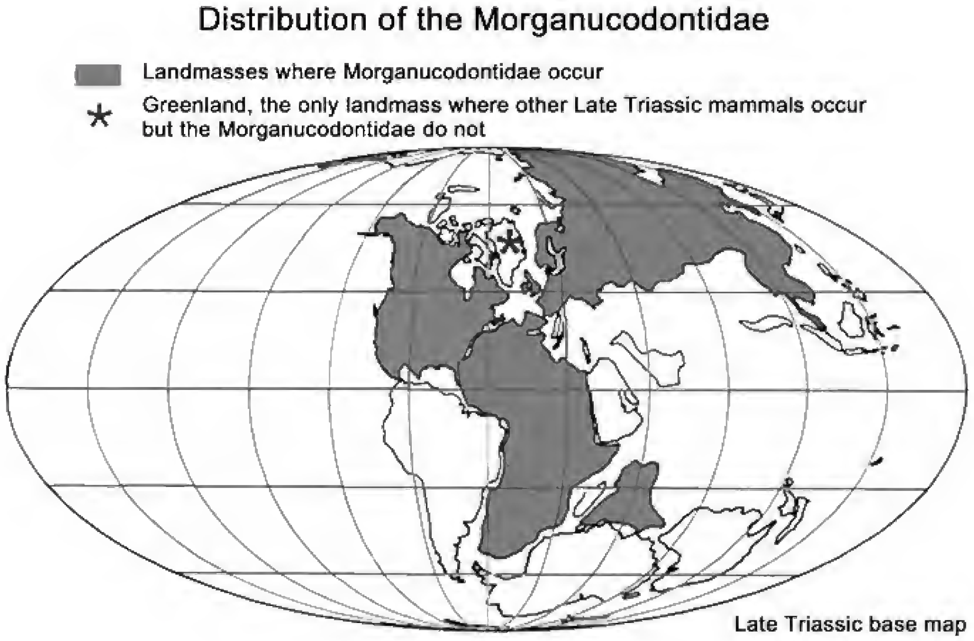


Fig.6- Known distribution of the Morganucodontidae. Base map Late Triassic.

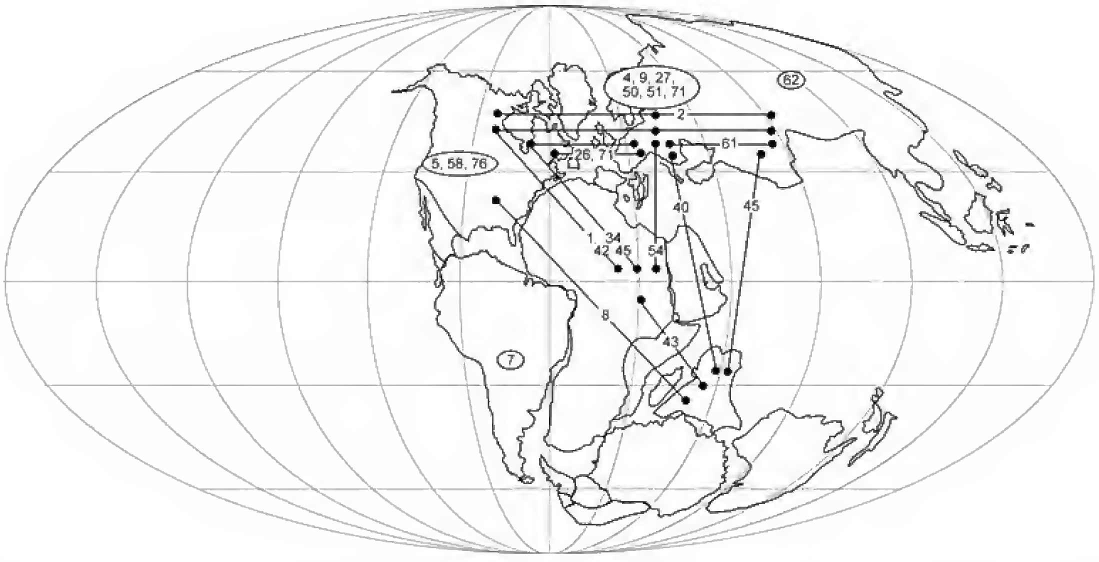


Fig.7- Records of Jurassic mammalian families on a Bajocian basemap. The same families found on two or more landmasses are linked together by a solid line. The linkage lines do not necessarily imply migration routes or directions of separation of land masses in vicariant events. For example, the Morganucodontidae are known both in India and Asia. The line linking them passes through Europe, North America, and Africa. Despite this, the interchange between Asia and India could have been more direct. 1. "Amphilestidae"; 2. Aegialodontidae; 3. Aguitheriidae; 4. Albionbaataridae; 5. Allodontidae; 6. Alphadontidae; 7. Ameghinichnidae; 8. Amphidontidae; 9. Amphitheriidae; 10. Arctocyonidae; 11. Arginbaataridae; 12. Arguimuridae; 13. Asiatheriidae; 14. Asioryctidae; 15. Ausktribosphenidae; 16. Austrotriconodontidae; 17. Barbereniidae; 18. Bobolestidae; 19. Bondesiidae; 20. Cimolodontidae; 21. Cimolomyidae; 22. Deltatheridiidae; 23. Djadochtatheriidae; 24. Docodontidae; 25. Donodontidae; 26. Dryolestidae; 27. Eleutherodontidae; 28. Eobaataridae; 29. Eucosmodontidae; 30. Ferugliotheridae; 31. Glasbiidae; 32. Gobiconodontidae; 33. Hahnodontidae; 34. Haramiyidae; 35. Hyopsodontidae?; 36. Kennalestidae; 37. Kermackiidae; 38. Kogiaononidae; 39. Kollikodontidae; 40. Kuehneotheriidae; 41. Kulbeckiidae; 42. Leptictidae; 43. Megazostrodontidae; 44. Mesungulatidae; 45. Morganucodontidae; 46. Neoplagiaulacidae; 47. Nyctitheriidae; 48. Otlestidae; 49. Palaeoryctidae; 50. Pappotheriidae; 50½ Paulchoffatiidae; 51. Paurodontidae; 52. Pediomyidae; 53. Peradectidae?; 54. Peramuridae; 55. Periptychidae; 56. Picopsidae; 57. Pinheirodontidae; 58. Plagiaulacidae; 59. Ptilodontidae; 60. Reigitheriidae; 61. Shuotheriidae; 62. Sinoconodontidae; 63. Sloanbaataridae; 64. Spalacotheriidae; 65. Stagodontidae; 66. Steropodontidae; 67. Sudamericidae; 68. Taeniolabididae; 69. Thereuodontidae; 70. Theroteinidae; 71. Tinodontidae; 72. Triconodontidae; 73. Vincelestidae; 74. Zalambdalestidae; 75. Zhelestidae; 76. Zofiabaataridae.

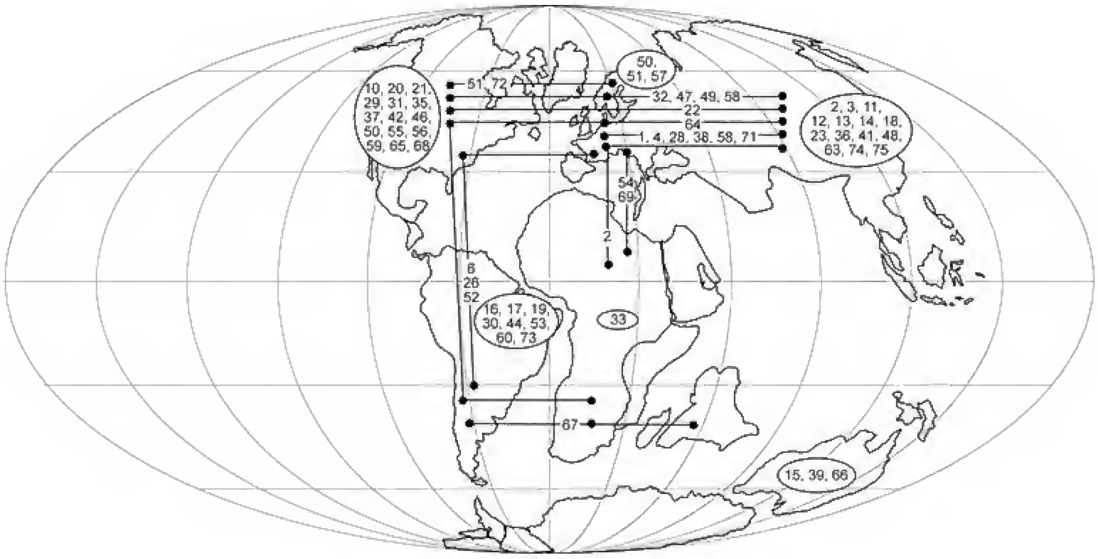


Fig.8- Records of Cretaceous mammalian families on an Albian basemap. For explanation, see caption for figure 7. 1. "Amphilestidae"; 2. Aegialodontidae; 3. Aguitheriidae; 4. Albionbaataridae; 5. Allodontidae; 6. Alphadontidae; 7. Ameghinichnidae; 8. Amphidontidae; 9. Amphitheriidae; 10. Arctocyonidae; 11. Arginbaataridae; 12. Arguimuridae; 13. Asiatheriidae; 14. Asioryctidae; 15. Ausktribosphenidae; 16. Austrotriconodontidae; 17. Barbereniidae; 18. Bobolestidae; 19. Bondesiidae; 20. Cimolodontidae; 21. Cimolomyidae; 22. Deltatheridiidae; 23. Djadochtatheriidae; 24. Docodontidae; 25. Donodontidae; 26. Dryolestidae; 27. Eleutherodontidae; 28. Eobaataridae; 29. Eucosmodontidae; 30. Ferugliotheridae; 31. Glasbiidae; 32. Gobiconodontidae; 33. Hahnodontidae; 34. Haramiyidae; 35. Hyopsodontidae?; 36. Kennalestidae; 37. Kermackiidae; 38. Kogiaononidae; 39. Kollikodontidae; 40. Kuehneotheriidae; 41. Kulbeckiidae; 42. Leptictidae; 43. Megazostrodontidae; 44. Mesungulatidae; 45. Morganucodontidae; 46. Neoplagiaulacidae; 47. Nyctitheriidae; 48. Otlestidae; 49. Palaeoryctidae; 50. Pappotheriidae; 50½ Paulchoffatiidae; 51. Paurodontidae; 52. Pediomyidae; 53. Peradectidae?; 54. Peramuridae; 55. Periptychidae; 56. Picopsidae; 57. Pinheirodontidae; 58. Plagiaulacidae; 59. Ptilodontidae; 60. Reigitheriidae; 61. Shuotheriidae; 62. Sinoconodontidae; 63. Sloanbaataridae; 64. Spalacotheriidae; 65. Stagodontidae; 66. Steropodontidae; 67. Sudamericidae; 68. Taeniolabididae; 69. Thereuodontidae; 70. Theroteinidae; 71. Tinodontidae; 72. Triconodontidae; 73. Vincelestidae; 74. Zalambdalestidae; 75. Zhelestidae; 76. Zofiabaataridae.

Another questionable record is a jaw fragment with three teeth, *Reigitherium,* from the Late Cretaceous Los Alamitos Formation of Argentina that was regarded in its original description as a docodont (Bonaparte, 1990) but is now regarded as Mammalia *incertae sedis* (Kielan-Jaworowska *et al.*, 2004).

Reflecting the fact that Mesozoic mammal sites are much more abundant in Laurasia, the eutriconodonts are much more frequent and diverse in Asia, Europe, and North America than in South America and Africa, the two Gondwana land masses with any record at all of this group. There are questionable records in the Early Jurassic of North America and India. By the Middle Jurassic, the eutrionodonts are well established in Asia and in the Late Jurassic, they occur in North America, Asia, and Africa. They are most widespread in the Early Cretaceous and persist into the Late Cretaceous in North and possibly South America. In Laurasia, there is enough of a record to at least suggest that some families were not present over that entire land mass. For example, while the Amphilestidae are known from North America and Asia including India, the Triconodontidae are known only from North America and Europe, and the Gobiconodontidae are known only from Asia and North America.

The Haramiyida are first known and most widely known in the Late Triassic of Europe. Subsequently, there are records from single sites in the Early Jurassic of North America and the Late Jurassic of Africa. On the sparse evidence that exists, the group would seem to have dispersed from Europe to North America and Africa.

The most diverse group of Mesozoic mammals are the Multituberculata. Eighteen families are recognised of which only four occur on more than one continent, all in Laurasia. This pattern is quite different from their modern analogues, the rodents, which are much more widely spread. Of the 19 Recent rodent families, 13 have records on two or more continents. Although there are records of multituberculates on two of Gondwana continents, Africa and South America, these are based on few specimens whereas in Laurasia their remains are common and taxonomically diverse.

Although not a highly diverse group, the "Symmetrodonts" are one of the most widespread of Mesozoic mammals between the Late Triassic and mid Cretaceous. This situation persisted from the time of Pangea in the Late Triassic to when the continents had split into Gondwana and Laurasia and those land masses in turn had begun to split apart by the mid Cretaceous. Five of the eight symmetrodont families are known from more than one continent. Two of the three that are restricted to one continent are known from the Late Cretaceous Los Alamitos fauna of Patagonia. They may have survived as long as they did in South America because of the isolation of that continent. The Spalacotheriidae, in contrast to these restricted families, are known from Africa, Asia, Europe, South America, and North America in the Early to mid Cretaceous.

Monotremes are now known from the Cretaceous and Cainozoic of Australia, the Cainozoic of New Guinea, and the Early Cainozoic of South America. The only evidence to support the hypothesis that they originated in Australia is the fact that they are unknown in the Campanian Los Alamitos local fauna of Patagonia. That this diverse mammalian assemblage does not include a monotreme implies that they had not yet reached South America at a time when they had been in Australia for at least 30 million years. Given that monotremes are generally regarded as quite primitive mammals and hence presumably a distinct lineage that came into existence in the early Mesozoic (Rich *et al.*, 2005), it is odd that they occur nowhere else in light of the configuration of the continents. However, given the meagre nature of the record of Jurassic fossil terrestrial vertebrates in Australia (one temnospondyl and one sauropod), monotremes quite likely thrived there through that period and are simply unknown and quite probably never will be.

Three of the eight families of eupantotheres are widespread geographically and have more than one genus in them. The other five have a single genus and are restricted to one continent. In addition to these, there are two African taxa which are not assigned to a genus and a number of European specimens that cannot be assigned to a genus or species, much less a family. Eupantotheres are most diverse in the Late Jurassic to Early Cretaceous. They occur on all the landmasses of Laurasia together with South America. The two South American families and species occur in the Late Cretaceous Alamitos fauna.

The oldest marsupials are in Laurasia, *Sinodelphis* from China being 125 myBP (Luo *et al.*, 2003) and *Kokopellia* from North America being 100 myBP (Cifelli & Muizon, 1997). As the diverse Los Alamitos local fauna of Patagonia has a variety of archaic mammals more like those of the Jurassic elsewhere and lacks therians of any kind (Bonaparte, 1990) while the early Palaeocene Tiupampa of Bolivia has both marsupials and placentals (Marshall *et al.*, 1995), this supports the conventional idea that marsupials arose in Laurasia and spread to South America. From South America, they reached Antarctica no later than the Eocene (Woodburne & Zinsmeister, 1982) and finally entered Australia in the Palaeocene or Eocene (Godthelp *et al.*, 1992, 1999). What is not clear is whether there was a single marsupial dispersal event between South America and Australia, or multiple ones. Extant marsupials can be divided quite sharply into the Ameridelphia and the Australodelphia. As the names imply, the former is found in the Americas and with one exception, the latter in Australasia. This division was first recognised on the basis of foot structure (Szalay, 1982) and subsequently supported by molecular data (Nilsson *et al.*, 2004). The one exception is the microbiothere *Dromiciops* from Chile, which is clearly an australodelphian. As *Dromiciops* appears to have been derived within the australadelphians, either its ancestors returned to South America after the dasyuromorphs plus peramelamorphs on the one hand and diprotodontians on the other differentiated in Australia, or the differentiation of the australodelphians into those two major groups occurred in South America and they independently reached Australia.

Turning to the eutherians, their Mesozoic palaeobiogeography is currently the most uncertain, particularly with regard to the placentals, those eutherians placed in extant orders. There are basically two schools of thought. The first is the "classical" school based primarily on the fossil record. The second is the "molecular" school based primarily on the analysis of DNA sequences.

The classic school holds that the eutherians arose in Laurasia and subsequently dispersed to Gondwana. This accords well with the vast bulk of the known mammalian fossil record, the oldest eutherian being *Eomaia scansoria* (Ji *et al.*, 2002). The view that despite its unevenness, the fossil record is adequate to accurately characterise these events is defended by Foote *et al.* (1999), and Archibald & Deutschmann (2001). Using statistical arguments regarding the completeness of the fossil record, they see the appearance of the eutherians as having taken place in the Early Cretaceous of Laurasia. Likewise, they regard the placentals as having arisen close to the time of their appearance in the fossil record; *i.e.*, in the aftermath of the KT boundary probably owing to the ecological release caused by the demise of the dinosaurs.

The molecular school is epitomised by Murphy *et al.* (2001). Based on analysis of the DNA structure of modern species, four major clades of placentals are recognised: Afrotheria (Africa), Xenarthra (South America), Laurasiatheria, and Euarchontoglires. Laurasiatheria and Euarchontoglires are combined into the Boreutheria (Laurasia) (Murphy *et al.*, 2001). The Afrotheria separated from the Xenarthra about 110 million years ago, the same time that the separation of Africa and South America occurred with the incursion of the South Atlantic. From there, under this view, the Boreutheria, which constitute the bulk of the placentals, reached North America and spread from there to Europe and Asia. The molecular data have been interpreted to mean that the majority of the modern placental orders arose ten to forty million years before their fossils are found in the fossil record. This constrains the time of movement of these placental groups to the Late Cretaceous when the Afrotheres gave rise to the Xenarthra which moved across the South Atlantic about 103 million years ago (Murphy *et al.*, 2001), the Xenarthra gave rise to the Boreosphenidians after that when they moved into Laurasia.

In the view of the classic school, the major weakness of the molecular school is the calibration points used to determine the age in years of the separation of the various placental clades from one another and thus the age of the clades themselves. In the view of the molecular school, the major weakness of the classic school is the incompleteness of the fossil record.

In the past eight years, a few tribosphenic mammal specimens have been found in the Middle Jurassic and Early Cretaceous of Gondwana. If they are not only indeed tribosphenic mammals, but also eutherians, this does not accord with the classic school. The fossils in question include the Middle Jurassic *Ambondro* (Flynn *et al.*, 1999) based on a single lower jaw fragment from Madagascar, Middle Jurassic *Asfaltomylos* (Rauhut *et al.*, 2002) based on a single lower jaw fragment from Argentina, and the Early Cretaceous *Ausktribosphenos* (Rich *et al.*, 1997) and *Bishops* (Rich *et al.*, 2001) based on about twenty lower jaw fragments from Australia (Fig.9). These forms have been variously interpreted. On the basis of their apparent tribosphenic dental morphology and dental formula, they have been allocated to the eutherians (Woodburne *et al.*, 2003).

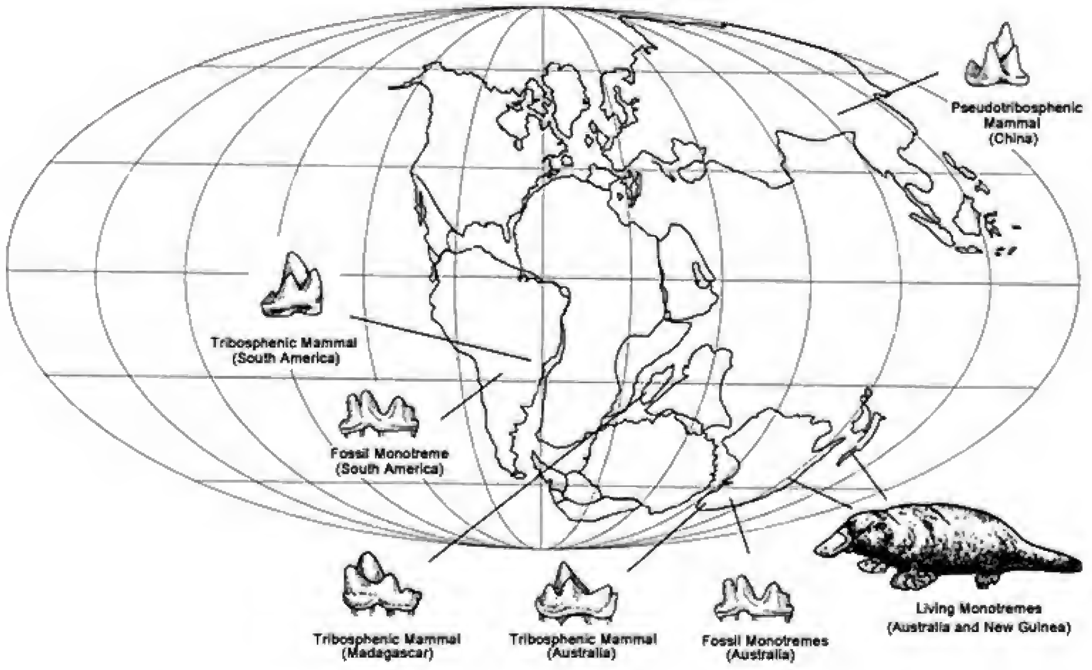


Fig.9- Geographic distribution of the Australosphenida of Luo *et al.* (2001). (Modified with permission from Zhe-Xi Luo. After Press Release of the Carnegie Museum of Natural History).

If this is the case, on the present evidence, eutherians arose earlier in Gondwana rather than in Laurasia. This accords with the idea based on molecular studies that placentals arose in Gondwana and subsequently spread to Laurasia. Alternatively, these forms have been united with the monotremes and the Middle Jurassic Chinese *Shuotherium* (Chow & Rich, 1982), under the hypothesis that a separate radiation of mammals with a therian-like but not true tribosphenic dentition on a structurally primitive jaw took place in Gondwana (Fig.10) (Luo *et al.*, 2001, 2002). The primitive nature of the jaw was manifested in the presence of an internal mandiblar groove. This group was dubbed the Australosphenida. The Laurasian eutherians were designated the Boreosphenida.

A cladogram of the Mammalia was constructed which grouped all of these australosphenidans together (Fig.11) (Luo *et al.*, 2001, 2002). Examination of the data matrix suggested that some important characters to this hypothesis could be interpreted quite differently (Woodburne *et al.*, 2003). The essential aspects of the tribosphenic molar pattern are first that a cusp on the upper molar, the protocone acts as a mortar in a basin formed on the lower molar by the talonid. Second, that shearing occurs by successive upper molars abrading against the triangular pillar or trigonid of the lower molars, forming vertical or near vertical facets (Fig.12). The molars of the monotremes do not have the pattern of wear to be expected in a tribosphenic mammal (Luo *et al.*, 2002) (Fig.13, see especially D_2). There is no talonid on the lower molars into which a protocone occludes. Likewise, no near vertical wear facets are present. Most mammals in fact do not have a tribosphenic dentition although they are clearly descended from ancestors that did. It could very well be that monotremes are descended from an ancestor with a tribosphenic dentition. But if so, the modifications that the teeth have undergone are so great that there is no trace of them having had a tribosphenic ancestor. In any case, the morphology of these teeth does not add evidence allying the monotremes with the tribosphenic australodelphidans (Rich *et al.*, 2002).

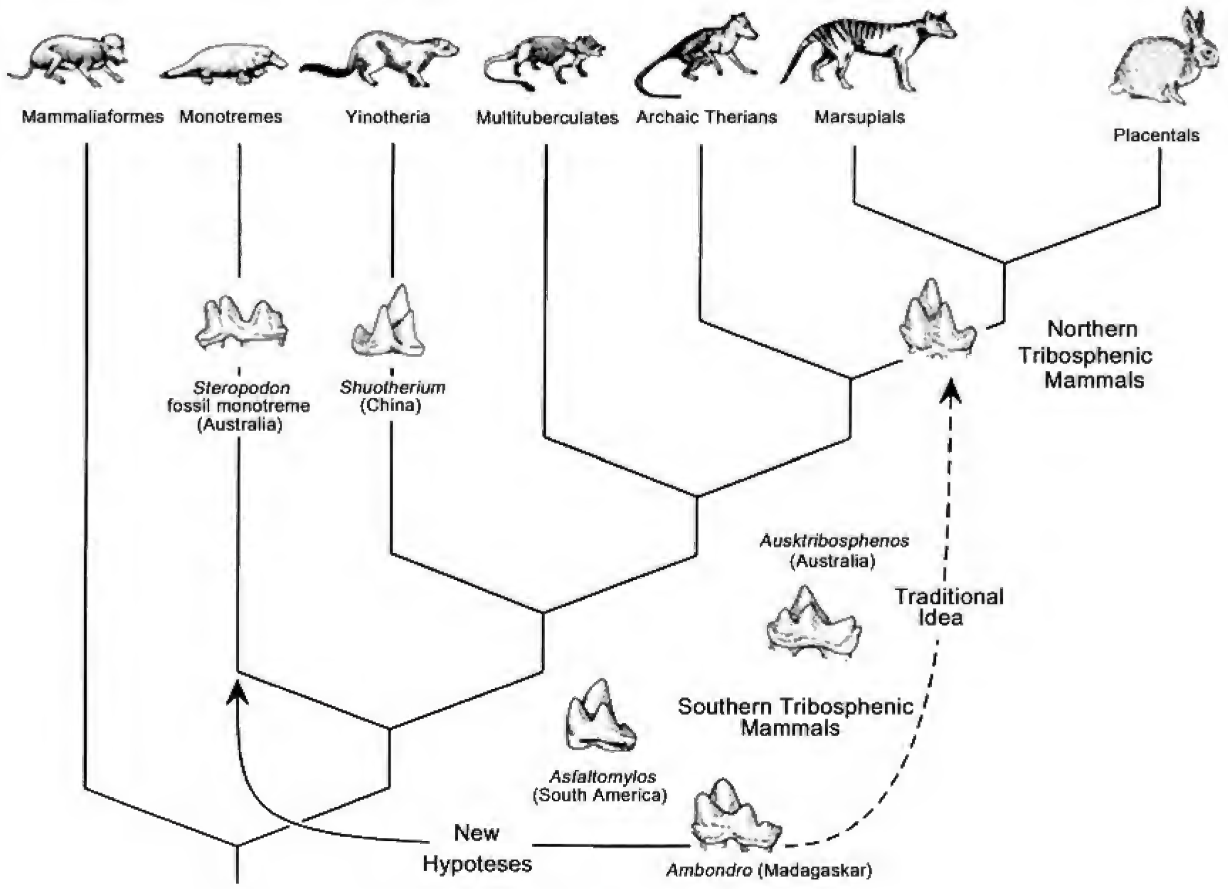


Fig.10- Alternative phylogenies of the tribosphenic members of the Australosphenida of Luo *et al.* (2001). (Modified with permission from Zhe-Xi Luo. After Press Release of the Carnegie Museum of Natural History).

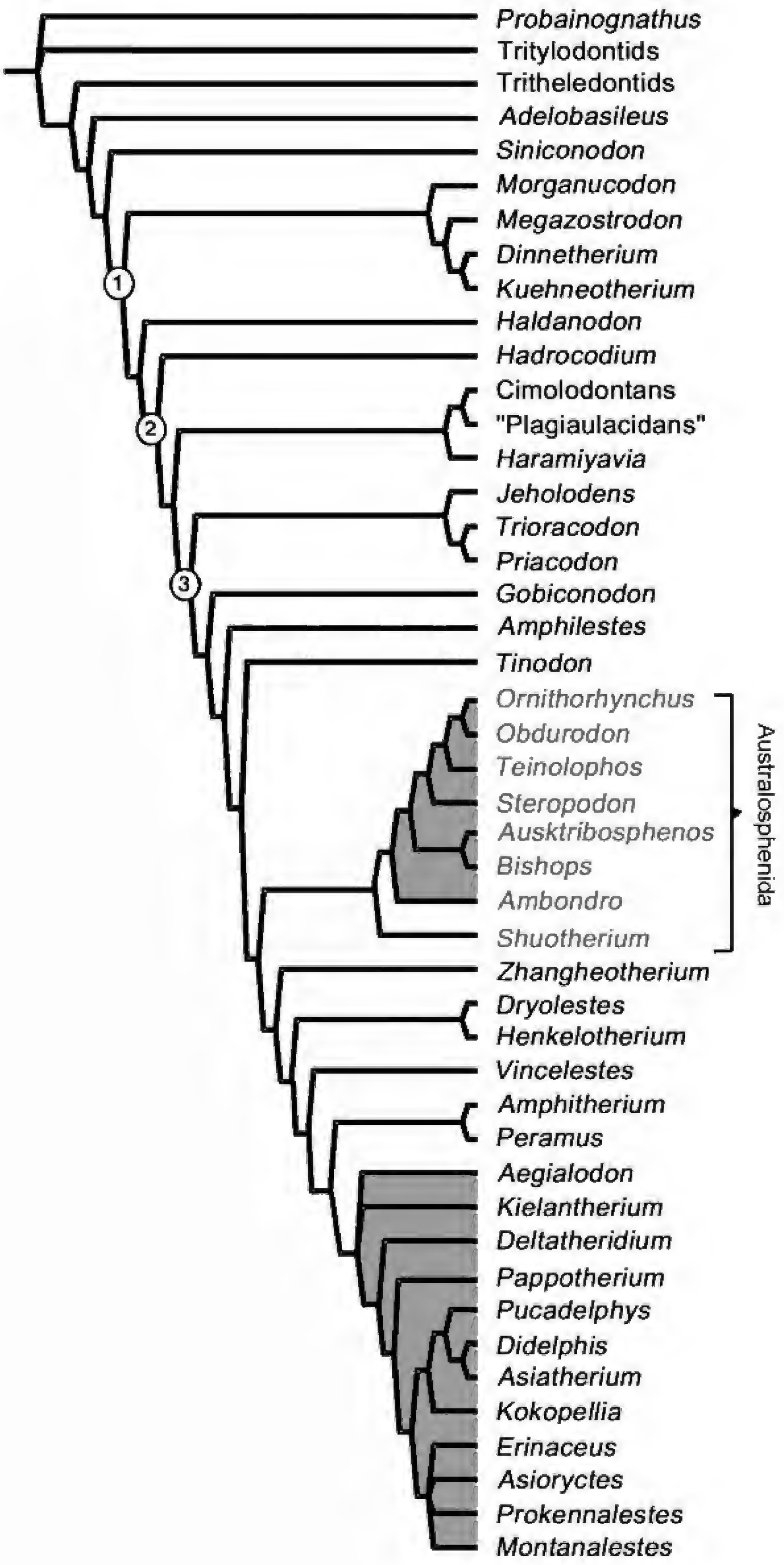


Fig.11- Cladogram of the relationships of the Mammalia in Luo *et al.* (2002). Note that the members of the Australosphenida are all clustered together.

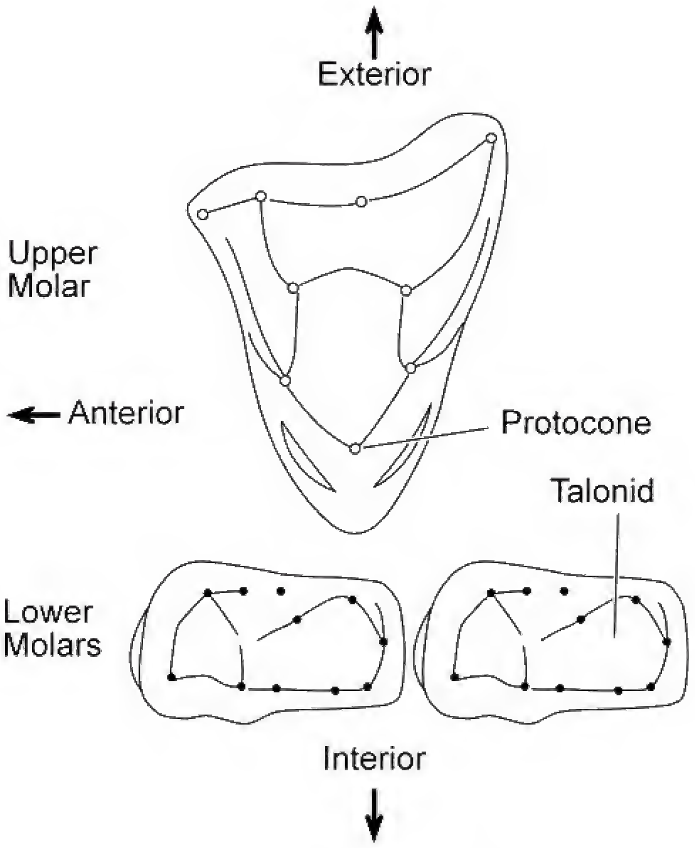


Fig.12- Diagrammatic tribosphenic upper and lower molars. Note that the protocone occludes in the talonid basin with a mortar and pestle action while the preprotocrista forms a vertical shearing surface in slicing past the posterior vertical side of the talonid basin and the postprotocrista forms a vertical shearing surface in slicing past the posterior side of the trigonid.

For that matter, the dental pattern of the monotremes is as close to the boreosphenidians as to the australosphenidans.

The australosphenidans are characterised as having an advanced tribosphenic dentition on a primitive mandible (Luo *et al.*, 2002). The primitive feature being a Meckelian groove. This character of the jaw is quite variable in the taxa regarded as australosphenidans. On the monotreme *Teinolophos* (Fig.14), the groove is quite deep while in the monotreme *Steropodon,* it is non-existant. In the ausktribosphenidan *Austribosphenos* (Fig.15), there is a shallow groove while in the other known ausktribosphenid *Bishops* (Fig.16), there is no groove at all. The yinothere *Shuotherium* (Fig.17) has a shallow groove as does the unquestioned boreosphenidian *Prokennalestes* (Kielan-Jaworowska & Dashzeveg, 1989) (Fig.18). Thus it seems that this feature of the jaw is not a consistent one within the australosphenidans. In any case, the presence of an internal mandibular groove is a plesiomorphic character and thus of little value in establishing relationships.

The australosphenidans and boreosphenidans have been separated on the basis of the height of the condyle and the orientation of the angle (Fig.19). Whilst this division holds in the specimens shown in the lefthand column of figure 19 (Fig.5 in Luo *et al.*, 2002) additional erinaceids shown in the righthand column (various figures in Butler, 1948) have the orientation of these structures similar to the australosphenidans and thus this character does not distinguish the australosphennidans from the boreosphenidans.

A cingulum wrapping around the paraconid of the australosphenidans is considered to be a principal feature of that group distinguishing it from the boreosphenidans (Luo *et al.*, 2002). Unfortunately, the view of the lower molar of *Teinolophos* shown in Luo *et al.* (2002) is lingual (Fig.20D) whereas all the other teeth in that figure are in labial view. The actual labial view is to the right of figure 20D.

When these character differences were incorporated into the data matrix of Luo *et al.* (2002), the tribosphenic australosphenidans clustered with the eutherians whereas the monotremes and *Shuotherium* were quite remote from that group (Fig.21) (Woodburne *et al.*, 2003).

In light of this, it is tempting to conclude that the eutherians arose in Gondwana and subsequently spread to Laurasia. However, the Middle Jurassic when *Ambondro* and *Asfaltomylos* lived is extremely poorly known. So, on the basis of the fossils, Lillegraven's conclusion, "somewhere on the Earth's dry surface," is probably the most realistic conclusion to come to regarding the place of origin of the eutherians.

Molecular studies suggest that the majority of the living orders of placentals arose well before the KT boundary. This is in contrast to the fossil record which only identifies a few pre-Tertiary orders. If the molecular interpretation is correct and there are many extant placental orders which originated in the Late Cretaceous, it implies that there is a significant missing fossil record. If that is the case, it is likely to be in areas that until now have been poorly sampled. This is the Garden of Eden. Hypothesis of Foote *et al.* (1999).

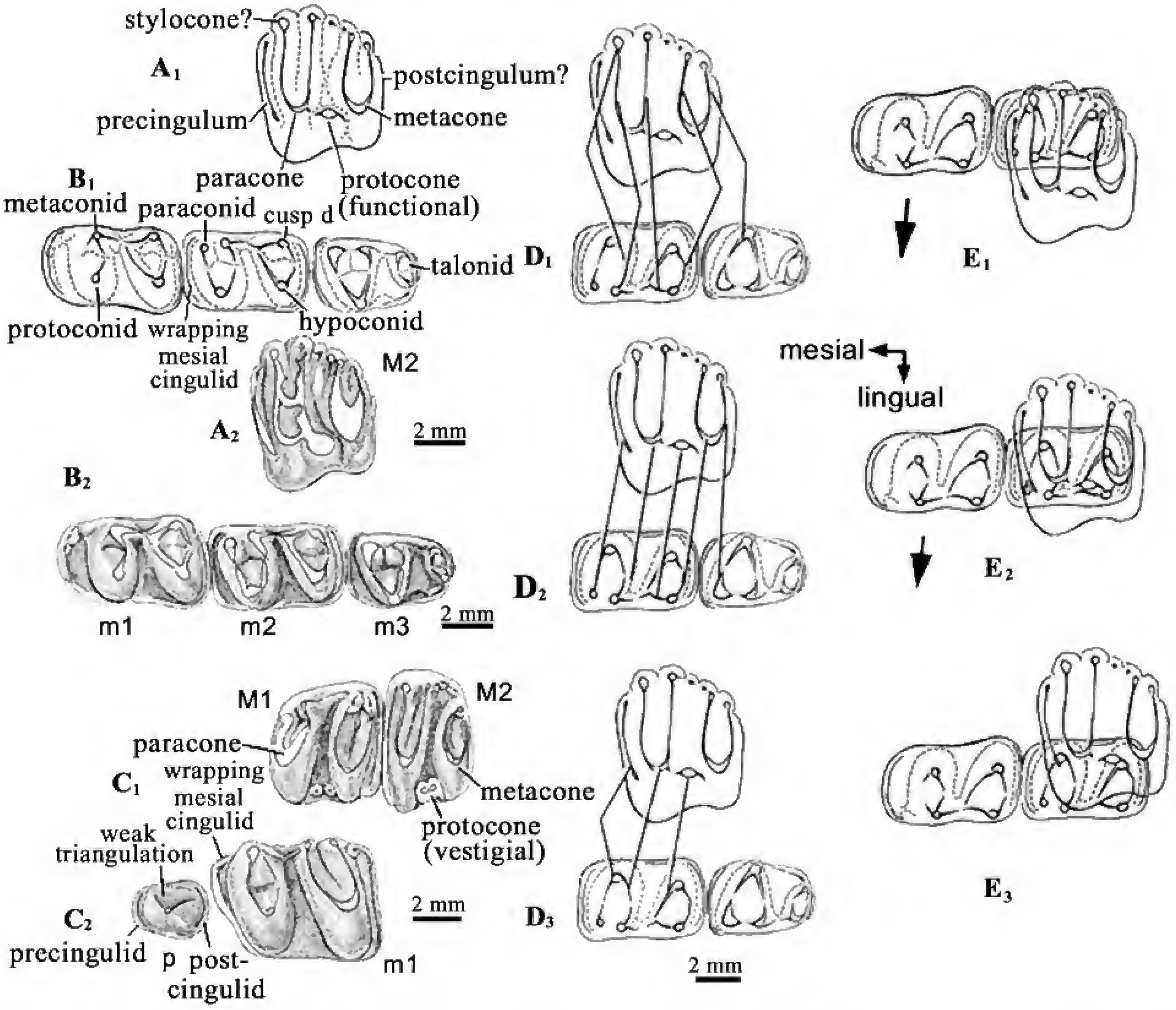


Fig.13- Diagrammatic monotreme occlusal patterns. A$_{1-2}$. Upper molar pf *Monotrematum sudamericanum*. B$_{1-2}$. Lower molars of *Steropodon galmani*. C$_{1}$. Upper molars of *Obdurodon dicksoni*. C$_{2}$. Lower premolar and molar of *Obdurodon dicksoni*. D. Hypothetical occlusal relationships between upper and lower monotreme molars. D$_{1}$. Beginning of occlusal cycle. D$_{2}$. Middle of occlusal cycle which shows a functional protocone that is interpreted as having had a mortar and pestle action against cusp d. Even if this occlusal relationship did exist, it is analogous, not homologous to the tribosphenic pattern. D$_{3}$. End of occlusal cycle. E$_{1-3}$. Superimposed relationship of upper and lower monotreme molars, each numerical stage corresponding to the equivalent number in D$_{1-3}$. After Luo *et al.* (2002).

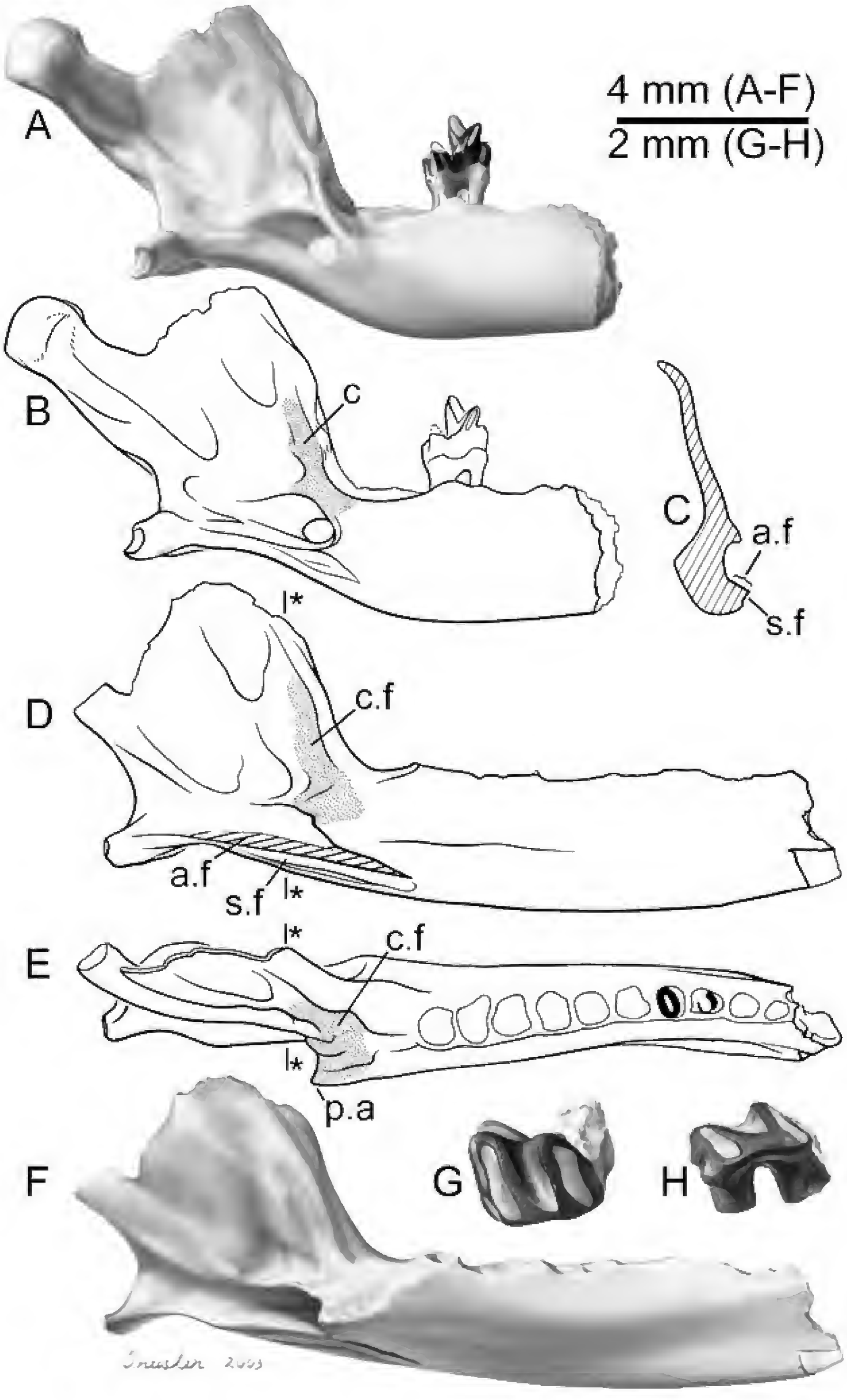


Fig.14- A. Medial view of holotype of *Teinolophos trusleri*, NMV P208231. B. Diagrammatic medial view of NMV P208231; the stippled area indicates the position of the fused coronoid bone. C. Cross section of mandible of referred specimen of *T. trusleri,* NMV P212933; position of cross section indicated in figures 14D and 14E, by lines terminated with stars. D. Diagrammatic medial view of NMV P212933. The stippled area indicates the position of the contact facet for the coronoid bone. Traces of roots of a molar can be seen in alveoli three and four. E. Diagrammatic dorsal view of NMV P212933. Traces of roots of a molar can be seen in alveoli three and four. F. Medial view of NMV P212933, rotated slightly medially towards the viewer. G. Occlusal and (H) medial views of isolated lower molar associated with dentary, NMV P212933. Abbreviations: a.f, angular facet; a.p, angular process; c, coronoid; c.f, coronoid facet; m.f, mandibular foramen; m.t, mandibular trough; p.a, posterointernal angle; s.f, splenial facet. (From RICH *et al.*, 2005).

Fig.15- Right mandible of the tribosphenic mammal *Ausktribosphenos nyktos* Rich, Vickers-Rich, Constantine, Flannery, Kool & Van Klaveren, 1997 (Fig.2). From the Aptian Strzelecki Group, Flat Rocks, Victoria, Australia.

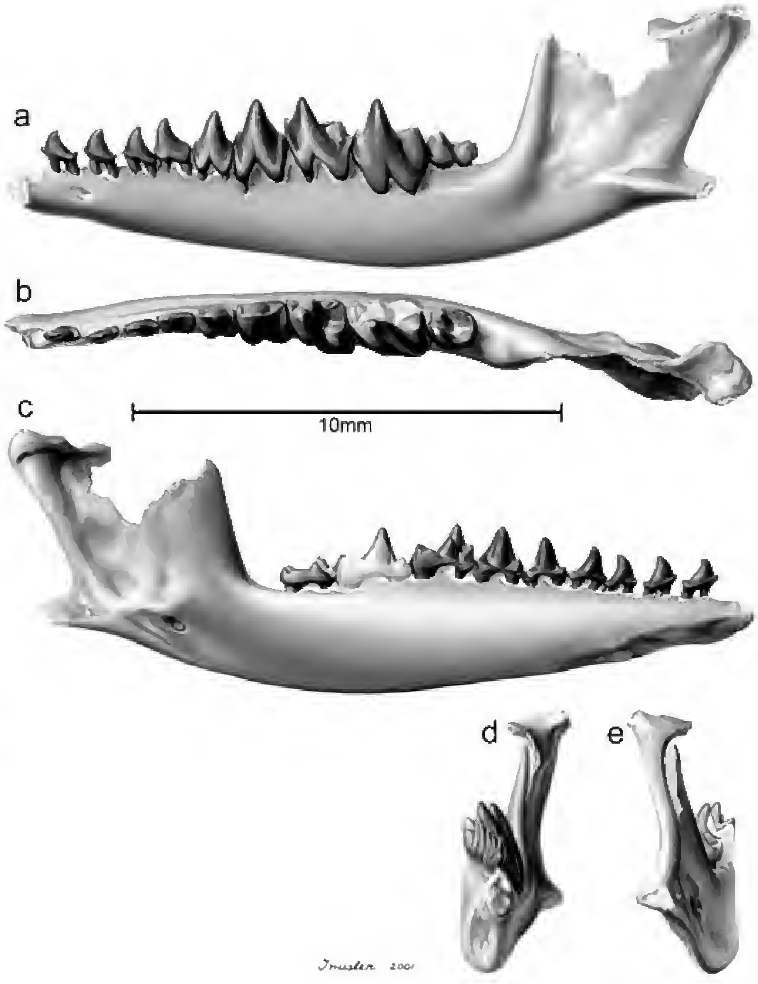


Fig.16- Left mandible of the tribosphenic mammal *Bishops whitmorei* Rich, Flannery, Trusler, Kool, Van Klaveren & Vickers-Rich, 2001 (Fig.1). From the Aptian Strzelecki Group, Flat Rocks, Victoria, Australia.

Fig.17- Left mandible of the yinothere *Shuotherium dongi* Chow & Rich, 1982 (Fig.5B).

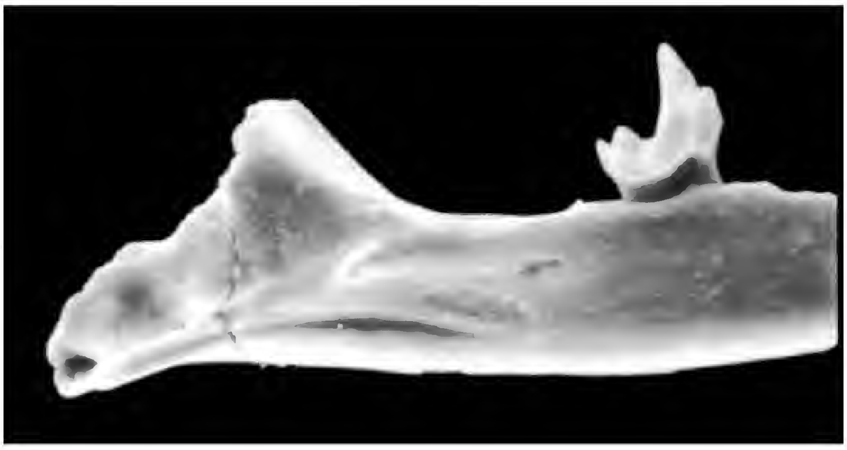


Fig.18- Left mandible of the placental *Prokennalestes minor* Kielan-Jaworowska & Dashzeveg, 1989 (Fig.23).

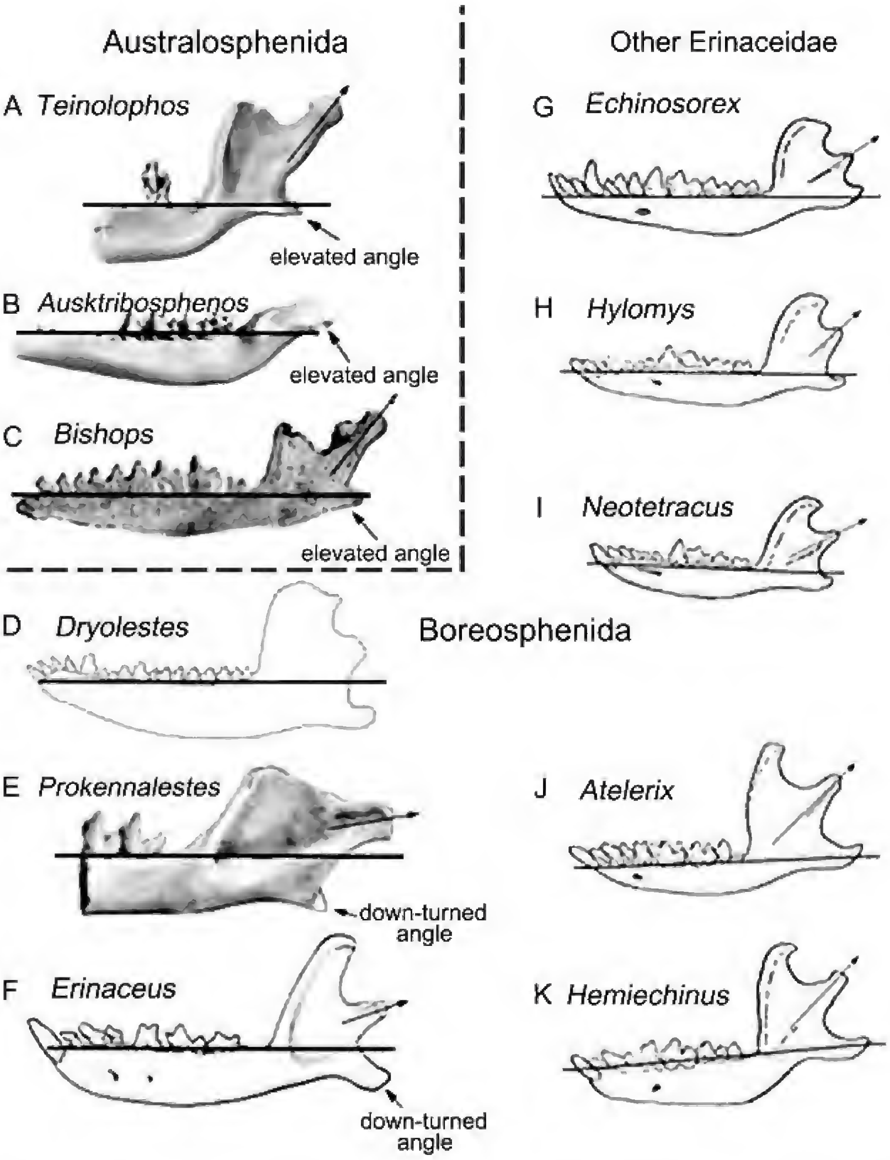


Fig.19- Comparison of the height of the condyle and orientation of the condyle on the mandible of boreosphenidians and australosphenidians. See text for discussion. From Butler (1948) and Luo *et al.* (2002).

Foote *et al.* (1999) and Archibald & Deutschmann (2001) both present actuarial arguments that the fossil record should be taken as given. That is, it is reliable enough to accept the dates of first appearance of groups as close to their dates of origin. Where this approach is weak in this instance is evaluating the record of land masses with no Late Cretaceous mammal sites; *i.e.*, Antarctica, Africa, and Australia.

Hunter & Janis (2006) put forward a hypothesis asserting that the placentals arose in the Northern Hemisphere. This was based in part on two parsimony arguments. The first was minimization of the amount of missing evolutionary history (Foote *et al.*, 1999). While this may be the best procedure to handle the data available, whether, given the uneven record of fossil placentals on various continents, it is even close enough to the actual events to be a useful guide rather than misleading is not clear. Second, it is not certain that a model which has the fewest number of continental interchanges for the various placental mammalian orders is the best estimate of their places of origin. In this instance, parsimony is regarded as a trustworthy guide for deciding between one geographic model and another because intercontinental interchanges are considered unlikely (McKenna, 1973).

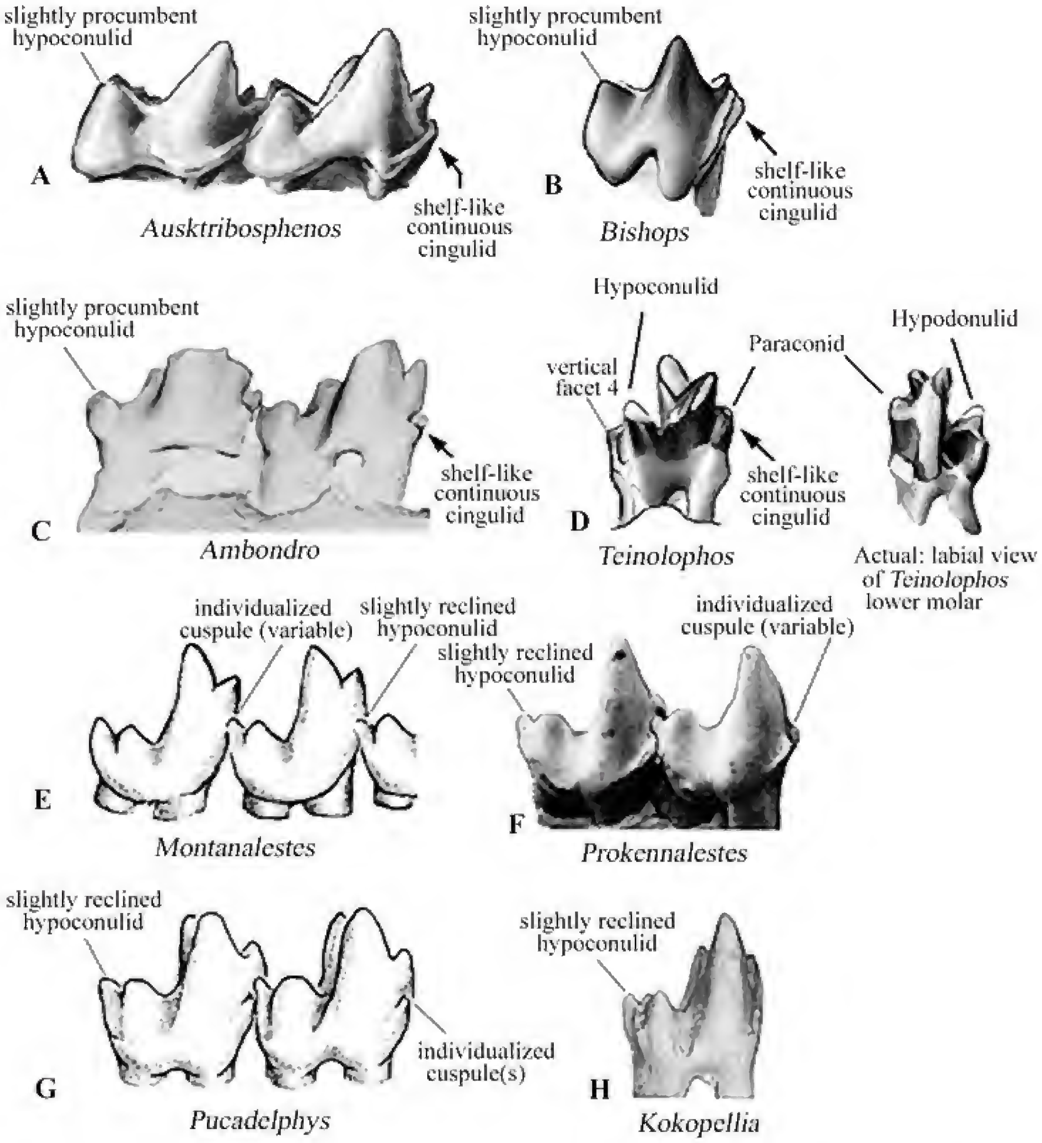


Fig.20- Comparison of the dentitions of australosphenidians and boreosphenidians. See text for discussion. From Luo *et al.* (2002).

However, such interchanges are not always rare. For example, between North and South America in the Pliocene Great American Interchange, 46 different genera individually passed from one continent to the other (Webb, 1985). This is far more than the ordinal interchanges analysed by Hunter & Janis (2006). If exchanges are possible at all does their number provide a meaningful measure of the likelihood? Given the smaller numbers in the models compared by Hunter & Janis (2006), one can only wonder at just how meaningful the significance of the numerical differences is.

CONCLUSIONS

Knowledge of the palaeobiogeography of Mesozoic mammals is extremely meagre and uneven both in time and space. Reconciliation of the interpretations of the fossil and molecular evidence relating to this problem is as central to future progress about this question as the discovery of additional fossils.

Woodburne *et al.* (2003) Fig. 2

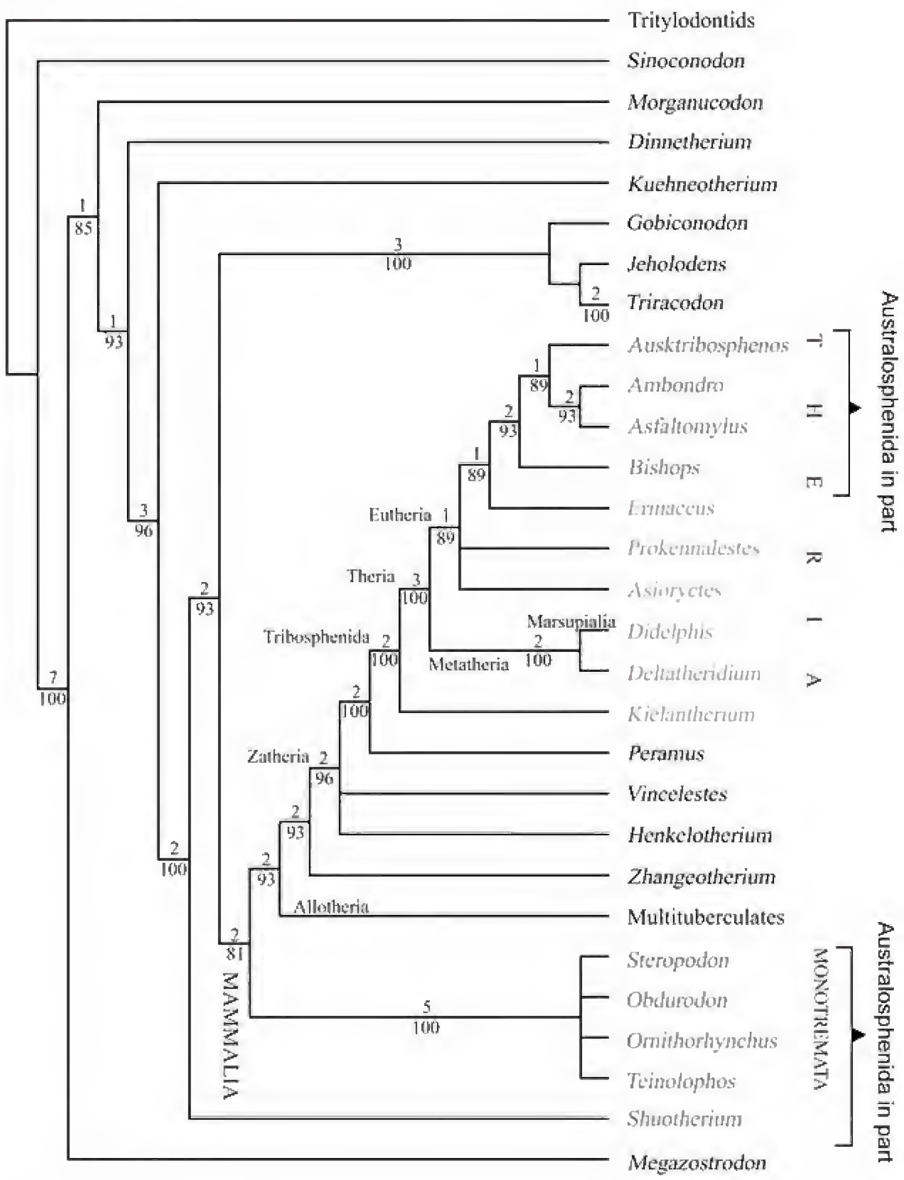


Fig.21- Alternative cladogram of the relationships of the Mammalia (Fig.2 in Woodburne *et al.*, 2003). The characters analysed in this cladogram were virtually the same as those in figure 11. That the cladograms are not the same is owing to differences in the assignment of character states. Whereas the australosphenidians were recognized by Luo *et al.* (2002) as a single entity, they are divided into the three groups indicated here: (1) eutherians?, (2) monotremes, and (3) *Shuotherium* (yinothere).

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This contribution is dedicated to the memory of Malcolm Carnegie McKenna (21 July 1930 - 3 March 2008), generous and inspiring mentor to numerous students and renowned palaeomammalogist.

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THE ORIGIN AND EVOLUTION OF NEOTROPICAL PRIMATES [1]

(With 4 figures)

MARCELO F. TEJEDOR [2]

ABSTRACT: A significat event in the early evolution of Primates is the origin and radiation of anthropoids, with records in North Africa and Asia. The New World Primates, Infraorder Platyrrhini, have probably originated among these earliest anthropoids morphologically and temporally previous to the catarrhine/platyrrhine branching. The platyrrhine fossil record comes from distant regions in the Neotropics. The oldest are from the late Oligocene of Bolivia, with difficult taxonomic attribution. The two richest fossiliferous sites are located in the middle Miocene of La Venta, Colombia, and to the south in early to middle Miocene sites from the Argentine Patagonia and Chile. The absolute ages of these sedimentary deposits are ranging from 12 to 20 Ma, the oldest in Patagonia and Chile. These northern and southern regions have a remarkable taxonomic diversity and several extinct taxa certainly represent living clades. In addition, in younger sediments ranging from late Miocene through Pleistocene, three genera have been described for the Greater Antilles, two genera in eastern Brazil, and at least three forms for Río Acre. In general, the fossil record of South American primates sheds light on the old radiations of the Pitheciinae, Cebinae, and Atelinae. However, several taxa are still controversial.

Key words: Neotropical Primates. Origin. Evolution.

RESUMO: Origem e evolução dos primatas neotropicais.

Um evento significativo durante o início da evolução dos primatas é a origem e a radiação dos antropóides, com registros no norte da África e da Ásia. Os representantes dos Primates do Novo Mundo, Infraordem Platyrrhini, provavelmente se originaram a partir dos antropóides mais primitivos, morfologica e temporalmente anteriores ao ramo Catarrhini/Platyrrhini. O registro fóssil dos Platyrrhini procede de regiões distantes no Neotrópico. Os mais antigos procedem do Oligoceno Superior da Bolívia, com atribuições taxonômicas difíceis. Os dois sítios fossilíferos mais ricos estão localizados no Mioceno Médio de La Venta, Colômbia, e ao sul, em sítios do Mioceno Inferior à Médio da Patagônia Argentina e Chile. A idade absoluta desses depósitos sedimentares varia de 12 a 20 Ma sendo os mais antigos depósitos os da Patagônia e do Chile. Essas regiões, ao norte e ao sul, tem uma notável diversidade taxonômica e os diversos táxons extintos certamente representam clados viventes. Somado a isto, três gêneros foram descritos para as Grandes Antilhas em sedimentos mais recentes, variando do Mioceno Superior ao Pleistoceno, dois gêneros para o leste do Brasil, e pelo menos três formas para o Río Acre. Em geral, o registro fóssil dos primatas sul-americanos permite de certa forma esclarecer as antigas radiações dos Pitheciinae, Cebinae e Atelinae. Contudo, vários táxons ainda são controversos.

Palavras-chave: Primatas neotropicais. Origem. Evolução.

INTRODUCTION

The origin and evolution of the Order Primates have been always controversial, but the fossil record has increased considerably especially in the last two decades (Hartwig, 2002). Currently, the most accepted macrosystematics of Primates is a division between Strepsirrhini and Haplorrhini. The Haplorrhini is a grouping joining Tarsiiformes and Anthropoidea, and the Anthropoidea is the suborder that joins the Infraorders Platyrrhini and Catarrhini. As a native South American infraorder, finding the closest ancestral stock of the platyrrhines may be a useful tool in reconstructing their phylogeny. As anthropoids, the potential ancestors of the platyrrhines might be found in Africa, where primitive anthropoids that lived before the platyrrhine-catarrhine split have been discovered during the last 100 years (Simons, 1995, and references therein). The relevant fossils are mostly of late Eocene and early Oligocene age, and the most popular and rich fossil primate assemblages are located in the Fayum, Egypt.

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The taxa are generally included in the families Propliopithecidae, Parapithecidae, Proteopithecidae, and Oligopithecidae. Traditionally, the Propliopitheciidae (*Aegyptopithecus*, *Propliopithecus*) are viewed as morphologically primitive catarrhines, and the Parapithecidae (*Apidium*, *Parapithecus*, *Qatrania*) alternatively as a sister group of platyrrhines plus catarrhines, or as primitive catarrhines (FLEAGLE & KAY, 1987; HARRISON, 1987; KAY *et al.*, 1997). The Oligopitheciidae (*Oligopithecus*, *Catopithecus*) are considered either basal catarrhines or basal anthropoids (SIMONS & RASMUSSEN, 1994; KAY *et al.*, 1997). The Proteopithecidae (*Proteopithecus*, *Serapia*) are morphologically primitive anthropoids, and have been linked with platyrrhines dentally (KAY *et al.*, 1997) and also based on postcranial anatomy (SIMONS & SEIFFERT, 1999).

Outside of the Fayum, northern Africa has yielded a small collection of additional primate fossils, some of them possible anthropoids. *Biretia*, from the late Eocene, was largely based on a single lower molar from Algeria originally described as a catarrhine (DE BONIS *et al.*, 1988), but reinterpreted as a parapithecid (RASMUSSEN & SIMONS, 1992; KAY *et al.*, 1997). SEIFFERT *et al.* (2005) reported two new species of *Biretia* from a late Eocene locality of the Fayum, Egypt, suggesting parapithecid relationships. Also from Algeria, but of early Eocene age, *Algeripithecus* (GODINOT & MAHBOUBI, 1992) and *Tabelia* (GODINOT & MAHBOUBI, 1994) are tiny primates with anthropoid affinities. *Djebelemur* came from the early Eocene of Tunisia (HARTENBERGER & MARANDAT, 1992), and was considered as an adapid by its discoverers, but as an anthropoid by GODINOT (1994), as well as *Omanodon* and *Shizarodon* (GHEERBRANT *et al.*, 1993), from the early Oligocene of Oman, in the Arabian Peninsula.

From the late Paleocene of Morocco, *Altiatlasius* was previously known by isolated teeth originally allocated among the Omomyidae, thus being the oldest anatomically modern primate ever discovered. However, recent discoveries of plesiadapiforms shed light on the possible plesiadapiform status of *Altiatlasius* (HOOKER *et al.*, 1999).

Several discoveries from Asia have potentially added information on the anthropoid origin, but the affinities of these forms are highly uncertain. Eosimiidae is a family that includes two species of *Eosimias*, from the middle Eocene of China, considered by some authors as the oldest known anthropoids (BEARD *et al.*, 1994; 1996; GEBO *et al.*, 2000). However, other authors question its anthropoid status (GODINOT, 1994; SIMONS & RASMUSSEN, 1994). A second genus has also been included among eosimiids, *Bahinia*, found in the late-Middle Eocene of Myanmar (JAEGER *et al.*, 1999; BEARD, 2002).

From the late-Middle Eocene of Myanmar are *Poundangia* and *Amphipithecus*, which were originally described in the 1930s and alternatively considered as adapiforms or anthropoids by different authors (see CIOCHON & HOLROYD, 1994). Along with *Siamopithecus*, from the late Eocene of Thailand (CHAIMANEE *et al.*, 1997), they were recently classified to constitute the family Amphipithecidae (BEARD, 2002).

In sum, these Afro-Arabian and Asian findings reflect a broad radiation of euprimates. Most researchers who have described and evaluated the material regard them as anthropoid or anthropoid-related primates. Several authors also tend to emphasize that this adds new information about an Asian geographic origins of the suborder. For the platyrrhines, their only potential ancestors proposed in this context have been some Fayum forms, as mentioned above (KAY *et al.*, 1997). The fact that some overall similarities are shared between platyrrhines and some parapithecids and proteopithecids is until now speculative, since there was no in depth comparative and phylogenetic studies to sharpen this hypothesis.

MATERIAL AND RESULTS

THE FOSSIL RECORD OF NEOTROPICAL PRIMATES

Since the times of Peter Lund and later Carlos and Florentino Ameghino, fossil primates have been found in South America and the Caribbean. Figure 1 shows the localities of fossil platyrrhines, and table 1 is a detailed taxonomic and temporal scheme for the platyrrhine fossil record.

BOLIVIA

The oldest records in South America, *Branisella boliviana* and *Szalatavus attricuspis*, come from the locality of Salla, Bolivia (HOFFSTETTER, 1969; ROSENBERGER *et al.*, 1991a; WOLFF, 1984; TAKAI & ANAYA, 1996; TAKAI *et al*, 2000). This locality is 26 Ma (KAY *et al.*, 1998), or late Oligocene age (Deseadan South American Land Mammal Age, SALMA). The phylogenetic relations of *Branisella* and *Szalatavus* are still under debate.

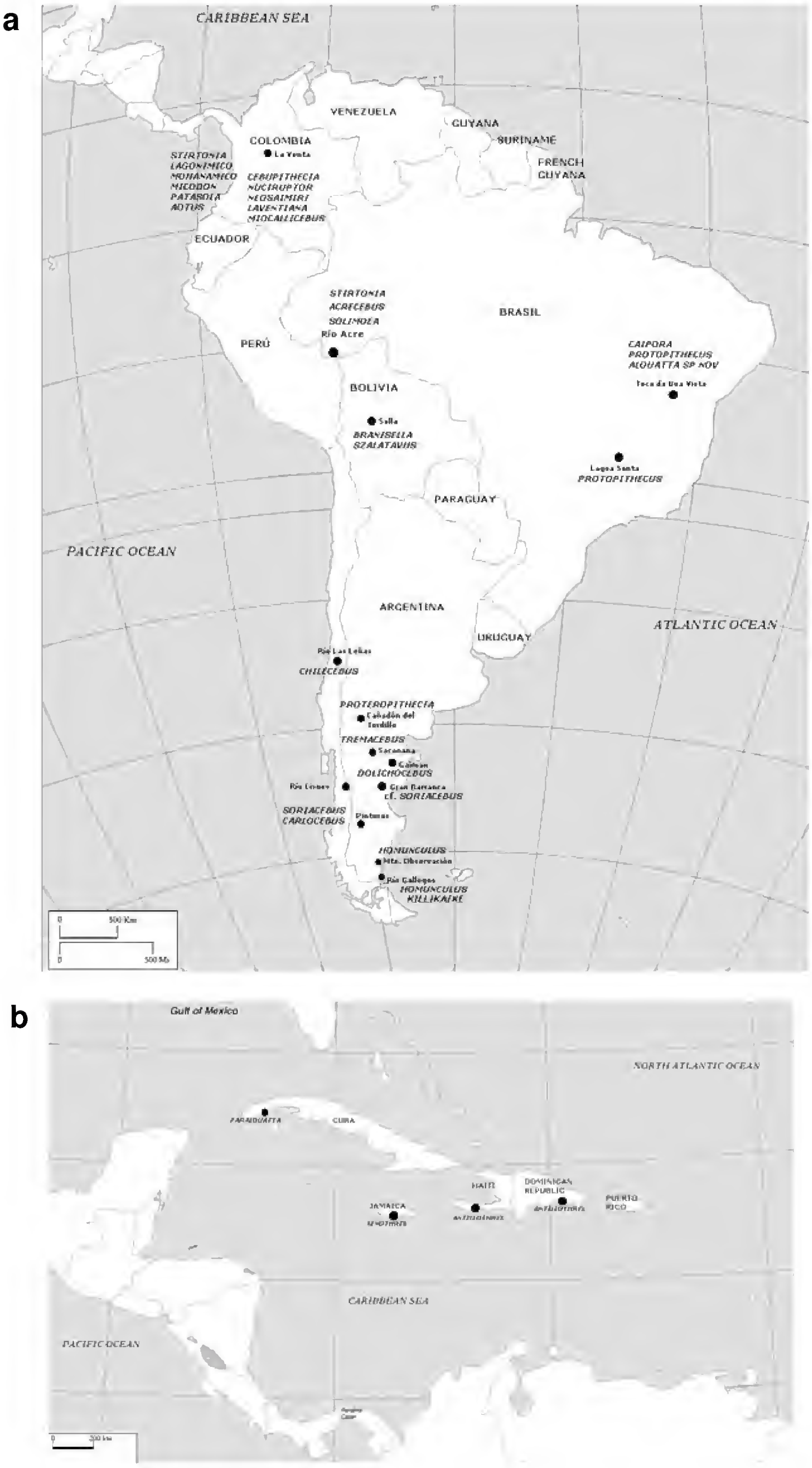

Fig.1- Geographic distribution of the fossil platyrrhine localities and genera in South America (a) and the Caribbean (b).

TABLE 1. Temporal and geographic distribution of the platyrrhine fossil genera.

AGE (MA)	EPOCH	SALMA	PRIMATE-BEARING SITES	FOSSIL TAXA
	HOLOCENE		Hispaniola	*Antillothrix*
10,000		Lujanian	Lagoa Santa-Toca da Boa Vista	*Protopithecus-Caipora-*
	PLEISTOCENE			*Alouatta sp nov*
		Ensenadan	Caribbean localities	*Xenothrix*
2-		Uquian		*Paralouatta*
5-	PLIOCENE	Chapadmalalan		
		Montehermosan		
		Huayquerian	Rio Acre	*Solimoea- Stirtonia-*
		Chasicoan		*Acrecebus*
		Mayoan		*Stirtonia-Neosaimiri-*
		Laventan		*Cebupithecia-Aotus-*
8-				*Mohanamico-Micodon-*
11-	MIOCENE			
		Colloncuran		*Lagonimico-Patasola-*
14-		Santacrucian	La Venta	*Laventiana-Nuciruptor-*
17-				*Miocallicebus*
20-		Colhuehuapian	Cañadón del Tordillo	*Proteropithecia*
			Santa Cruz Fm	*Homunculus- Killikaike*
			Pinturas Fm	*Soriacebus-Carlocebus*
		Deseadan	Sacanana-Gaiman-Gran Barranca	cf. Soriacebus
				Tremacebus-Dolichocebus
			Río Las Leñas	*Chilecebus*
23-				
26-			Salla	
29-				*Branisella-Szalatavus*
32-	OLIGOCENE			
35-				

Some characters relate them more closely to the Callitrichinae, such as triangular shape of the upper premolars and molars (ROSENBERGER *et al.*, 1991a), as well as the shape of p2 (TAKAI & ANAYA, 1996). Based on several new specimens found more recently, some authors (*i.e.*, Takai, Kay) suggested that *Szalatavus* is a synonym of *Branisella*.

CHILE

In the western Andean cordillera, south of the city of Santiago, in Chile, a remarkable primate skull was discovered in the 1990s. The taxon, *Chilecebus carrascoensis*, is 20 Ma old (Colhuehuapian SALMA; early Miocene; FLYNN *et al.* (1995) and is another odd fossil primate with a rare combination of traits. Following FLYNN *et al.,* 1995; see also FLEAGLE & TEJEDOR, 2002), *Chilecebus* may be related more closely to the Cebinae, based on the premolar morphology, which are buccolingually elongated. *Chilecebus* also has a rounded skull, small orbits, and dental arcade diverging posteriorly; the upper molars are quadrate with a well developed hypocone; M3 is considerably reduced and has no metacone nor a hypocone, which is also characteristic or consistent with cebine morphology. Unusual characters for a cebine are the very small P2 compared with P3-4, and also the small upper canine.

An isolated primate talus from the type locality of the "Friasian" SALMA (Middle Miocene), Alto Río Cisnes, in southern Chile, was described by TEJEDOR (2003). It shares overall similarities and locomotor adaptations with some Pinturas tali reported previously (MELDRUM, 1990).

ARGENTINA

There are somewhat younger records of fossil platyrrhines in the Argentine Patagonia, coming from the provinces of Neuquén, Chubut, and Santa Cruz, with diverse and relatively abundant taxa (TEJEDOR, 2000, and references therein; FLEAGLE & TEJEDOR, 2002). The primates from Chubut Province are all of the Colhuehuapian SALMA, with an age of *ca.* 20 Ma, and come from three classic localities: Gaiman, Sacanana, and Gran Barranca. From Gaiman, a locality in the lower valley of the Chubut river, the edentulous type skull of *Dolichocebus gaimanensis* is known since 1942, after the original description by Bordas (1942, see also Kraglievich, 1951). This taxon is closely related to the living genus *Saimiri* (Rosenberger, 1979a; Rosenberger & Fleagle, 1981). The skull shows small orbits with a narrow interorbital region and long braincase, as in the living *Saimiri*, and an apparently well developed interorbital fenestra (Rosenberger, 1979a; for an alternative view, see Hershkovitz, 1982), also typical of *Saimiri*. Unfortunately, all of the teeth are missing but, judging from the alveolous and broken roots, it is possible to observe buccolingually broad postcanine dentition. Some isolated teeth from Gaiman have been also attributed to *Dolichocebus* (Fleagle & Bown, 1983; Fleagle & Kay, 1989), but they are still under study. Their specific attribution to *Dolichocebus* appears difficult.

Fig.2- Lateral views of the type of *Tremacebus harringtoni* (a; courtesy of Alfred L. Rosenberger) and a partial skull of *Homunculus patagonicus* (b; courtesy of Adán Tauber).

Also from the Colhuehuapian is *Tremacebus harringtoni*, from the locality of Sacanana, in north-central Chubut Province (Rusconi, 1935; Hershkovitz, 1974). *Tremacebus* is represented by another edentulous skull that shows large orbits and a short face (Fig.2a), certainly synapomorphies shared with the living *Aotus*. The broken upper molars of *Tremacebus* do not provide much information. From the same locality, Fleagle & Bown (1983) described a mandibular fragment preserving a distal p4 and complete m1 that was tentatively allocated to *Tremacebus*; however, Fleagle (1990) later suggested that it is most probably related to *Soriacebus ameghinorum* (see below). In a recent paper, Tejedor (2005a) has compared several specimens of *Soriacebus* along with the mandible from Sacanana and reached similar conclusion. The molar has a short trigonid and long and wide talonid, but poorly developed cusps and crests.

Also Colhuehuapian, but from the locality of Gran Barranca, is another mandibular fragment with p4 described as *Homunculus* sp. by Heshkovitz (1984). Fleagle (1990) also related this mandible to *Soriacebus*, mainly because of the expanded buccal enamel. Kay *et al.* (1999) briefly reported some specimens from Gran Barranca that resemble *Soriacebus*, but they are still undescribed. However, the most significant contribution of that abstract is the age for the Colhuehuapian primates from Argentina, which was placed at around 20 Ma (Kay *et al.*, 1999).

The Pinturas Formation (Bown & Larriestra, 1990), in the northwest of Santa Cruz Province, has yielded a relatively abundant and moderately diverse collection of early Santacrucian primates. This material has the potential to contribute to the phylogeny of platyrrhine primates in Patagonia because it includes representatives of early stages in the evolution of some clades. Early researchers (Ameghino, 1906) as well as more recent ones (de Barrio *et al.*, 1984) observed several faunistic differences between the taxa from Pinturas and others from the typical Santa Cruz Formation, which comes from the Atlantic coast of the homonymous province. They concluded that the former was a little more primitive. Actually, Fleagle *et al.*, (1995) have determined an age of *ca.* 17 Ma for the Pinturas fauna, thus being early Santacrucian, compared with the younger Santa Cruz Fm, dated in about 16.4 Ma (Fleagle *et al.*, 1995; Tejedor *et al.*, in press). Four species included in two genera have been described so far for Pinturas. *Soriacebus ameghinorum* and *S. adrianae* (Fleagle *et al.*, 1987; Fleagle, 1990; Fleagle & Tejedor, 2002; Tejedor, 2005a; 2005b) are early representatives of the tribe Pitheciini, subfamily Pitheciinae (from now on pitheciins and pitheciines, respectively), characterized by having a derived anterior dentition with procumbent and styliform incisors, and big and projecting canines that resemble those of living pitheciins; also, the p2 is huge and projecting. This morphology was probably an adaptation as a hard seed predator, as in living pitheciins (Kinzey, 1992; Rosenberger, 1992). However, the posterior dentition has some autapomorphies that has generated controversy (Kay, 1990; Rosenberger *et al.*, 1990; Tejedor, 2000). Unlike modern pitheciins, *Soriacebus* lower molars are elongated with well developed trigonids, and the upper molars present a relatively small hypocone with a well developed talon. However, the presence of a well developed talon in upper molars and the anterolingual cingulum pattern are clearly pitheciin features (Tejedor, 2000). In addition, as in pitheciines, the entire ramus of the mandible of *Soriacebus* deepens posteriorly. The derived condition of the anterior dentition is clearly similar not only to living pitheciines, but also to the slightly younger Pinturas species, *S. adrianae* (Figs.3a, b), and to the even younger *Proteropithecia*, *Cebupithecia* and *Nuciruptor* (see below), all of which show a large suite of derived pitheciin features which reinforce the relationships of *Soriacebus*.

Other Pinturas species are *Carlocebus carmenensis* (Fig.3d) and *C. intermedius* (Fleagle, 1990; Fleagle & Tejedor, 2002). These are probably more closely related to *Homunculus* or the living *Callicebus*; however, several specimens tentatively attributed to *Carlocebus* are certainly different in morphology (Fleagle, 1990), and thus may be alocated to a different species (Tejedor, 2000). The dental proportions of *Carlocebus* differ from *Soriacebus* basically in having small anterior dentition and large, quadrate molars with wide basins and more prominent cusps. *Carlocebus* has a large hypocone in the upper molars and strong lingual cingulum, features considered to be primitive for platyrrhines (Tejedor, 2000). The p4 of *Carlocebus* is molariform, and P4 surprisingly has a hypocone, whose phyletic significance remains controversial (Kay, 1990; Tejedor, 2000). Adding to the dental, maxillary and mandibular material, several postcranial remains are preserved, all suggesting quadrupedal or climbing locomotor adaptations (Anapol & Fleagle, 1988; Meldrum, 1990; Stevens & Fleagle, 1998).

Several isolated canines from Pinturas suggest the presence of additional primate taxa (Tejedor, 2002), representing at least one small and one large morph, the latter closely similar to the living *Alouatta*. Moreover, a recently discovered mandibular fragment may represent either a different species of *Soriacebus* or a morphological variant within the species *S. ameghinorum* (Fig.3c) (Tejedor, 2005b), since the lower molars are not as elongate and the talonid is broader than in described species of the genus. Thus, the diversity of fossil primates in the Pinturas Formation appears the second richest in all of South America, after the La Venta of Colombia (see below).

Also in Santa Cruz Province, the Santa Cruz Formation has produced fossil primates since the time of the Ameghino's brothers. *Homunculus patagonicus* is the oldest fossil primate found in Argentina (Ameghino, 1891) and the second discovered in South America, following Lund's (1840) description of *Protopithecus* from a Pleistocene cave in Brazil. All the *Homunculus* specimens were found along the Atlantic coast of southestern Santa Cruz, south of the town of Piedrabuena through the city of Río Gallegos (Ameghino, 1891, 1906; Bluntschli, 1931; Fleagle *et al.*, 1988; Tauber, 1991; Tejedor, 1996, 2000; Kay *et al.*, 2005). *Homunculus* is the best known Argentine fossil primate, and is represented by partial skulls, teeth, mandibles, and postcranial bones.

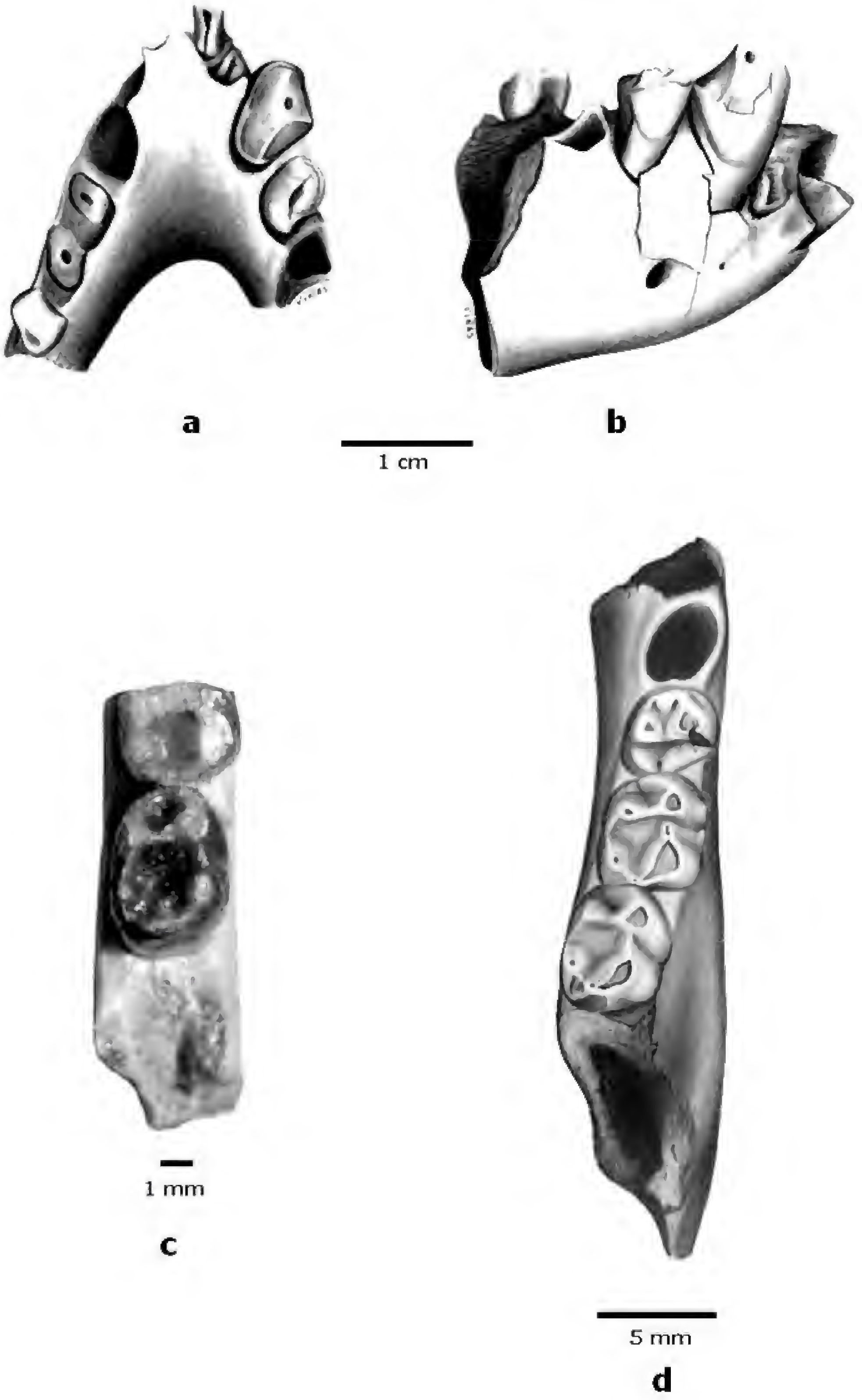

Fig.3- Occlusal (a) and buccal view (b) of *Soriacebus adrianae* (MPM-PV 1605, modified from Tejedor, 2005a). Occlusal views of, *Soriacebus* cf. *ameghinorum*, MPM-PV 36 (c), and MACN-SC 266, holotype of *Carlocebus carmenensis* (d).

The dentition appears also primitive in several characters, such as broad molars with well developed hypocone and lingual cingulum, relatively small anterior teeth, and moderately developed canines. It is similar in general aspects to *Carlocebus*, but the latter has lower and more bunoid cusps, as well as less sharp crests (Fleagle, 1990; Tejedor, 2000). The skull of *Homunculus* has moderate-sized orbits, a relatively low frontal bone, and a well developed interorbitum. As for *Carlocebus*, the postcranium exhibits adaptations for climbing and quadrupedal habits.

There is a remarkable new partial skull, the new genus and species *Killikaike blakei* (Fig.4), from the coastal Santa Cruz Formation, near Río Gallegos, that shows strong affinities with cebines and which figures as the southernmost fossil platyrrhine ever described (Tejedor *et al.*, 2006). It is the first fossil platyrrhine that preserves the entire face undistorted and an unworn, little damaged dentition that is the best anatomical evidence of the maxillary teeth of any Santacrucian fossil monkey, also providing the first relatively complete and undistorted evidence of the anterior braincase of a fossil platyrrhine. A second maxillary specimen provides additional information on the upper molar morphology. This new taxon lacks diagnostic derived characteristics of the lower face and premolar dentition that are shared by modern

Fig.4- Frontal view of the type of *Killikaike blakei* (MPM-PV 5000).

cebines, but its strongly vaulted frontal bone and capacious anterior cranial fossa indicate the early evolution of an enlarged forebrain.

In the northwest of Patagonia, the Province of Neuquén has yielded a poorly represented fossil pitheciin, *Proteropithecia neuquenensis* (Kay *et al.*, 1998, see also Pardiñas, 1991). It is known only by 15 isolated teeth and a talus. However, the interrelationships of this fossil can be firmly established. It has lower incisors that are compressed and procumbent as in pitheciins, and lower molars with low crown relief, shallow basins and crenulated enamel, also as expected for pitheciins. The talus shows overall resemblances to *Callicebus*.

Colombia

An important region where a diverse fauna of middle Miocene primates was found is La Venta, in the valley of the Magdalena River, Colombia. The work at La Venta began in the 1940s, when several primate species were found by Stirton and co-workers (Stirton, 1951). These first Laventan primates were *Cebupithecia sarmientoi*, *Neosaimiri fieldsi* and *Stirtonia tatacoensis*, originally described as "*Homunculus*" *tatacoensis*, then properly reassessed as a new genus by Hershkovitz (1970). *Cebupithecia* is one of the most complete fossil platyrrhines ever found (Stirton, 1951) and is undoubtedly linked with pitheciins. The type is a partial skeleton represented by rather complete hindlimbs and forelimbs, vertebrae, tail and pelvic girdle, and a mandible and maxilla with several teeth. The dentition is clearly synapomorphic with the living pitheciins, displaying procumbent upper incisors, huge and projecting canines that are triangular in cross-section, and quadrate molars with poorly developed cusps and crests.

Neosaimiri fieldsi is an undoubtedly squirrel-monkey fossil relative. It is represented by mandibles and abundant isolated teeth (Stirton, 1951; Takai, 1994) that shows strong affinities with *Saimiri*; some authors have also proposed that it differs from *Saimiri* only at the species level (Rosenberger *et al.*, 1991b). However, the upper incisors of *Neosaimiri* are slightly smaller, the upper P4 shows a hypocone and the upper molars are trapezoidal in outline, with a moderate hypocone and well developed crests, and M3 is the smallest molar, a synapomorphy shared with *Saimiri* and *Cebus*. The lower molars develop a buccal cingulum. Postcranial elements of *Neosaimiri* shares similarities with *Saimiri*, *Saguinus* and *Aotus* (Meldrum *et al.*, 1990, Nakatsukasa *et al.*, 1997).

Laventiana annectens is a closely related taxon represented by a rather complete mandible and a talus (Rosenberger *et al.*, 1991c), very similar to *Saimiri* and *Neosaimiri* in general morphology and size. A buccal cingulid is present in the molars, and also an autapomorphic distinct post-entoconid notch.

Nuciruptor rubricae is another pitheciin primate, represented by a right mandibular corpus with well preserved teeth (Meldrum & Kay, 1997). The lower incisors clearly show the pitheciin pattern, as in *Cebupithecia*, but the canine and premolars are distinct. The canine is moderately developed by comparison and the premolars do not show a molarized p4; instead, the talonid is short. Although presenting primitive features such as well developed cusps and crests, the molars display distinctive pitheciin morphology.

Mohanamico hershkovitzi (Luchterhand *et al.*, 1986) is represented by a mandible and is most probably related to *Callimico* (Rosenberger *et al.*, 1990), although pitheciin affinities have been also proposed (Kay, 1990). It has relatively high-crowned incisors, a tall canine, large p2, and molars with broad trigonids, moderate talonids and moderate crown relief.

Aotus dindensis is placed among the species of the living genus *Aotus* (Setoguchi & Rosenberger, 1987) and it is represented by a mandible, a maxillary fragment and an isolated talus. Despite the presence of smaller incisors and less elevated premolar trigonids, the general molar morphology is basically identical to the living species. The talus was referred to *A. dindensis* on the basis of some characters seen in the living *Aotus* and *Callicebus* (Gebo *et al.*, 1990). More recently, Takai *et al.* (2001) mentioned a maxillary fragment with P4-M1of an *Aotus*-like taxon from La Venta, with a general morphology indistinguishable from the living *Aotus*.

Patasola magdalenae is a small callitrichine-like primate known by a right mandible with all molars and the deciduous premolars (Kay & Meldrum, 1997). Lower molars are narrow but still lack the trigonid enlargement seen in callitrichines. However, it has a third molar, which is slightly smaller than that of *Callimico*.

Another callitrichine from La Venta is *Micodon kyotensis* (Setoguchi & Rosenberger, 1985), represented by an upper molar tentatively referred to as an M1. There is not much to say about this taxon since it is so poorly represented. The morphology suggests callitrichine affinities especially with reference to its small size, and reduced hypocone and lingual cingulum.

Lagonimico conclucatus is a flattened skull described originally as a giant callitrichine (Kay, 1994) that preserves most of the dentition. *Lagonimico* is larger than any known callitrichine, about the size of *Callicebus*. Among the characters that supposedly link it to marmosets and tamarins are the lack of a hypocone in the upper first and second molars, a very small M3/m3, and wasted upper premolars. However, it has also been suggested that *Lagonimico* is related to pitheciines because of its deep mandible with a flaring gonial region, as in all pitheciines, and also because of the shape of its ascending ramus, which resembles *Callicebus* and *Aotus* (Rosenberger, 2002).

Miocallicebus villaviejai is the most recently described primate from La Venta (Takai *et al.*, 2001). It has preserved a piece of maxilla with root of M1, damaged M2, and broken M3. Takai suggests it is closely related to the living *Callicebus*, a homunculin taxon of the Pitheciinae clade. Due to the heavy wear, the crown morphology is not clear but the large hypocone and quadrate molar outline resembles that of *Callicebus*.

Stirtonia tatacoensis and *S. victoriae* (Stirton, 1951; Hershkovitz, 1970; Kay *et al.*, 1987) are closely comparable in size and dental morphology to the living *Alouatta*. This genus is well known by dental, mandibular and maxillary material, including large molars with tall cusps and sharp crests, prominent buccal cingulum and reduced lingual cingulum in upper molars, a long cristid obliqua, a high and relatively small trigonid in the lower molars, and broad talonids with well developed talonid basin. In general, these characters strongly resemble those of living species of *Alouatta*, thus the generic status of *Stirtonia* - which has already been questioned (Delson & Rosenberger, 1980) - ought to be re-examined.

Río Acre

The Solimões Formation, in the border between Brasil, Perú and Bolivia, has preserved a late Miocene fauna of Huayquerian SALMA (late Miocene, ca. 9-6 Ma), including some isolated primate teeth (Kay & Frailey, 1993). The Solimões Fm represents a geologic time with no record of primates in South America, about 12 Ma since the middle Miocene of La Venta through the Pleistocene of Brazil and Caribbean (see below). Two molars were collected at the Bolivian margin of the Acre River. One isolated lower molar has been tentatively assigned to *Stirtonia* sp., for it is similarity in crown morphology and size to *Stirtonia tatacoensis*, with the well developed crests that are also seen in the living *Alouatta* species (Kay & Frailey, 1993). Another primate from Solimões is an upper molar of a large cebine (Kay & Frailey, 1993) that has been named recently as *Acrecebus fraileyi* by Kay & Cozzuol (2006), having inflated cusps, a large hypocone and a metaconule, thus resembling *Cebus* in many aspects. In the same paper, Kay & Cozzuol (2006) described an additional taxon, *Solimoea acrensis*, from the Acre river in Brazil, based on an isolated lower molar and a maxillary fragment with P3-4 that they included in their ateline subfamily (Tribe Atelini for the present work), this is the clade formed by *Ateles*, *Lagothrix* and *Brachyteles*, basically because they interpret that the specimens have moderate shearing crests. The authors allocated the two specimens into *Solimoea* based on some dental traits and because they were found in the same locality. However, the upper premolars are heavily worn and do not allow to predict confidently the morphology, thus leaving some doubts on their generic status.

BRAZIL

Although published later, *Protopithecus brasiliensis* was found by Lund in 1836 inside a Pleistocene cave from the state of Minas Gerais (LUND, 1840). Thus, *Protopithecus* is not only the first fossil primate discovered in South America but also the first in the world. In addition to the partial femur and humerus that Lund discovered in the XIXth century, a skull and mandible along with several postcranial bones were discovered by Cástor Cartelle in the early 1990s in late Pleistocene cave deposits of Toca da Boa Vista, state of Bahía (HARTWIG & CARTELLE, 1996).

Although presenting a mix of traits, *Protopithecus* does display several derived characters shared by all atelines. The skull, which shows some similarities to *Alouatta* (HARTWIG & CARTELLE, 1996), also lacks of the usual specializations for folivory found in the dentition of Howler monkeys. The postcranium is apparently more similar to atelins (*Ateles*, *Lagothrix*, *Brachyteles*), with traits that characterize brachiating locomotor adaptations (HARTWIG & CARTELLE, 1996). However, the postcranium is also much more robust than in other atelines. This is related to the fact that the estimated body weight of *Protopithecus* is about 25kg (HARTWIG, 1995), much larger than the largest living platyrrhines, weighting about 12kg (FLEAGLE, 1999).

Caipora bambuiorum is another "giant" primate genus from Toca da Boa Vista, Bahía, represented by a nearly complete skeleton (CARTELLE & HARTWIG, 1996). It is also considerably larger than *Brachyteles*, weighing around 20kg. *Caipora* is more similar to *Ateles* in cranial morphology, with a large, rounded braincase. Its molars are quadrate, bunoid and have low cusp relief. As with *Protopithecus*, the postcranium is generally similar to atelins and exhibits brachiating locomotor adaptations.

Another extinct primate appeared in a Pleistocene cave of Bahía; it is a new species of the living *Alouatta* (TEJEDOR *et al.*, in press) with most major traits undoubtedly demonstrating a relationship to the Howler monkeys.

GREATER ANTILLES

In Cuba, Jamaica, Dominican Republic, and Haiti, several fossil primate remains of controversial affinities have been found. A remarkable example is *Xenothrix macgregori*, from the late Pleistocene of Jamaica (WILLIAMS & KOOPMAN, 1952; ROSENBERGER, 1977; MACPHEE & FLEAGLE, 1991), a primate that lacks the third molars, among other unusual features. On the basis of several traits of the type mandible, the pitheciine status of *Xenothrix*, as a member of a subclade possibly linked with *Callicebus* and *Aotus*, was proposed years ago by ROSENBERGER (1977). HOROVITZ & MACPHEE (*e.g.*, 1999; MACPHEE & HOROVITZ, 2004) have proposed that *Xenothrix* is part of a unique clade of pitheciines that is more closely related to *Callicebus*. The type mandible has a very deep corpus and preserved m1-2 of bunoid aspect, long and broad with low cusp relief and enamel crenulation. A more recently discovered partial face, with flat P4-M2 on both sides (HOROVITZ & MACPHEE, 1999; MACPHEE & HOROVITZ, 2004), shows pitheciin traits such as expanded trigon/talon basins and poorly developed crown relief. Its morphology suggested to ROSENBERGER (2002) the possibility of closer affinities with genus *Aotus*, a proposal challenged by MACPHEE & HOROVITZ (2004). Another remarkable but non-pitheciin character of *Xenothrix* is the small canine and second premolar in both jaws, evidenced by the small roots. However, moderate canine and p2 characterize the homunculins.

Antillothrix bernensis was originally described as "*Saimiri*" *bernensis* by RÍMOLI (1977), later renamed by MACPHEE *et al.* (1995). The type is a partial maxilla with P4-M2, and other material include a lower m1 in a mandibular fragment, and a distal tibia found in the southeast of Domincan Republic, Hispaniola. The estimated age is 3850 +-150 rcybrp, thus being late Holocene. Although the affinities with *Saimiri* have been debated, the upper molars resemble at least cebines in its buccolingually broad P4 – a key synapomorphy of cebines – expanded bucal side of M1-2, reduced cingulum and reduced M2 with the hypocone almost absent. To the contrary, based on four unambiguous characters of the skull and canine, MACPHEE *et al.* (1995) and HOROVITZ & MACPHEE (1999) suggested a sister group relationship between *Antillothrix* and *Paralouatta* (see below). As noted above, they hypothesize that *Antillothrix* forms a monophyletic clade along with *Xenothrix*, and that this clade also includes *Callicebus*. However, the dental morphology evidence supports a phylogenetic link with cebines.

Paralouatta varonai was described from a well preserved skull with a damaged dentition and a good part of the face (RIVERO DE LA CALLE & ARREDONDO, 1991). Later, a mandible and isolated teeth were found and described (HOROVITZ & MACPHEE, 1999). This material came from the Pleistocene (probably early?) of Cuba. The face appears projecting upward, as in *Alouatta*; the braincase is long and low, relatively large with strong temporal and nuchal crests, and large orbits, a set of characters strongly resembling *Alouatta*. But the dentition exhibits several strong differences; the canine is very small, and the cheek teeth are not large and crested like *Alouatta*. While as mentioned above, some associate *Paralouatta* with pitheciines, along with *Xenothrix*, *Antillothrix*, and *Callicebus* (MACPHEE *et al.*, 1995; HOROVITZ, 1999; HOROVITZ & MACPHEE, 1999), several cranial and dental novelties of *Paralouatta* are shared with the howlers, indicating they are cladistically related.

Adding to the above mentioned three taxa of Caribbean platyrrhines, there are other records of importance, such as an astragalus from the early Middle Miocene of Cuba (MACPHEE & ITURRALDE-VINENT, 1995), the oldest platyrrhine recorded until now in the Greater Antilles as well as in the northern Neotropical Region. This talus appears similar to one broken talus assigned to *Paralouatta*, and has been named as the new species *Paralouatta marianae* (MACPHEE *et al.*, 2003). "*Montaneia anthropomorpha*" (AMEGHINO, 1910, later renamed *Ateles anthropomorphus* (ARREDONDO & VARONA, 1983), is an upper dentition currently thought to pertain to the living species *Ateles fusciceps* (MACHPHEE & RIVERO DE LA CALLE, 1996). A tibia from Hispaniola with uncertain taxonomic affinities has been related morphologically to callitrichines, but it approached the size of a *Cebus* (FORD, 1986). Two femora from Jamaica (FORD & MORGAN, 1986; HERSHKOVITZ, 1988) are similar to each other in size and morphology and could be attributable to *Xenothrix* (see MACPHEE & HOROVITZ, 2002), while a third femur is rather unusual (MACPHEE & FLEAGLE, 1991). Finally, several materials from Haitian caves have been mentioned by FORD (1990) but remain undescribed.

DISCUSSION AND CONCLUSION

Before considering particular questions, the systematics of much of the above is summarized here, in the form of a classification. This classification of platyrrhines includes all known living and fossil genera. These taxa are the evidence of a very small part of a history of more than 26 Ma of evolution in South America and the Antilles. An impressive number of genera – twenty four, and twenty eight species, of extinct platyrrhines are described at the present time, as compared with 16 living genera.

- Infraorden Platyrrhini E. Geoffroy, 1812
  - Superfamily Ateloidea Gray, 1825 (Rosenberger, Setoguchi & Shigehara, 1990)
    - Family Atelidae Gray, 1825
      - Subfamily Atelinae Gray, 1825 (Pocock, 1925)
        - Tribe Atelini Gray, 1825 (Szalay & Delson, 1979)
          - *Ateles* E. Geoffroy, 1806
          - *Lagothrix* E. Geoffroy, 1812
          - *Brachyteles* Spix, 1831
          - †*Protopithecus brasiliensis* Lund, 1838
          - †*Caipora bambuiorum* Cartelle & Hartwig, 1996
        - Tribe Alouattini Trouessart, 1897 (Szalay & Delson, 1979)
          - *Alouatta* Lacépède, 1799
          - †*Stirtonia* Hershkovitz, 1970
          - †*Alouatta* sp. nov. (Tejedor, Rosenberger & Cartelle, MS accepted)
      - Subfamily ?Atelinae
        - Tribe Aotini Poche, 1908 (Tejedor, 2000)
          - *Aotus* Illiger, 1811
          - †*Tremacebus* Hershkovitz, 1974
          - †*Aotus dindensis* Setoguchi & Rosenberger, 1987
      - Subfamily Pitheciinae Gray, 1849 (Mivart, 1865)
        - Tribe Pitheciini Gray, 1849
          - *Pithecia* Desmarest, 1820
          - *Chiropotes* Lesson, 1840
          - *Cacajao* Lesson, 1840

†*Cebupithecia* Stirton & Savage, 1951
†*Soriacebus* Fleagle, Powers, Conroy & Watters, 1987
†*Nuciruptor* Meldrum & Kay, 1997
†*Proteropithecia* Kay, Johnson & Meldrum, 1998
Tribe Homunculini Ameghino, 1894 (Rosenberger, Setoguchi & Shigehara, 1990)
Callicebus Thomas, 1903
†*Homunculus* Ameghino, 1891
†*Carlocebus* Fleagle, 1990
†*Miocallicebus* Takai, Anaya, Suzuki, Shigehara & Setoguchi, 2001
Tribe indet.
†*Xenothrix* Williams & Koopman, 1952
Subfamily ?Pitheciinae
†*Lagonimico* Kay, 1994
Subfamily *incertae sedis*
†*Antillothrix* Rímoli, 1977 (Mac Phee, Horovitz, Arredondo & Jimenez-Vasquez, 1995)
Family Cebidae Bonaparte, 1831
Subfamily Callitrichinae Thomas, 1903 (Cabrera, 1958)
Callithrix Erxleben, 1777
Cebuella Gray, 1886
Saguinus Hoffmannsegg, 1807
Leontopithecus Lesson, 1840
Callimico Thomas, 1913
†*Micodon* Setoguchi & Rosenberger, 1985
†*Patasola* Kay & Meldrum, 1997
†*Mohanamico* Luchterhand, Kay & Madden, 1986
Subfamily *incertae sedis*
†*Branisella* Hoffstetter, 1969
†*Szalatavus* Rosenberger *et al.*, 1991
†*Chilecebus* Flynn, Wyss, Charrier & Swisher III, 1995
Subfamily Cebinae Bonaparte, 1831 (Mivart, 1865)
Cebus Erxleben, 1777
Saimiri Voigt, 1831
†*Dolichocebus* Kraglievich, 1951
†*Laventiana* Rosenberger, Setoguchi & Hartwig, 1991
†*Neosaimiri* Stirton, 1951
†*Killikaike blakei* Tejedor, Tauber, Rosenberger, Swisher & Palacios, 2006

THE OLDEST, THE RAREST

The oldest platyrrhines, *Branisella* and *Szalatavus*, of late Oligocene age, are still controversial. However, their closest affinities appear to be with the cebids, though probably not with either cebines or callitrichine but with another extinct subfamily. A similar case is *Chilecebus*, the younger Colhuehuapian skull from Chile, a taxon especially difficult to understand. *Chilecebus* shows the rare combination of a small but long braincase with large teeth. But the upper premolars are clearly broad, a strong synapomorphy undoubtedly shared with the cebines, as well as a small M3 relative to the other molars. However, unlike cebines, *Chilecebus* has large quadrate molars with a prominent hypocone; also, the interorbitum appears wider than in a cebine pattern. The early radiation of cebines appears to have been a complex event, and the scarcity of fossil cebids does not help our understanding of their phylogeny. But it is clear that other clades are involved in their diversification.

AUSTRAL PLATYRRHINES

Patagonia has preserved an important record from the early stages of platyrrhine evolution. The Colhuehuapian primates, *Dolichocebus* and *Tremacebus*, are ancient relatives of *Saimiri* and

Aotus, respectively (ROSENBERGER, 1979b; ROSENBERGER & FLEAGLE, 1981). *Dolichocebus* is the oldest cebine known thus far, and *Tremacebus* is the oldest aotin. If it is confirmed that the Aotini are atelines, as suggested by TEJEDOR (2001), thus the early Miocene *Tremacebus* would be the oldest record of the whole Subfamily Atelinae.

The Santacrucian Pinturas primates display an interesting diversity of ancient models of modern patterns. The most remarkable story is the status of *Soriacebus*, certainly the oldest pitheciin known to date. The anterior dentition and mandibular morphology of *Soriacebus* strongly support this hypothesis, and the more recently described *Protopithecia*, from the younger Colloncuran, reinforces the fact that there was a major pitheciin radiation in Patagonia. *Carlocebus*, as a possible homunculin, is probably related to another Santacrucian monkey, *Homunculus*, coming from a different formation but close in age. Homunculins are generalized, morphologically more primitive representatives of the Pitheciinae, and in this sense they are also the oldest. In addition, as FLEAGLE (1990) pointed out, some material from Pinturas pertain to a bigger monkey, morphologically different from *Carlocebus*, whose affinities are currently under study. And TEJEDOR (2002), on the basis of isolated canines has commented on the possible existence of alouattins in Pinturas, as well as a morph even smaller than *S. adrianae*. Finally, *Killikaike blakei*, the new cebine genus is another example of the diverse and still poorly known radiation in Patagonia (TEJEDOR *et al.*, 2006). In summary, during the early to middle Miocene, Patagonia was the geographic reservoir for pitheciines, pitheciins, aotins, and cebines, four major clades that still survive, as well as possibly alouattins.

LAVENTAN PLATYRRHINES

This middle Miocene rich fossiliferous area is, along with Patagonia, one of the two most important regions for fossil platyrrhines. Two additional pitheciin taxa are present there, *Cebupithecia* and *Nuciruptor*, both with more advanced characters than their Patagonian counterparts, relative to the moderns. *Lagonimico* has been allied either to pitheciines of an indeterminate tribe, basically on the basis of its mandibular morphology (ROSENBERGER, 2002), and to callitrichines, based on the dental morphology (KAY, 1994). Abundant remains of *Saimiri*-like cebines are also present in La Venta, *Neosaimiri* and *Laventiana*, both with a general morphology and size very close to living *Saimiri*. The three taxa attributed to callitrichines, *Mohanamico*, *Micodon*, and *Patasola*, none of which are convincing beyond a doubt, have several characters non-typical for that subfamily, but their closest affinities are more likely to be with callitrichines than any other clade. The complex callitrichine radiation in La Venta appeared transitional to more modern lineages (HARTWIG & MELDRUM, 2002).

Among the callitrichine's sister clade, the cebines, saimiriins are quite distinct but there is no trace of the *Cebus* lineage. One may speculate that the more typical callitrichines appeared later in the evolutionary history of cebids, and if all these rare forms (*i.e.*, *Patasola*, *Micodon*, *Mohanamico*) should be considered true callitrichines of cebids indet., or if the lack of typical callitrichines is due to sampling error. Aotins are also present in La Venta, represented by *Aotus dindensis*, which is almost identical to the living species of *Aotus*, thus exemplifying the old branching, conservative morphology, and independent evolution of aotins. Finally, *Stirtonia* is a witness of another old lineage, the howler monkeys. There is no question about the relationships between *Stirtonia* and *Alouatta*, and probably a deeper analysis may demonstrate that they are congeneric.

GIANTS FROM BRAZIL

Protopithecus and *Caipora* are outstanding examples of the complex ateline radiation, and the only two possible atelins (Tribe Atelini) discovered thus far, although the status of *Protopithecus* is still under debate (see also GUEDES & SALLES, 2005). These two giant atelines are filling the latest part of what should have been a long ateline history - virtually unknown - during the Tertiary. As noted by MACPHEE & HOROVITZ (2002), *Protopithecus* and *Caipora* may have been part of the megafauna that became extinct in the late Pleistocene, while other primates associated in the same sites still survive. This means there is probably a large taxonomic gap between the relatively abundant and widespread platyrrhines between the early-middle Miocene and the late Pleistocene that hides much of the information we need to understand the modern radiations. The large-bodied platyrrhines today, subfamily Atelinae, are widely distributed and have a broad adaptive spectrum, but there are no traces of larger ancestors or ancient relatives except for the odd *Caipora* and *Protopithecus*.

FROM THE ISLANDS

If one must choose non-typical platyrrhines, the Antillean genera are outstanding examples. *Paralouatta* resembles *Alouatta* in several aspects, but has very unusual teeth, unusual even compared with all other platyrrhines. *Xenothrix* is very odd, not only because it lacks the third molars, but also for its strange dental morphology, having small p2/P2, a very small canine that may have been functionally incisiform. Apparently, the alveolous for the upper central incisors are enlarged relative to the lateral ones and there is a large intralveolar distance between both I1s, as observed by ROSENBERGER (2002; but see MACPHEE & HOROVITZ, 2004). Also, the orbit appears to be large and preserve the inferior orbital fissure, another argument used by ROSENBERGER (2002) to relate *Xenothrix* with *Aotus*. The P4 and upper molars of *Xenothrix* are certainly related to pitheciins, due to the expanded talon and low occlusal relief with weak crests; P4 has the crest connecting paracone and protocone that divides the tooth in two closely symmetrical parts. This pattern of P4 is not shared by any platyrrhines other that the living pitheciins. The lesson from this rare Antillean primate is that the pitheciins (and the pitheciines as a whole) had a diverse radiation with several "mosaic" patterns. For example, *Xenothrix* differs from pitheciins by having a proportionally smaller anterior dentition, especially a small second premolar and canine, the reverse condition seen in pitheciins.

Antillothrix could be considered as a cebine mainly because of the especially strong synapomorphy of highly transverse P4. The remaining traits (*i.e.*, hypocone reduction and structure, shape of the lingual cingulum, M2 reduction) suggesting cebine affinities may be secondarily important.

And the third case, *Paralouatta varonai*, is the last but best example of oddity among the Caribbean primates. It combines a rather normal, albeit primitive, Howler monkey skull with unusual cheek teeth and very small canines. But, after all, the most readily interpretable traits are in the skull, and they spell Howler.

QUESTIONS TO BE ANSWERED...

As final thoughts based on the descriptions and discussions above, I close with several sets of questions:

a) LESS KNOWN FOSSIL RECORD
- Callitrichinae: origin, radiation, and phylogenetic status. If the Deseadan primates from Bolivia are callitrichines, then the ancestral morphotype we are searching for probably didn't exhibit the expected pattern. Laventan callitrichines are rather unusual and do not contribute to clarify their phylogenetic relationships at all.
- *Cebus lineage*: lack of fossils, virtually unknown; origin of thick enamel and big brain. There is no fossil record of *Cebus*-like platyrrhines anywhere in the Neotropics. The only related specimen is the upper molar from Río Acre. However, the origin of the extreme bunodonty and thick enamel of the living *Cebus* is unknown, as well as its branching from the sister taxon *Saimiri*.
- *Ateles, Lagothrix, Brachyteles*: oldest radiation?, origin?, significance of the Brazilian giants?: The tribe Atelini has no representatives in the fossil record excepting for *Caipora* and, possibly, *Protopithecus*. Even when all atelines are large-bodied, there are no traces of their ancestral morphotypes. The Tertiary had no relatives of the living *Ateles*, *Lagothrix*, and *Brachyteles*.

b) CARIBBEAN RADIATION
- Why is *Xenothrix* so unique? Although its pitheciine affinities are convincing, the origin and adaptive significance of its dental adaptations are confusing.
- Combination of alouattin skull and rare teeth in *Paralouatta*. Following the unusual Caribbean radiation, *Paralouatta* combines rare teeth with an almost typical Howler monkey skull, possibly indicating a long and relatively independent evolution that remains unexplained.
- Examples of island endemisms? This is one of the most probable hypothesis to explain the particular adaptations of all the Caribbean primates, only speculative for now.
- Where do these monkeys come from? The presence of a middle Miocene primate talus in Cuba led us to speculate if the platyrrhines originated first in South America and moved to the Caribbean to undertake such an odd radiation. If so, we should investigate the Caribbean platyrrhines in a different way taking into account a history of an early branching about 17 million years ago.

c) THE MOST CONTROVERSIAL TAXON AMONG PLATYRRHINES, THE *AOTUS* LINEAGE:
- Pitheciine (Rosenberger, 1979b), cebid (Schneider *et al.*, 1996; Horovitz, 1999), ateline (Tejedor, 2000, 2001), something else? Present in the middle Miocene of La Venta, and older relative in the early Miocene of Argentina, *Aotus* is the last

systematic problem among platyrrhines due to its jumping position in the taxonomy. The recent evidences, both morphological and molecular, are far from resolve the controversies.

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PALEONTOLOGICAL TOURISM IN BRASIL: EXAMPLES AND DISCUSSION [1]

(With 9 figures)

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ABSTRACT: The paleontological tourism in Brazil is still at the beginning. Several fossiliferous sites were already transformed into parks or routes, but the main visiting targets are the museums. A broad perspective of interesting paleontological sites is provided here, as well as a discussion on the implementation of such tourism, in the need of an integrated project (scientific, social, economic, cultural, educational, and protective).

Key words: Paleontological tourism. Ecotourism. Scientific tourism. Education. Preservation.

RESUMO: O turismo paleontológico no Brasil: exemplos e discussão.

O turismo paleontológico no Brasil está ainda em fase inicial. Vários sítios fossilíferos já foram transformados em parques ou rotas, mas os principais alvos de visitação são os museus. Uma ampla perspectiva de sítios paleontológicos importantes é fornecida aqui, assim como uma discussão sobre a implementação deste tipo de turismo, com a necessidade de um projeto integrado (científico, social, econômico, cultural, educacional e preservacionista).

Palavras-chave: Turismo paleontológico. Ecoturismo. Turismo científico. Educação. Preservação.

INTRODUCTION

Paleontology is a science that attracts so many people attention, through the discovery of new fossils, behavior aspects, or the identification of new species. It is an important area of the Geosciences, easy to understand and highly educative, which supports cultural tourism around the world, mainly connected with the knowledge of the pre-history. In this case, an important industry is responsible for the creation of movie and TV pictures, books, documentaries, souvenirs, food, clothes, temporary and permanent exhibits, congresses and symposia, and scientific tourism.

Paleontological tourism is a specific type of scientific tourism or ecotourism, related to the history of life on earth. It is performed in museums, parks, trails, routes, and in guided excavations (Da Rosa, this volume), as a link between preservation of the paleontological patrimony and regional socioeconomic development (Schwanke & Silva, 2004).

Thus, preservation of the paleontological patrimony is important in distinct ways: scientific, cultural and economic. In scientific terms, it is fundamental in the approach of the biologic and ecologic evolution on Earth, as well as on the analysis of the environmental changes of our planet, both past and present. In a legal approach, preservation of the paleontological patrimony is justified (Wild, 1988), as fossils are "cultural monuments", of scientific importance and interesting for the global society.

The interdisciplinary approach of Paleontology with other sciences such as Biology, Physics, Genetics, Geology, Mathematics, Chemistry, and many others, provided a new vision of its importance and application. The use of fossils in research institutes and resources exploration (oil, gas, coal) brings more comfort to the world, extremely based on thermal energy for industrial and residential use; classic and molecular paleontology, seeking the parent affinities of living and extant species, and the reconstitution of vanished species, turn Paleontology into a dynamic science, with profound theoretical and applied interest.

In Brazil, the paleontological science goes back nearly two centuries ago. Its history is marked by several relevant scientific discoveries, based on important collections housed at museums or research and graduation institutes. However, this patrimony has been continuingly threatened by the predatory and organized action of great international museums or

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private collectors. Despite a specific legislation on fossils preservation, they perform an institutional procedure of illegal dealing of the scientific material. Preservation of this cultural legacy, important for both the Brazilian nation and the mankind as a whole, is certainly the great challenge of Paleontology in Brazil, now and in the future (Carmo & Carvalho, 2004).

MATERIAL AND METHODS

To discuss on the Brazilian fossiliferous patrimony, a summary of the fossiliferous sites and associated museums detailed by Carmo & Carvalho (2004) were addressed here; for a further description, refer to those authors. More museums may be reached in the homepage of the Paleontological Brazilian Society <www.sbpbrasil.org>.

RESULTS

Preservation of the fossiliferous patrimony and its use by local communities

Preservation of the fossiliferous patrimony at Brazil is generally too complex. Although society recognizes the cultural importance of the fossiliferous sites and its fossils, predation and unauthorized excavations still occur. In the other hand, mining activities performed in sedimentary rocks have an important economic impact on local communities, where those fossiliferous sites are being used for economic transformation, and thus constraining the adoption of more efficient strategies for the paleontological tourism and preservation.

Preservation, evaluation, and consolidation of the fossiliferous sites as cultural elements, vital for the development of regional economic activities (through the scientific tourism), are necessarily linked to educational actions and legal responsibilization. The educational institutions (from fundamental education to university) are responsible for the social and community consciousness of the importance of our natural patrimony, and the urgent need for its preservation. The government (national, regional and local) is in charge for the inspection and on the assurance that the public patrimony will be properly guarded and used.

A restrictive law, prohibiting the commerce of fossils, goes back to March 4th, 1942 (Decreto-Lei n. 4,146); however, there are many cases of commerce and depredation of our fossiliferous sites (see examples in Carmo & Carvalho, 2004). The Araripe Basin ("Chapada do Araripe") is certainly the most brutal one, due to an inefficient inspection, the low life conditions of local population, and an organized system of national and illegal dealing. Protection of the fossiliferous sites is not only a legal problem, but also an educational issue.

The paleontological societies around the world are now in the search of different manners to avoid the commerce of fossils, through specific laws, as well as avoiding the publication of papers based on private collections. Nevertheless, the population living near the fossiliferous sites may also act in their protection, with projects of patrimonial education (Schwanke & Silva, 2004).

The paleontological patrimony and the scientific tourism

Fossiliferous sites must be regarded as "natural cultural monuments", due to their scientific importance and public interest. They represent unique moments of geologic history of our planet, helping to understand past and present ecologic and environmental changes, both catastrophic or not, the evolution of living beings and the meaning of life in our planet. That is the main fascination produced by Paleontology. A growing interest on this science comes from this perception of life, and how extemporaneous our existence can be.

Some of the fossiliferous localities in Brazil show both an exceptional preservation of its fossils and a basic infrastructure (access, lodging, guided tours), and thus an excellent potential for the paleontological tourism (Fig.1; Tab.1; Carmo & Carvalho, 2004). Associations with regional museums, in which the local fauna and flora can be viewed, are extremely relevant for the outcome of paleontological tourism. The fossiliferous sites and associated museums detailed by Carmo & Carvalho (2004) are the following:

A. The Permian Petrified Forest from Central Brazil

Located among the states of Tocantins, Maranhão and Piauí, the great Petrified Forest from Central Brazil includes trunks and ferns of pteridophyts, silicified or preserved as impressions. The genus *Psaronius* is the most important, but many specimens are not formally described yet. Specimens are very well preserved, mainly by histometabasis (Fig.2), in outcrops from the Pedra de Fogo Formation, Parnaíba Basin.

There is no local museum, and the area was 'mistakenly' mined. It is considered one of the greatest outcrops from the Permian flora of South America.

Fig.1- Location of selected fossiliferous sites in Brazil, in which paleontological tourism already occurs, or is in preparation (letters refer to the text). For a more complete map of the Brazilian paleontological museums and research centers, see the Brazilian Geological Survey website, at <http://www.cprm.gov.br/bases/novapale/paleind.php>.

B. The Paleontological Route

At the central region of the State of Rio Grande do Sul (Paraná Basin, Santa Maria and Caturrita formations), a Triassic fauna and flora composes the Paleontological Route, arranged in museums and guided visits to fossiliferous outcrops. Visiting comprehends the 'Petrified Forest from Mata' (Minello, 1995) and the 'Fossil vertebrates from Santa Maria region' (Schultz, 1995) (Fig.3). A more in-depth description is provided elsewhere (Da Rosa, this volume).

C. Cretaceous Dinosaurs, from Uberaba and Monte Alto

A good example of the importance of the fossiliferous patrimony on the modification of the local budget comes from Peirópolis, Municipality of Uberaba, State of Minas Gerais, an important fossiliferous site. The Municipality of Uberaba created the "Centro de Pesquisas Paleontológicas Lewellyn Ivor Price" (CPPLIP), at the district of Peirópolis, in a very innovative and visionary way. Since the 1980's, Peirópolis was an economically decadent place, due to the abandonment of the railroad and despite the mining activities on the area. As many industrial activities in Brazil, mining reverted a very few social and economic benefits to the local population. Deactivation of the nearby quarry could have turned life difficult, but the creation of the CPPLIP helped to improve local economy, by creating new jobs, increasing property values and promoting a more distributed budget. The abandoned rail station was transformed into a research lab and preparation room, which supports an exhibit (Fig.4).

The 'Museu de Paleontologia de Monte Alto' (Fig.4; <http://www.montealto.sp.gov.br>) is located at the homonymous city, in the State of São Paulo (central portion of Bauru Basin). The mentor and present director is Prof. Antonio Celso de Arruda Campos, who gathered fossils of dinosaurs, crocodiles, turtles, bivalve mollusks, ichnofossils, and microfossils from the Upper Cretaceous. These fossils are both matter of university research and elements of educational activities with local students of fundamental and middle course teaching.

D. 'Chapada do Araripe'

'Chapada do Araripe' is a flat-lying mountain developed over the Araripe Basin, a large Cretaceous intracratonic sedimentary basin. It is located at the limits of the states of Ceará and Pernambuco, northeastern Brazil. There are several fossiliferous sites, in which microfossils, ichnofossils, plants, vertebrates, and invertebrates can be found (Carvalho, 2001; Lima, 1978; Nuvens, 1994; Maisey, 1991).

TABLE 1. Brazilian paleontological sites protected and published by SIGEP till 2002 (www.unb.br/ig/sigep/sitios.htm and Schobbenhaus *et al.*, 2002).

1. O Membro Crato da Formação Santana, Chapada do Araripe, CE - M. S. Sales Viana; V. H. L. Neumann	Crato Member of the Santana Formation, rich in animal and plant fossils – Paleontological
2. Sítios Paleobotânicos do Arenito Mata, Municípios de Mata e São Pedro do Sul, RS - M. Guerra-Sommer; C.M. S. Scherer	Triassic Petrified Forest – Paleontological
3. *Mesosaurus* da Serra do Caiapó-Montividiu, GO, e Passo de São Borja, RS - D. Araújo-Barberena; J. V. de Lacerda Filho; L. de L. Timm	Permian *Mesosaurus* – Paleontological
4. Pegadas de dinossauros das bacias Rio do Peixe, PB - G. Leonardi; I. de S. Carvalho	Early Cretaceous dinosaurs tracks, with the third longest world track (more than 20 m) – Paleontological
5. Caverna Aroe Jari ou das Almas, Chapada dos Guimarães, MT - L. B. de Almeida, M. I. C. Moreira	*Arthrophycus* ichnofossils – Paleontological
6. O Sítio Fossilífero de Pirapozinho, Ramal dos Dourados, Pirapozinho, SP - J. M.Suarez	Bone bed of fossils turtles – Paleontological
7. Tufas Calcárias da Serra da Bodoquena - P.C. Boggiani; A. M. Coimbra; A. L. D. Gesicki; A. N. Sial; V. P. Ferreira; F. B. Ribeiro; J. -M. Flexor	Carbonate deposits with foliar imprints and Pleistocene mammals – Speleological and Paleobiological
8. Ilha de Fortaleza, PA - V. de A. Távora; A. C. S. Fernandes; C. S. Ferreira	Fossiliferous limestone of Pirabas Formation, Lower Miocene – Paleontological
9. Fazenda Arrecife, Chapada Diamantina, Morro do Chapéu, BA - N. K. Srivastava; A. J. D. Rocha	Exposures of Neoproterozoic stromatoliths – Paleontological and Stratigraphic
10. Sítio Jaguariaíva, PR – R. T. Bolzon; I. Azevedo; M. L. Assine	Fossiliferous area of Devonian rocks – Paleontological
11. Toca da Janela da Barra do Antonião, São Raimundo Nonato, PI - C. Guerin; M. Faure; P. R. Simões; M. Hugueney; C. Mourer-Chauvire	Parque Nacional da Serra da Capivara: Pleistocene megafauna – Paleontological and Speleological
12. Jazigo icnofossilífero de Ouro, Araraquara, SP - G. Leonardi; I. S. Carvalho	Ichnofossiliferous sandstones, with vertebrate tracks (mammals and dinosaurs) – Paleontological
13. Afloramento Bainha, Criciúma, SC - R. Iannuzzi	Permian *Glossopteris-Gangamopteris* Flora – Paleontological
14. Fazenda Cristal, Morro do Chapéu, BA - N. K. Srivastava; A. J. D. Rocha	Mesoproterozoic stromatolithic bioherms – Paleoenvironmental, Stratigraphic and Paleontological
15. Fonseca, MG - C. L. Mello; L. G. Sant'Anna; L. Paglarelli Bergqvist	Tertiary plant fossils – Paleontological
16. Tetrápodes triássicos, RS - M. C. Barberena, C. L. Schultz, C. M. S. Scherer & M. Holz	World famous reptiles, cradle of the dinosaurs and mammals – Paleontological
17. Jazigo rodovia Quiririm-Campos do Jordão, km 11 (Tremembé), SP - M.E.C. Bernardes-de-Oliveira, A. F. M. de Lacerda, M. J. Garcia & C. C. Campos	Tertiary plant macrofossils – Paleontological
18. Fazenda Santa Fé (Tremembé), SP - M. E. C. Bernardes-de-Oliveira, A. F. M. Lacerda, M. J. Garcia & C. C. Campos	Brazilian biggest association of Tertiary fossils – Paleontological
19. Membro Romualdo da Formação Santana, Chapada do Araripe, CE - A. W. Kellner	Cretaceous fossiliferous carbonate concretions – Paleontological

Fig.2- The Great Petrified Forest from Central Brazil: a) outcrops of the Pedra de Fogo Formation (Parnaíba Basin); b) permineralized log (*Psaronius* sp.).

Fig.3- The Paleontological Route, at southern Brazil: a) 'Museu Guido Borgomanero' at Mata; b) 'Museu de Ciência e Tecnologia – PUCRS', at Porto Alegre.

In order to avoid depredation and illicit fossil commerce (Fernandes & Carvalho, 2000), several museums now exist:

'Museu de Paleontologia da Universidade Regional do Cariri', at Santana do Cariri (Fig.5), is constituted by permanent and temporary exhibits, library, TV and video room, and a research area. The museum was founded by Prof. Plácido Cidade Nuvens, when he was the University Rector, and contains more than 3,000 specimens, such as silicified logs, coniferophyt imprints, flowering plants, mollusks, arthropods, fish, amphibians, and reptiles. Very delicate anatomic structures were preserved, like insects bristles and vertebrate muscle remains;

'Museu de Ciências Naturais e de História Barra do Jardim', at Jardim, is maintained by the 'Fundação Francisco de Lima Botelho', which works on citizenship development through an educational program. The museum houses arthropods, fish, reptiles and conifers from the Araripe Basin;

'Museu dos Fósseis – Centro de Pesquisas Paleontológicas da Chapada do Araripe' (CPPCA), at Crato, is supported by the federal mining agency 'Departamento Nacional da Produção Mineral' (10th District, Ceará). The exhibit presents insects, crustaceans, mollusks, permineralized logs, foliar imprints of different plant groups, fish, reptiles, and specimens from the Pleistocene megafauna. CPPCA was created as an effort to establish a research center, performing educational activites and helping to protect the fossiliferous patrimony. Its paleontological collection partially comes from the apprehension of smuggled specimens, which unfortunately is the exception, as there is few material and human resources to protect all the area.

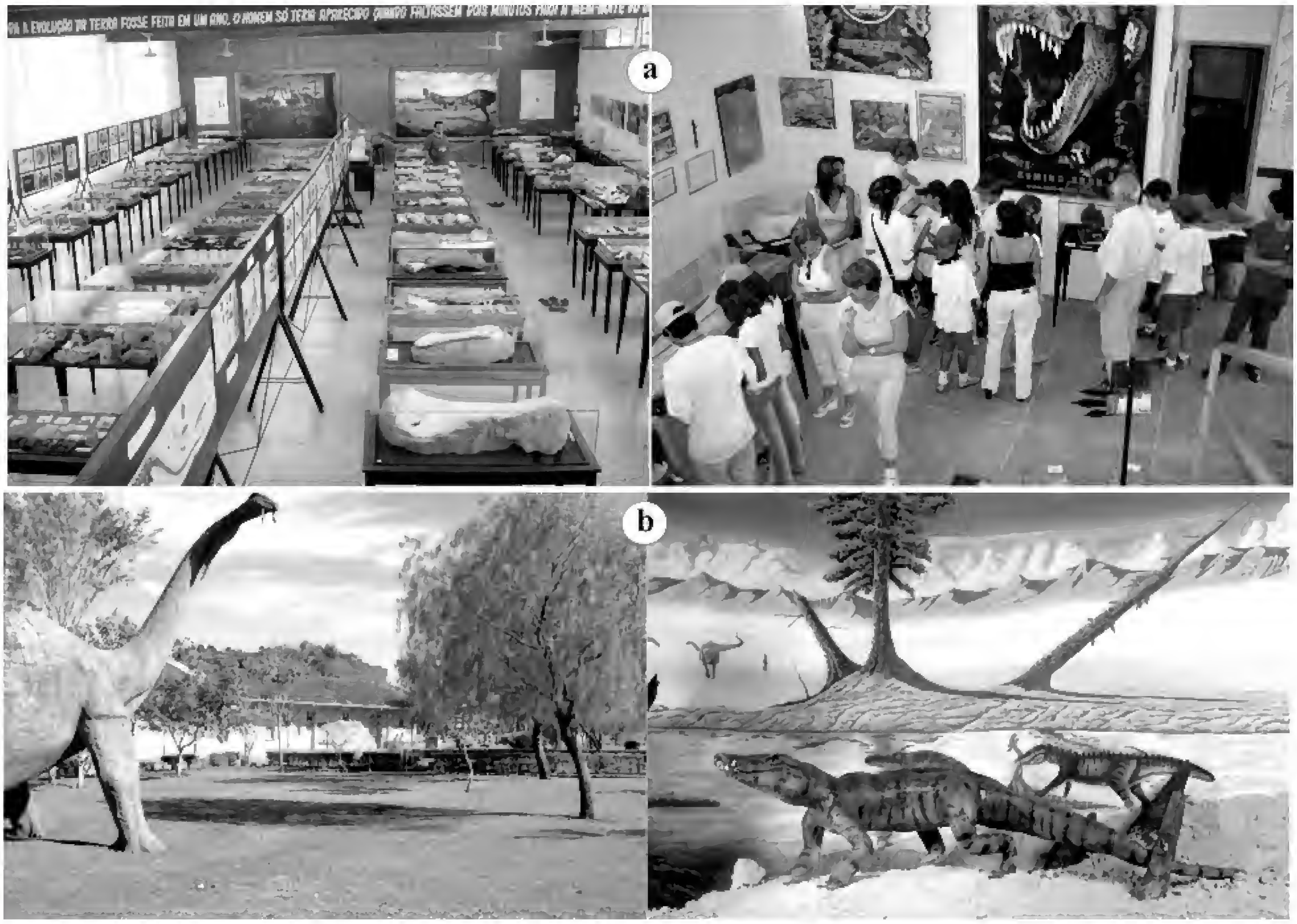

Fig.4- Cretaceous dinosaurs, at southeastern Brazil: a) 'Museu de Paleontologia' at Monte Alto, São Paulo; b) 'Museu dos Dinossauros', at the 'Centro de Pesquisa Paleontológica Lewellyn Ivor Price', at Peirópolis, Uberaba.

Fig.5- 'Chapada do Araripe', at northeastern Brazil: a) outcrops of the Crato Member (Santana Formation, Araripe Basin; b) 'Museu de Paleontologia', at Santana do Cariri; c) well preserved insects.

E. 'Museu do Homem Americano'

Located at São Raimundo Nonato (State of Piauí), it gathers prehistoric information from the 'Parque Nacional Serra da Capivara', which turned to be the most important paleontological collection of northeastern Pleistocene megafauna. Fossils in exhibition are *Palaeolama*, *Hippidion*, *Eremotherium*, *Catonyx*, *Pampatherium*, *Glyptodon*, *Panochtus*, *Toxodon*, *Macrauchenia*, *Haplomastodon*, and *Smilodon* (Museu do Homem Americano, 1998), showing the region paleodiversity and climatic and environmental conditions in the past.

The 'Museu do Homem Americano' is maintained by the 'Fundação Museu do Homem Americano' (FUMDHAM), that is responsible for the scientific research and the preservation of the cultural and natural patrimony of the 'Parque Nacional Serra da Capivara'. Besides the museum, there is also a guided tour to the park, where the visitor receives information about the rock paintings, the cultural traditions of the pre-history, and the environmental context of the megafauna sites.

F. 'Museu de Ciências da Terra – Departamento Nacional da Produção Mineral'

It is a museum that received the paleontological collection and documents of the Brazilian mining agency 'Departamento Nacional da Produção Mineral'. Located at Rio de Janeiro, contains fossils, rocks, minerals and meteorites. The fossil specimens are more than 50,000, from many sedimentary basins, and show the paleodiversity of our country, both fauna and flora. Many fossils are unique, and/or come from destructed or presently inaccessible outcrops.

G. 'Parque Vale dos Dinossauros'

Sousa and Uiraúna-Brejo das Freiras are Cretaceous sedimentary basins, with dinosaur tracks (Carvalho, 1996; Godoy & Leonardi, 1985; Leonardi, 1979 a,b; Leonardi, 1980). They are located at the region of Peixe River, west of the State of Paraíba, northeastern Brazil. The basins were originated during the opening of the Atlantic Ocean, due to transcurrent faults movement (Carvalho, 2000; Carvalho & Leonardi, 1992).

The sedimentary basins have a rich dinosaurian and non-dinosaurian ichnofauna (Leonardi & Carvalho, 2002). The most important site is located at 'Passagem das Pedras', transformed into a park with guided tours, and a whole infrastructure for the preservation of the ichnofossiliferous site (Fig.6). Investments already exceeded US$ 800,000.00, in the infrastructure detailed in Carmo & Carvalho (2004): modification of the main course of the river, to protect the fossil levels; reforestation of native vegetation; road access to the park; steel bridges over the fossiliferous rocks; construction of a reception center. The park contains a permanent exhibit, TV and video room, library, souvenirs store, snack bar, restrooms and administration rooms, as well as reconstructed fossils outside.

Fig.6- 'Parque Vale dos Dinossauros' at Sousa, Paraíba: a) sauropod track; b) steel bridge over dinosaur tracks; and c) reconstruction of theropod track-makers.

I. Ilha do Cajual

The Cajual Island is located at the São Marcos bay, Municipality of Alcântara, State of Maranhão. It is an environmental protection area, with fossiliferous Cretaceous rocks. Fossils are more common near the 'Estação Ecológica da AMAVIDA', in a bone bed called 'Laje do Coringa' (MARTINS, 1996; MEDEIROS, 2001; MEDEIROS, 2003). MEDEIROS *et al.* (1996) recognized teeth and bones of dinosaurs, crocodiles, scales and bony plates of holostean fish, as well as huge tracheophyt logs. Thus, the State of Maranhão created the 'Centro de Pesquisa de História Natural e Arqueologia do Maranhão' (Fig.7), in which there is a paleontological and archeological research area.

J. 'Parque Paleontológico São José de Itaboraí'

The paleontological park is located over Paleocene deposits of the São José de Itaboraí sedimentary basin, at the Municipality of Itaboraí, State of Rio de Janeiro. The area was formerly mined for cement production. According to MEDEIROS & BERGQVIST (1999), the limestone provided a rich fossil fauna and flora: fungi, pollens, angiosperms, gastropods, ostracods, amphibians (Gymnophiona and Anura), reptilians (chelonians, snakes, and crocodiles), birds and mammals (marsupials, Condilarthra, Litopterna, Notoungulata, Astrapotheria, Xenungulata, Edentata, and Proboscidea). The park was created in 1995 and occupies an area of more than 1km^2, being also used in studies of Landscape Archaeology (BELTRÃO *et al.*, 2001). In an effort to revitalize tourism at the park, the local community works with researchers and technicians in a working group to improve local activities and an educational program (RODRIGUES, 2005).

K. Neogene Megafauna from the Amazonian Region

Several Neogene fossiliferous deposits can be found in Amazon, preserving the environmental, climatic and biotic shifts of the northern Brazil. In the State of Acre, many rivers present outcrops of the Solimões Formation (Upper Miocene – Pliocene), studied by the 'Laboratório de Pesquisas Paleontológicas da Universidade Federal do Acre'. A rich fauna is recorded: bivalves, gastropods, decapods, crocodilomorphs, chelonians, mammals, as well as permineralized logs (Fig.8, COSTA & ROSAS JR., 2001; MAIA & MAIA, 2001; MELO, 2001). The Juruá River also shows some Pleistocene deposits, in which crocodilomorphs and mammals were found (RAMOS & SOUZA FILHO, 2001), indicating a widespread distribution over the western Amazon (RANZI, 2001).

At Belém, the Museu Paraense Emílio Goeldi houses a collection concerning the main fossil groups found in the Northern Brazilian basins.

Fig.7- 'Cajual Island', at northern Brazil: external view (a) and exhibit room (b) of the 'Centro de Pesquisa de História Natural e Arqueologia do Maranhão', at São Luís –Maranhão.

L. Pleistocene Megafauna from Minas Gerais and Bahia caves

The states of Minas Gerais and Bahia present many limestone caves, in which there is a broad record of Pleistocene mammals (see Cartelle, 1994 for a detailed description). These caves are also important for the study of early occupation of South America, as the discovery of "Man from Lagoa Santa", by the Danish paleontologist Peter Wilhelm Lund, on the XIX century, and present studies of "Luzia", by the Brazilian anthropologist Walter Neves.

The Pleistocene fossils may be seen at: the 'Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais', an important collection of the Pleistocene megafauna; the 'Museu de História Natural da Universidade Federal de Minas Gerais'; and at the 'Zoológico de Pedra' (StoneZoo), located at Cordisburgo, State of Minas Gerais, in which concrete sculptures represent the megafauna (Fig.8).

M. Paleontological Center of Mafra

Located at the city of Mafra, State of Santa Catarina, the Paleontological Center of Mafra (CENPALEO) was

Fig.8- The Megafauna: a) Neogene from western Amazon, a skull replica of the giant crocodile *Purussaurus brasiliensis*; b) Pleistocene from Minas Gerais, 'Zoológico de Pedra' (StoneZoo), at Cordisburgo; c) at the 'Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais', which shows a diorama with a replica of the office of Peter Wilhelm Lund (d).

created at 2002, to house the collection of mesosaurs. It performs educational and research activities, as well as an integrated effort to protect the fossiliferous sites in the area (Fig.9)

N. Taubaté Natural History Museum

The Taubaté Natural History Museum is centered on a rich Cenozoic fauna from the Taubaté Basin, and also on fossil and present skeletons and taxidermized specimens. The main attraction is a complete specimen of the giant non-flying bird *Paraphysornis brasiliensis* (ALVARENGA, 1982, 1985a,b, 1990, 1993; ALVARENGA & HÖFLING, 2003). The museum performs research and educational activities, integrating the local community (Fig.9).

O. Geological Museum from Bahia

The Fossils Room of the Geological Museum from Bahia, among other attractions, exhibits a complete replica of the proboscidean *Haplomastodon waringi*, a common Pleistocene mammal exhumed from carbonatic caves. The museum is presently in the process of integrating research and educational activities.

P. Mineralogical Museum Professor Djalma Guimarães

Located downtown at Belo Horizonte (MG), the Mineralogical Museum is dedicated to the work of Professor Djalma Guimarães, a brilliant Brazilian geologist. There are fossils and replicas in the collection, mainly from the "Oficina das Réplicas – USP".

Q. Estação Ciência

The integration of the research, education, and leisure is very well established at this interactive museum. Born as an extension project of the Universidade de São Paulo, the Estação Ciência is a center of scientific, technologic and cultural diffusion, in which a mix of long term and itinerant exhibits are displayed next to shows, short courses, workshops, and cultural gatherings. Their main objective is centered on providing multiple and interdisciplinary educational resources to teachers and lecturers from school grades.

DISCUSSION

The non-academic community must realize that fossils are part of the cultural, public patrimony, which may be important to the local economic reactivation and/or development, an increase on population self-esteem, as well as on helping to rescue regional cultural values and identity. In a world of globalization, the paleontological heritage comes to be the outmost benefit for the population.

The use of the fossiliferous sites and the fossils found there must be based on an educational program, fiercely attached to a strong legislation. In this case, fossil commerce and depredation may diminish, or even finish. However, the government (federal, regional and local) must always provide the means to protect and inspect the use of the paleontological patrimony.

Fig.9- Fossil exhibits at: a) 'Centro de Paleontologia de Mafra', state of Santa Catarina; b) the Natural History Museum of Taubaté, State of São Paulo.

Success in protecting the public patrimony is generally linked to activities that return knowledge and welfare to these communities. These simple, but long-lasting elements may also help in understanding the true meaning of Citizenship (Carvalho *et al.*, 1999).

According to the World Tourism Organization (World Tourism Organization, 2003), many tourist sites, including the paleontological parks, may not 'pay for themselves', in a first moment. In general, they are unable to guarantee a monetary influx greater than their construction, development, and operational costs. However, the influx of tourists and the widespread use of commercial services generally justify a huge money cost, on equipments and operation. Thus, there is an economic purpose, but not strictly financial.

As in any other commercial enterprise, financial return is not immediate. Also, the financial return volume is associated with how much money is invested first (Tab.2). So, as any kind of industry, there is no space for 'quick return'. The bigger is the investment for the construction, maintenance, and renovation of the tourist spaces and products; larger is the volume of visitors and a socio-economic return. To the local community, the financial quest may be the most interesting, but in a long term, the maintenance of the natural patrimony matters to the entire community.

In summary, the paleontological tourism in Brazil may be viewed as an alternative way of protecting the national paleontological patrimony, through visiting museums, parks and fossiliferous sites, in an organized and educational way, for the visitor and the community around. This kind of cooperation among science, economics, and workfare generally allows a better-distributed welfare, a more disseminated knowledge and culture, and the formation of citizens that are engaged on the fossils protection.

CONCLUSIONS

The Brazilian paleontological patrimony is incredibly rich and important, both in scientific and touristic terms. However, the use of fossils and fossiliferous sites without the participation of the local communities, integrated in educational activities, as well as an inefficient governmental inspection are the main causes for the destruction or illegal dealing of this worldwide legacy.

The paleontological tourism in Brazil is just beginning. So, it is extremely important that all the agents take extreme care on the implementation of parks and routes. In our point of view, only an integrated effort, joining researchers, technicians and the community, can prevent the destruction of the paleontological patrimony and improve the socio-economic-cultural development of the local population.

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TABLE 2. Examples of socio-economic return of four museums with paleontological exhibits in the State of Rio Grande do Sul.

	INITIAL INVESTMENT VOLUME	VISITORS (PER YEAR)	RAW ECONOMIC RETURN*
Museu Paleontológico Walter Ilha, São Pedro do Sul (Secr. Turismo, personal com.)	not informed	1,450	not informed
Museu Guido Borgomanero, Mata (Secr. Turismo, personal com.)	not informed	11,000	R$ 20,000.00
Museu de Ciências Naturais – UCS, Caxias do Sul (P. Reginatto, personal com.)	not informed	60,000	not informed
Museu de Ciência e Tecnologia – PUCRS, Porto Alegre (J. Bertoletti, personal com.)	R$ 10,000,000.00	100,000	R$ 1,000,000.00

(*) = Annual estimates.

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PALEONTOLOGICAL TOURISM: AN ALTERNATIVE INCOME TO VERTEBRATE PALEONTOLOGY [1]

(With 3 figures)

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ABSTRACT: In the Centro Paleontológico Lago Barreales, Neuquén Province, paleontological tourism is in permanent development due to the activities related to The Dino Project. This place is the first paleontological tourism center with educational purposes that uses the resources obtained to finance the scientific research carried out in the area. We have defined three categories of paleontological tourism: the simple visit to a museum, or Classic Paleontological Tourism (CPT); the visit of site museums, or External Paleontological Tourism (EPT), and the Alternative Paleontological Tourism (APT), that comprises the interaction between the visitor and the specialists at the site, as well as the direct participation of the visitor in the technical paleontological work and in research activities. We consider that paleontological tourism in Neuquén Province helps not only to preserve the patrimony and to divulgate the cultural and educational importance of fossils to the general public, but also to collect funds to maintain The Dino Project alive.

Key words: Paleontological Tourism. Education. Neuquén Province. The Dino Project. Tourism categories.

RESUMO: Turismo Paleontológico: uma alternativa rentável para a Paleontologia de Vertebrados.

No Centro Paleontológico Lago Barreales, Província de Neuquén, o turismo paleontológico está em desenvolvimento permanente devido às atividades relacionadas ao Projeto Dino. Neste local encontra-se o primeiro centro de turismo paleontológico com objetivos educacionais que utiliza os recursos obtidos para financiar a pesquisa científica realizada na área. Nós definimos três categorias de turismo paleontológico: a simples visita a um museu, ou Turismo Paleontológico Clássico (CPT, Classic Paleontological Tourism); a visita a museus localizados no próprio afloramento, ou Turismo Paleontológico Externo (EPT, External Paleontological Tourism), e o Turismo Paleontológico Alternativo (APT, Alternative Paleontological Tourism), que compreende a interação entre o visitante e os especialistas no local do afloramento, assim como a direta participação do visitante no trabalho técnico paleontológico e em atividades de pesquisa. Nós consideramos que o turismo paleontológico na Província de Neuquén ajuda não apenas a preservar o patrimônio e a divulgar ao público em geral a importância cultural e educacional dos fósseis, mas também a arrecadar fundos para manter vivo o Projeto Dino.

Palavras-chave: Turismo Paleontológico. Educação. Província de Neuquén. Projeto Dino. Categorias de Turismo.

INTRODUCTION

Tourist activities are developed when, for example, a natural, cultural, and social tourist resource together with the motivation of the visitors (tourists or not) that go to a certain place to relax or to get acquainted with this resource is present.

The aim of paleontological tourism is to provide the visitors the knowledge about this science as well as the necessary materials to carry out the scientific study. In fact, Paleontology is considered a resource that really motivates not only the visit of local people but also of those who come from very distant places. For this reason, one of the paleontologists' objectives is to encourage heritage preservation. Therefore, as Wearing & Neil (2000) points out when discussing about ecoturism, paleontological tourism implies "the management and control, by human beings, of the use of resources (biotic and abiotic) as well as the activities carried out in the planet, trying to restore, improve, protect and maintain, in qualitative and quantitative terms, a desirable mixture of species, ecosystems conditions and processes to be

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enjoyed not only by current generations, but also by future ones". From this point of view, tourism activities are developed in paleontological sites where the fossils found or under investigation are of interest.

In Argentina, the extremely important discoveries made in the Lago Barreales paleontological site since 2000, made it possible to create the Dino Project in 2001 and, as a result of it, in 2002, the first South American *in situ* fossil theme scientific and educational center - The Centro Paleontológico Lago Barreales. It is located 90km away from Neuquén, Patagonia, and its staff has been working to gather the pleasure of a tourist visit with the education of Paleontology. In this place the paleontological tourism is permanently developed.

Fossils in Argentina are protected by paleontological heritage laws. Only one of them is of national coverage (The National Act 25743/03) and the others are specifically of each state. In Neuquén state governs Provincial Act 2184/96 with its regulation decree N°2711/97. By these laws, all fossils are legally protected as they belong to the Nation or to the Provincial State. Museums are just a repository of this heritage. In other words, the care, the study, the protection, and the exhibition of the fossils are the State's responsibility. The problem is that there is no enough funding for the development of those activities. On the other hand, the resources obtained by museums from the received visits are not reinvested in scientific research. They are used to subsidize the maintenance of the buildings.

As the example of Sian Ka'an Biosphere Reserve (Ceballos Lascurian, 1987), a small ecotourism and education center in Mexico, the Centro Paleontologico Lago Barreales, by the development of the Dino Project's activities, use the revenue generated through visits to fund a conservational and educational program within the Lago Barreales site. This reinvestment allows the improvement of the investigation activities.

MATERIAL AND METHODS

In Neuquén Province, it is possible to see paleontological exhibits in five museums: Museo Ernesto Bachman, Museo Municipal Carmen Funes, Museo Municipal Argentino Urquiza, Museo Prof. Juan Olsacher, and Museo de Geología y Paleontología. Particularly, the Museo de Geología y Paleontología of the Universidad Nacional del Comahue, at Lago Barreales area, exhibits a wide collection of dinosaurs and mesozoic reptiles and it represents the unique permanent dinosaur digging accessible area to the general public. The fossils housed at this museum and the Project Dino as a whole are the object of the alternative income study here presented.

RESULTS AND DISCUSSION

Museums in the Neuquén Province

In the Neuquén Province, there are five museums that exhibit paleontological materials: the Museo Ernesto Bachman which is located at Villa El Chocón town and exhibits, among others, the original fossil remains of the famous carnivorous dinosaur *Giganotosaurus carolinii*; the Museo Municipal Carmen Funes which is located at Plaza Huincul city and exhibits, among others, the replica of *Argentinosaurus huinculensis*, the biggest herbivore dinosaur in the world; the Museo Municipal Argentino Urquiza which is located at Rincón de los Sauces city and exhibits original pieces and replicas, mainly of titanosaurids; the Museo Prof. Juan Olsacher which is located at Zapala city and exhibits Mesozoic marine reptiles and invertebrate material; and the Museo de Geología y Paleontología which is part of the Universidad Nacional del Comahue and is located at the Lago Barreales area, 90km away from Neuquén city. It exhibits a wide collection of dinosaurs and mesozoic reptiles.

The laboratories and exhibition rooms in there are the physical places where one can generally be in contact with the fossil material which are occasionally shown to the public. If these institutions do not count with an appropriate space, and the staff is not adequately trained for curatorial activities, the functions of the museums are really affected and fossils are at the risk of being damaged or lost. So, to maintain those repositories of fossil collections there is a need of permanent financial resources. However, most of the time the institutions face a scarcity of resources to preserve the heritage. In general, funds obtained are only sufficient to be applied to the maintenance of the buildings in order to keep the museums opened. Unfortunately, the resources are generally not sufficient to be directed to the reinvestment in scientific investigation. This situation occurs since funds are not subsidized by other entities, either the state or private ones. As a result, the paleontological heritage on the field is in constant dangerous situation and so are the fossil collections and research, activities that sometimes cannot be maintained.

The Museo de Geología y Paleontología is the only museum among the five located on the Neuquén Province that proves to be in a different condition due to the Paleontological Tourism developed in the Lago Barreales site.

The Paleontological Tourism

Since the terminologies "Visit a museum" and "Paleontological Tourism" are commonly used in a wrong and confused way, we have defined three categories of paleontological tourism. The visit to a Museum is defined as the Classic Paleontological Tourism (CPT) (Perini & Calvo, 2005). An alternative of this kind of tourism is to visit "*in site*" museums, with static paleontological sites as, for example, the Valle de la Luna (Moon valley) in San Juan, or dinosaurs' footprints in Neuquén, both in Argentina. We have defined this tourism activity as External Paleontological Tourism (EPT) (Perini & Calvo, 2005) since these sites in general depend on some established museum and are included as an extra visit.

The third category here defined is the Alternative Paleontological Tourism (APT) (Perini & Calvo, 2005) in which the paleontological tourism is shown in all its branches. It is considered a special kind of tourism that consists in the visitor's interaction with the science of Paleontology and the paleontological work itself. In this sense, the site is the key factor when planning the development of this activity. This kind of tourism can be defined as the visit to a paleontological site with the intention of learning and interacting with fossil remains. During the visits, besides the pleasure of the touristic activity, it is simplified the learning of the fossil's scientific value, its importance and its necessary protection. Nowadays, the Alternative Paleontological Tourism is carried out for few days in a year in few places in South America. However, in Centro Paleontológico Lago Barreales this is a constant activity due to the development of the Dino Project.

As the name suggests, the Paleontological Tourism is only developed in paleontological sites and it has educational and recreational purposes. It means that a fossiliferous site must be put in value in order to be used for tourist activities. In this sense, a site is the key factor when planning the development of this activity.

Considering the three presented categories, it is considered that the real Paleontological Tourism is the Alternative one. It consists in the visitor's participation in the excavations, fossil preparation and in getting acquainted with different methods of investigation and scientific information related to the fossil material and paleoenvironmental conditions.

In general, the activity is centered on the cohabitation with the scientific team, on the interaction with technicians and paleontologists, and on the learning of the techniques applied. The tourist participates in all the activities related to the field work, from putting up the bivouac to loading the truck with plaster jackets. The paleontologist's function is to distribute the cleaning tasks and the tourist's participation will depend on their working skills. In fact, this is an important detail, since those who are not capable of handle the materials, specially the delicate ones, cannot participate in this kind of activity. The priority is the fossil preservation and not the visitors self pleasure. It is the paleontologist who is in charge of the excavation and responsible for the scientific work that must evaluate the conditions.

The Paleontological Tourism into practice

Since 2002, in the Neuquén province, Argentina, there is a site in which the APT is permanently carried out. It is placed in the north coast of Lago Barreales, about 90km (60 miles) northwest of the city of Neuquén. The activities developed in the site are related to the Dino Project, a project that is considered a prototype in paleontological tourism practice.

The Centro Paleontológico Lago Barreales is the first paleontological tourist center with educational purposes. Paleontologists that carry out their task of investigation allow the participation of visitors whose main interest is to learn about this specific subject and to take part in the paleontological world

The interest of those who carry out this work is to spread the importance of the development of this science, as well as to collect funds to finance the paleontological scientific researches.

Spontaneous Tourism

The fossil discoveries in Lago Barreales during the development of Dino Project, their preservation, and their importance, were the paleontological novelty of 2002, in Argentina (Poblete & Gomes, 2002). In the weekends of February, 2002, while the works in the location were being carried on, the first onlookers arrived. At the beginning of the following month, on March, 2002, the number of visitors gradually increased. By that time, the weekends were completely dedicated to a guide tour for the visitors. Besides, the schools of the area also became interested in visiting the site, and they did it during weekdays. For this reason some spontaneous circuits had to be established. Then, the circuits and paths had to be strategically devised to turn the visit to the site enjoyable (Perini, 2003).

Along with the tourists, private companies began to collaborate with the rescue. So that, the Universidad Nacional del Comahue, the visitors and the private companies helped Dino Project to be a success and a tourist educational alternative (Calvo *et al.*, 2002).

Our Visitors

Almost 50.000 tourists have visited the excavation until last August 2006, turning Dino Project into the most visited dinosaur excavation of South America until that year. According to our guest book, visitors come in groups of an average of 15 people, mainly families, groups of friends or students. Their interest ranged from sightseeing, carrying out recreational activities, acquiring knowledge, and interacting with the team of technicians and paleontologists.

During the time spent in the center the visitor can interact with the technicians allowing them to become familiar not only with the paleontological work, but also with its cultural and scientific importance. They can also to learn how to protect this heritage of mankind. The fossil material is shown in a double function room, being at the same time a laboratory and a show-room. This is the guarantee that the information given to the visitors is always up to date. The average time of the visit is three hours, depending on the circuit to be chosen. In all cases, visitors are guided by a member of the team. Those who came to the site recognized that it is not frequent to find this kind of organized touristic development with educational purposes and considered these visits of a great valuable educational time.

In order to visit and complete the circuits, tourists have to pay a fee. These resources are exclusively directed to scientific investigations that range from excavation materials to supplies required by the scientist. Several paleontological fieldtrips can now be financed thanks to the income generated by tourism, whereas in the past they could not be launched due to the lack of funding or to the money shortage usually provided by annual subsidies of the state. As a result of the Paleontological Tourism activities, it is possible to guarantee the continuity of the paleontological work for a long time in the future.

CONCLUSION

The Centro Paleontológico Lago Barreales is the first South American *in situ* fossil theme scientific and educational center that joins touristic and paleontological permanent activities. In what concerns the diffusion of the paleontological knowledge the Dino Project showed of great importance since the information offered is not only related to the fossil material (sometimes so fragile) and its preservation, but also to the environmental conditions in which the local species coexisted with. Besides the University and private companies help, the obtained incomes generated by tourism made possible to get the necessary funds to finance several paleontological needs such as equipments for fieldtrips and laboratories. Otherwise, these funds are also essential to the development of scientific researches.

The interaction between Paleontology and Tourism is now considered a valid alternative to spread the importance of preserving and protecting the heritage and as an alternative income to vertebrate paleontology. Finally, we understand that paleontological resource must not be used with touristic ends if it does not favor its protection and sustainable development.

This initiative requires a great effort and in the case of the Centro Paleontológico Lago Barreales its organization is the responsibility of a Public University and a team of people that considers that the passion is the main engine to carry out a scientific-touristic activity.

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PALEONTOLOGICAL TOURISM AT SANTA MARIA CITY, SOUTHERN BRAZIL: POTENTIAL *VERSUS* REALITY[1]

(With 6 figures)

ÁTILA AUGUSTO STOCK DA ROSA[2]

ABSTRACT: The central region of the State of Rio Grande do Sul has a great potential for the development of paleontological tourism due to the rich and diverse Triassic fauna. A thoughtful and responsible tourism may help to protect the paleontological patrimony, if linked to educational activities and based on a project where public and private institutions operate in an integrated form.

Key words: Paleontological tourism. Scientific tourism. Ecotourism. Santa Maria. Brazil.

RESUMO: Turismo paleontológico na cidade de Santa Maria, sul do Brasil: potencial *versus* realidade.

A região central do Estado do Rio Grande do Sul possui grande potencial para a implementação do turismo paleontológico, graças a uma rica e diversificada fauna triássica. Um turismo correto e consciente deve ajudar na proteção desse patrimônio paleontológico, se ligado a atividades educativas e a um projeto integrado entre as instituições públicas e privadas.

Palavras-chave: Turismo paleontológico. Turismo científico. Ecoturismo. Santa Maria. Brasil.

INTRODUCTION

The central portion of the State of Rio Grande do Sul, southern Brazil, is known for the Triassic vertebrate fauna and plant fossils (*e.g.*, Schultz *et al.*, 2000). The evolution of early dinosaurs (Colbert, 1970; Bonaparte *et al.*, 1999; Langer *et al.*, 1999; Leal *et al.*, 2004; Bittencourt & Kellner, 2005) and mammalian cynodonts (Bonaparte & Barberena, 1975; Bonaparte *et al.*, 2003) are important highlights of that paleontological record. The occurrence of the *Dicroidium* flora in these sedimentary rocks constitute a significant link for the reconstruction of Gondwana (Bortoluzzi, 1974; Guerra-Sommer *et al.*, 1999; Guerra-Sommer & Klepzig, 2000), and further contribute to the studies on the early evolution of conifers (Guerra-Sommer & Scherer, 1999; Pires *et al.*, 2005) and the climatic shift from semi-arid to more humid conditions at the end of the Triassic (Pierin *et al.*, 2002; Holz & Scherer, 2000).

The geologic, climatic, tectonic, and paleobiologic events that occurred at the end of the Triassic can be used as educational tools for the understanding of evolution. Paleontological tourism, integrated education and protection of the fossiliferous patrimony are also important tools for the improvement of the local socio-economic framework (Carvalho & Da Rosa, this volume).

In this paper, the potentials and reality of the implantation of paleontological touristic activities at the city of Santa Maria, southern Brazil, is discussed.

Paleontological Tourism

There is no formal definition of paleontological tourism. It is certainly a "trip to the past", a specific type of scientific tourism, and related to ecotourism (SENAC, 1988a,b; Carvalho, 2004). The paleontological tourism is a form of interaction between the tourist (individually or in a group) and the paleontological knowledge of a certain region, as part of the understanding of evolution. This search for a mixture of scientific knowledge and pleasure is currently done at museums, parks, and on guided fieldtrips (Santos & Da Rosa, 2001).

Museums of natural history are the best option for people who are interested in paleontological and/or scientific tourism, as fossil can be seen in a planned and acclimatized visiting circuit environment. Two good examples are the Field Museum (Chicago, USA), which displays permanent and temporary exhibits based on fossils collected

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by its research teams from all over the world, and the British Museum of Natural History (London, UK), scientific home of Charles Darwin, which presents fossils from the beginning of life on Earth up to the human modifications done on our planet, which is already regarded as a "mass extinction" event by some.

Very rich fossiliferous sites can be protected *in loco*, what happens in parks or centers, where the visitor can see fossils still outcropping from the original sedimentary rocks. The Dinosaur National Monument (Utah, USA) is one example where the fossiliferous exposures are preserved under a building that was transformed into a visiting center. In some specific cases, tourists are allowed to join scientific expeditions, where they can explore new sites and collect fossils, which end up housed in the promoting scientific institutions.

Among South American museums and parks, there is only one case of scientific expedition for tourist. Many museums of natural history are old-fashioned or in need of adequate conservation of their permanent exhibits (KELLNER, 2004). One of the exceptions is the Museu Paleontológico Egidio Feruglio (Trelew, Argentina), that was recently transferred to a new building, totally planned to allocate research labs and a new exhibit. In the Centro Paleontológico Lago Barreales (CEPALB), of the Universidad Nacional del Comahue, Patagonia, Argentina, tourists are allowed to participate in excavations of fossils. It is estimated that CEPALB receives more than nine thousand visitors per year (PERINI, 2004).

In Brazil, there are several science or natural history museums, that can easily receive hundreds of thousands visitors per year. On the other hand, small local museums are trying to renew their exhibits, with or without scientific supervision. Very recently, some important fossiliferous sites have turned into paleontological parks, where protection, education and tourism were integrated (CARVALHO & DA ROSA, this volume) as follows: Centro de Pesquisas Paleontológicas Lewellyn Ivor Price (Peirópolis, State of Minas Gerais); Monumento Natural Vale dos Dinossauros (Sousa, State of Paraíba); Parque dos Pterossauros (Santana do Cariri, State of Ceará); Centro Paleontológico de Mafra (Mafra, State of Santa Catarina); Museu Paleontológico de Taubaté (Taubaté, State of São Paulo); and Parque Paleontológico de Itaboraí (Itaboraí, State of Rio de Janeiro). Another interesting initiative is the proposition of virtual (*e.g.*, in the internet) geological and paleontological guided tours: the *Caminhos Geológicos*, at Rio de Janeiro/RJ, produced by the Departamento Nacional de Produção Mineral; and the *Excursão Virtual da Serra do Rio do Rasto*, hosted at the Companhia de Pesquisa dos Recursos Minerais – Serviço Geológico do Brasil's homepage.

At the State of Rio Grande do Sul (RS), southern Brazil, there is a regional project that envisions the creation of a Paleontological Route, integrating several municipalities of the central portion of the state, which are rich in animal and plant fossils (Fig.1). This project intends to improve the rate of local development, provide paleontological knowledge to the respective community, and help to protect the paleontological patrimony (fossils and fossiliferous sites). More than fifteen municipalities are part of the Paleontological Route, in an area about 300km long and 30km wide, including the world known fossiliferous sites of São Pedro do Sul, Santa Maria, and Candelária. The federal and state roads are already signaled, but there is a general lack of information pointing to museums or other tourist attractions in the cities.

Some information on the geological and paleontological importance of the area will be here presented, as well as the present infrastructure for paleontological tourism, as a basis for the discussion on specific needs for its implementation.

GEOLOGY AND PALEONTOLOGY OF THE CENTRAL REGION OF RIO GRANDE DO SUL STATE

The central portion of RS is located over Triassic sedimentary rocks of the Paraná Basin (Fig.2). The following formal units represent the Brazilian Triassic (ANDREIS *et al.*, 1980): Sanga do Cabral Formation (Early Triassic), Santa Maria Formation (Middle to Upper Triassic), and Caturrita Formation (Upper Triassic). Approximate ages are based on the correlation of the vertebrate faunas (BARBERENA, 1978; BARBERENA *et al.*, 1985, 1991, 1993; SCHERER *et al.*, 1995; SCHULTZ *et al.*, 2000) and imprints of the *Dicroidium* Flora (BORTOLUZZI, 1974; GUERRA-SOMMER *et al.*, 1999; GUERRA-SOMMER & KLEPZIG, 2000).

In terms of sequence stratigraphy, the Santa Maria and Caturrita formations are grouped into the Sequence II (FACCINI, 2000), Supersequence Gondwana II (MILANI *et al.*, 1998), a Carnian-Eonorian Sequence (SCHERER *et al.*, 2000) or the Santa Maria Supersequence (ZERFASS *et al.*, 2003).

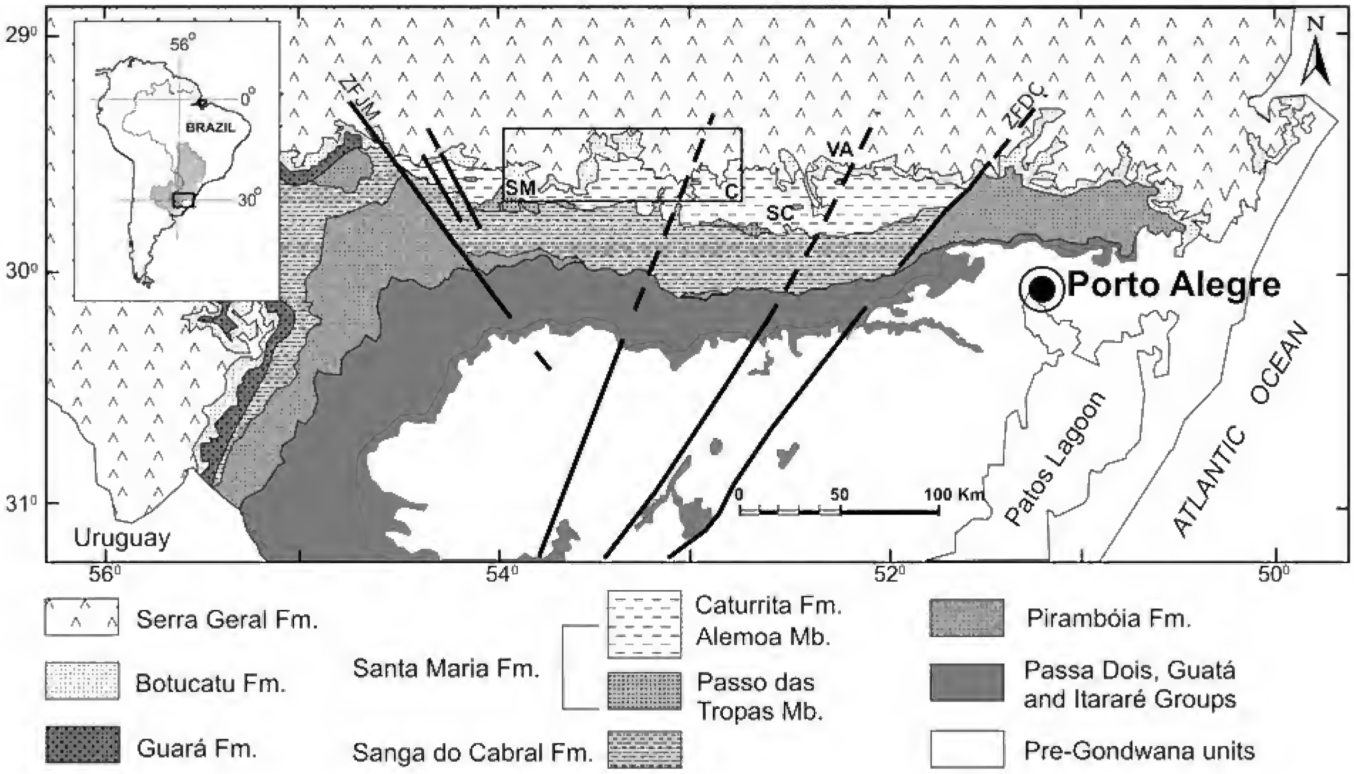

Fig.1- Location of the central region of the State of Rio Grande do Sul, in the context of Paraná Basin (modified from Da Rosa & Faccini, 2005).

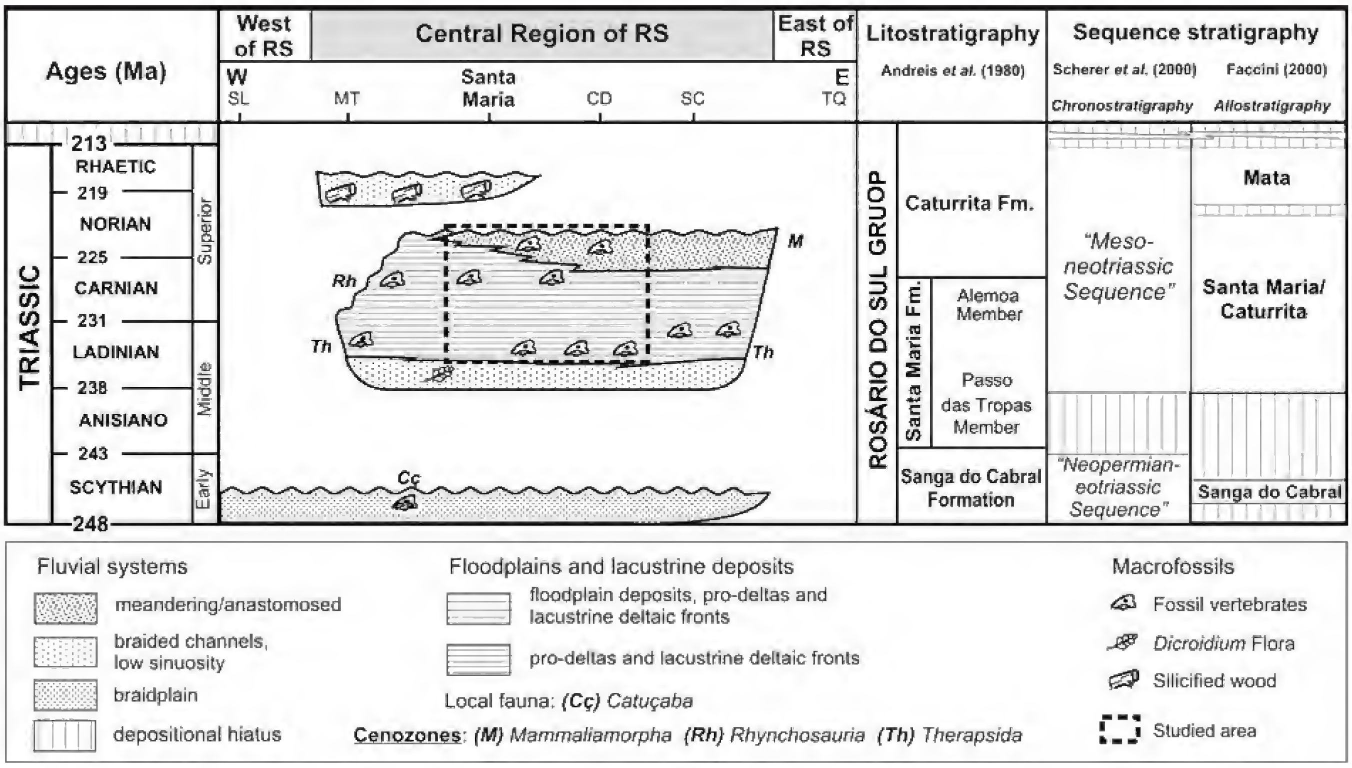

Fig.2- Schematic diagram of the stratigraphic relations and fossiliferous associations of analyzed lithologies (modified from Da Rosa & Faccini, 2005).

In lithostratigraphic terms (and relevant to biostratigraphy), the Santa Maria Formation is subdivided into (ANDREIS *et al.*, 1980): Passo das Tropas Member, formed by coarse to medium sandstones that were deposited in moderate sinuosity channels (FACCINI *et al.*, 2003), and the Alemoa Member, characterized by reddish mudstones, deposited on floodplains, with carbonate paleosoils, aeolian siltstones (*loess*) and secondary sandy channels (DA ROSA, 2005).

Fossil vertebrates at the Alemoa Member were known since the beginning of the XX Century (BELTRÃO, 1965; HUENE, 1990; SCHULTZ, 1995). The leaf imprints of the *Dicroidium* Flora, exclusive to the Passo das Tropas Member (BORTOLUZZI, 1974; GUERRA-SOMMER *et al.*, 1999; GUERRA-SOMMER & KLEPZIG, 2000); and the invertebrate fossils also registered to the Passo das Tropas Member (GALLEGO, 1996, 1999; KATOO, 1971; PINTO, 1959) for stratigraphy, evolution, and paleogeography (Tab.1).

The fossil content of the Santa Maria Supersequence (*sensu* ZERFASS *et al.*, 2003) may be subdivided into cenozones, based on the abundance of certain fossil vertebrates (BARBERENA, 1978; BARBERENA *et al.*, 1985; BARBERENA *et al.*, 1993; SCHERER *et al.*, 1995; SCHULTZ *et al.*, 1994; SCHULTZ *et al.*, 2000; ABDALA *et al.*, 2001; RUBERT & SCHULTZ, 2004). The following progressively younger cenozones are recognized (Tab.2): Therapsida, Traversodontidae, Rhynchosauria, and Mammaliamorpha. At the city of Santa Maria, only fossils from the Rhyncosauria cenozone are recorded (AZEVEDO & SCHULTZ, 1990; HUENE, 1990; LANGER *et al.*, 1999; DA ROSA & LEAL, 2002; DA ROSA, 2004).

The *Dicroidium* Flora has a Triassic range, with some species restricted to Middle to Upper Triassic. However, it is most important to realize that those ramified leafs that first appeared in this geological period represent an important evolution of terrestrial plants (GUERRA-SOMMER & KLEPZIG, 2000). They also confirm the ancient link of South America, Africa, India, Madagascar, Australia and Antarctica, and the existence of Gondwanaland.

The fossil vertebrates are divided into two distinct groups (Fig.3): the archosauromorphs, with reptilian characteristics, and the therapsids, with mammalian characteristics. Rhyncosaurs, primitive archosaurs (=‘thecodonts’), and dinosaurs represent the first ones. The therapsids are represented by dicynodonts and cynodonts.

TABLE 1. Animal and plant fossils recorded to the city of Santa Maria, according to litostratigraphic unit, and indicating its geological or paleontological importance.

UNIT	FOSSILS	LOCATION AND REFERENCES	IMPORTANCE
Caturrita Formation	Silicified logs (“madeira pedra”) and dinosaurs	Itararé, Água Negra (DA ROSA, 2004; LEAL *et al.*, 2004)	Vegetation change, from arbustive to forests, adaptation of dinosaurs and specialized herbivores
Passo das Tropas Mb.	Leaf imprints, insects wings, conchostracs, fish scales	Passo das Tropas Creek (GUERRA-SOMMER & KLEPZIG, 2000; PINTO, 1959)	*Dicroidium* Flora is an important element of stratigraphic correlation and paleogeographic and paleoenvironmental reconstruction
Alemoa Mb.	Rhynchosaurs, archosaurs, dinosaurs and cynodonts	Sanga Grande da Alemoa, Cerro da Alemoa, Faixa Nova, Vila Kennedy, Vila Caturrita (HUENE, 1990; DA ROSA & LEAL, 2002)	Vertebrate fauna represents the early evolution of dinosaurs, as well as the extinction of archosaurs

TABLE 2. Tetrapod-based cenozones of the Triassic of southern Brazil.

AGE		CENOZONE	TETRAPODS
Upper Triassic	EoNorian	Mammaliamorpha	‘Ictidosaurian’ cynodonts, sphenodonts, procolophonids, dinosaurs
	Carnian	Rhynchosauria	Rhynchosaurs, dinosaurs, absence of dicynodonts
Middle Triassic	NeoLadinian	Traversodontidae	Mostly traversodontid cynodonts
	EoLadinian	Therapsida	Dicynodonts, cynodonts, archosaurs and procolophonids

Not belonging to any presently known groups are the lizard-like parareptilian procolophonoids: *Candelaria barbouri* (Cisneros *et al.*, 2004); *Soturnia caliodon* (Cisneros & Schultz, 2003) *Procolophon pricei* (Lavina, 1983), and *Procolophon brasiliensis* (Cisneros & Schultz, 2002).

The rhynchosaurs are specialized herbivores, with an adapted skull similar to a parrot beak (Schultz, 1995). Three species are known: *'Scaphonyx' fischeri* (Woodward, 1907), *Scaphonyx sulcognathus* (Azevedo & Schultz, 1990), and *Hyperodapedon huenei* (Langer & Schultz, 2000).

Archosaurs are represented by the following taxa: *Cerritosaurus binsfeldi* (Dornelles, 1992 and references there), *Chanaresuchus* sp. (Dornelles, 1992 and references there), *Hoplitosuchus raui* (Huene, 1990), *Aetosauroides subsulcatus* (Zacarias, 1982; Da Rosa & Leal, 2002; Desojo & Kischlat, 2005). They are regarded as the precursors of the dinosaurs, the latter being represented by the basal theropod *Staurikosaurus pricei* (Colbert, 1970), the basal sauropodomorph *Saturnalia tupiniquim* (Langer *et al.*, 1999), the comparatively more derived theropod *Guaibasaurus candelariensis* (Bonaparte *et al.*, 1999), the 'prosauropod' *Unaysaurus tolentinoi* (Leal *et al.*, 2004), and the ornitischian *Sacisaurus agudoensis* (Ferigolo & Langer, 2006).

In a global stratigraphy, aetosaurs and rhynchosaurs are important to correlation and the establishment of land vertebrate faunas (Lucas, 1998). The most basal dinosaurs that are present at the region among northern Argentina, southern Brazil and southern Africa, evolved in less than 10 My (Sereno, 1999). An osteologic and functional comparison has confirmed that *Staurikosaurus* is the most primitive dinosaur, when compared to *Eoraptor* and *Herrerasaurus*.

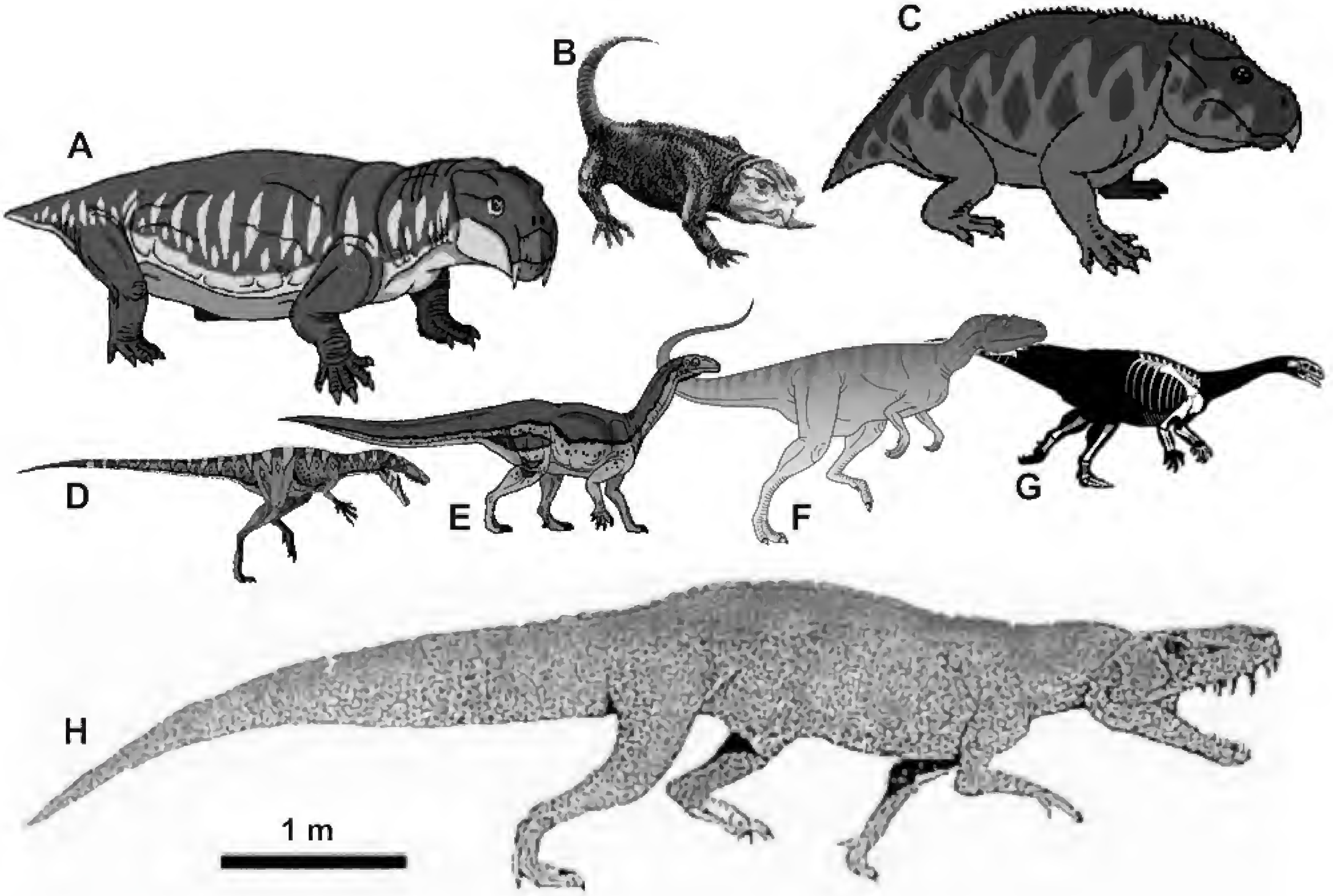

Fig.3- Examples of the fossil vertebrates of the central region, showing distinct forms of tourist interest. *Dinodontosaurus* sp., *Scaphonyx fischeri* and *Jachaleria* sp.; the archosaur *Karamuru vorax*; the dinosaurs *Staurikosaurus pricei*, *Saturnalia tupiniquim*, *Guaibasaurus candelariensis*, and *Unaysaurus tolentinoi*. Drawings from several paleoartists: Felipe A. Elias (A, C, D, E), Euverman (F), Maurílio Oliveira (G), and José Eduardo F. Dornelles (H).

The dicynodonts are huge herbivores from the Middle Triassic, therefore not present at the city of Santa Maria. Two genera are known, which need to be revised (Schwanke, 1998): *Stahleckeria potens*, *Dinodontosaurus oliverai*, and *D. turpior*. So far, fossiliferous sites of this cenozone are Chiniquá (Huene, 1990), Dona Francisca, Paraíso do Sul (Da Rosa *et al.*, 2004a), Novo Cabrais (Da Rosa *et al.*, 2004b), and Candelária (Romer, 1969; Price, 1946, 1947).

Cynodonts are distributed over all cenozones. They can be divided into mammalian and non-mammalian cynodonts, and both in herbivore and carnivore forms (Oliveira & Lavina, 2001). A revision of non-mammalian cynodonts is provided elsewhere (Abdala, 1996), but recent findings have greatly increased the knowledge of this group (*e.g.*, Abdala *et al.*, 2001). Non-mammalian cynodonts are known for the following species: *Therioherpeton cargnini* (Bonaparte & Barberena, 1975), *Charruodon* sp. (Abdala & Ribeiro, 2000), *Santacruzodon hopsoni* (Abdala & Ribeiro, 2003), *Riograndia guaibensis* (Bonaparte *et al.*, 2001), *Brasilodon* sp. and *Brasilitherium* sp. (Bonaparte *et al.*, 2003), and *Irajatherium hernandezi* (Martinelli *et al.*, 2005). Several *Exaeretodon* skeletons (a medium-sized cynodont) have been collected at the vicinities of Santa Maria and São João do Polêsine cities.

Fish scales are recorded at several outcrops (Lima *et al.*, 1984; Perez & Malabarba, 2002; Richter, 2001). A phytosaur was recently described for the Caturrita Formation (Kischlat & Lucas, 2003).

At the city of Santa Maria, it is very common to find silicified logs at the Itararé neighborhood, while excavating for construction of buildings foundations. At the backyard of the Escola Estadual Xavier da Rocha, cross-bedded coarse sandstones from the Caturrita Formation present logs at the stratification sets. In the same formation, there are conchostracs on the road BR 158 (Katoo, 1971), and fossil vertebrates at Água Negra (Azevedo *et al.*, 1998; Da Rosa *et al.*, 1998; Leal, 2001, 2005; Leal *et al.*, 2004), Quilombo (Da Rosa, 2005), and Campinas (Beltrão, 1965; Lyrio *et al.*, 2003, 2004).

Up to now, there are 21 fossiliferous sites at the urban area of the city of Santa Maria (Da Rosa, 2003, 2004). Those sites comprehend public and private areas, with different degrees of accessibility, thus needing an urgent protection.

Infrastructure for the Paleontological Tourism

According to Sommer & Scherer (2000), the 'Petrified Forest from Mata' represents one of the most important paleobotanic sites from South America. Fossil logs are conifer-related gymnosperms, which represent the climatic shift at the end of Triassic. The 'Fossil vertebrates from Santa Maria region' consist of a reptilian fauna, including the first dinosaurs and some mammal precursors (Schultz, 1995).

All these fossils occur in several cities from the region. The fossil logs also outcrop at São Pedro do Sul, Santa Maria, and Faxinal do Soturno. The fossil vertebrates are found in outcrops from São Pedro do Sul through Venâncio Aires. However, just a few cities have prepared themselves for the paleontological tourism. The Mata city, for example, relies on the work done by Daniel Cargnin (deceased), a Christian priest that helped in local conservation and education. His work was based primarily exhibiting large logs on the city public parks, numbered small logs on sidewalks, and some fossil vertebrates and plants at the Museu Pe. Daniel Cargnin (former Museu Guido Borgomanero) (Fig.4). A convention between the Prefeitura Municipal and the Universidade Federal de Santa Maria created an open-air exhibit, the Jardim Paleobotânico, where the visitor can see the trunks in the original outcrops.

Fossils from this region, including vertebrates and plants, are housed the following museums:

- ➢Museu Paleontológico e Arqueológico Walter Ilha - Located at the municipality of São Pedro do Sul, it was created due to the work and effort of Walter Ilha, who also acted fiercely on the preservation of the paleontological patrimony;
- ➢Museu Educativo Gama D'Eca – Located at the municipality of Santa Maria;
- ➢Museu Histórico e Cultural Vicente Pallotti – Located at the municipality of Santa Maria, it presents a paleontological section organized by the late priest Daniel Cargnin;
- ➢Museu de Ciências – Fundação Zoobotânica do Rio Grande do Sul – Located at the municipality of Porto Alegre, presents a paleontological section;
- ➢Museu de Paleontologia – Universidade Federal do Rio Grande do Sul – Located at the municipality of Porto Alegre, nowadays presents only one room exhibit;
- ➢Museu de Ciência e Tecnologia – Pontifícia Universidade Católica do Rio Grande do Sul – Located at the municipality of Porto Alegre, it presents a paleontological section.

In an early attempt to protect the paleontological patrimony, the municipalities of Mata, São Pedro do Sul, and Santa Maria have created local laws to avoid fossil commercialization and to obligate teachers to deal with that subject in local schools (Minello, 1995). Nowadays, the State Law 11.738/02 determines the legal protection of fossiliferous sites and their fossils.

Fig.4- Examples of museums near the city of Santa Maria. (a) The Museu Paleontológico e Arqueológico Walter Ilha, at São Pedro do Sul; (b) The Museu Pe. Daniel Cargnin, at Mata; (c, d) Fossil trunks on the public squares at Mata; (e) the Jardim Paleobotânico at Mata.

The implantation of a tourist route, based on the paleontological knowledge, necessarily involves a correct evaluation of the local infrastructure. Two museums, a research lab, and several important fossiliferous outcrops are recorded at the city of Santa Maria (Fig.5), but no improvement of the infrastructure so far can be recorded.

The Museu Educativo Gama D'Eça, a unit of the Universidade Federal de Santa Maria (UFSM) located at the downtown area, is divided in thematic rooms: history of the UFSM and its founder, Dr. José Mariano da Rocha; archaeology; paleontology; natural history; guns and cannons. At the paleontology room named after Dr. Mário C. Barberena, an exhibit of minerals, rocks, and fossils from southern Brazil was recently reorganized (Leal *et al.*, 1998).

The Museu Histórico e Cultural Vicente Pallotti, part of the religious society named Sociedade Vicente Pallotti, houses collections of stuffed animals, minerals and rocks, archaeologic and paleontologic specimens, tools and guns. The paleontological collection is greatly indebted to the Priest Daniel Cargnin (*in memoriam*), who was responsible for the preservation of the paleontological patrimony for the entire region. In his homage, several species were designated (*e.g.*, *Therioherpeton cargnini* Bonaparte & Barberena, 1975), as well as a public square (Pe. Daniel Cargnin square), that is located at the crossing of road BR 158 and the Fernando Ferrari Avenue.

There are four small municipal museums near the city of Santa Maria. Two of them located west at São Pedro do Sul and Mata and the other two located east at Faxinal do Soturno and Candelária municipalities.

The Museu Paleontológico e Arqueológico Walter Ilha, at São Pedro do Sul, is located at the building of the local Deputies House, as well as the Museu Histórico Fernando Ferrari. The paleontology room exhibits specimens of fossil vertebrates (dicynodonts, rhynchosaurs, and archosaurs) and plants (silicified logs and leaf imprints) of the region. Fossils from other localities from southern Brazil can also be seen. A few outcrops are easily reachable by car, as the Sítio da Piscina, Sítio da Ermida, Sítio Inhamandá, and Sítio Água Boa.

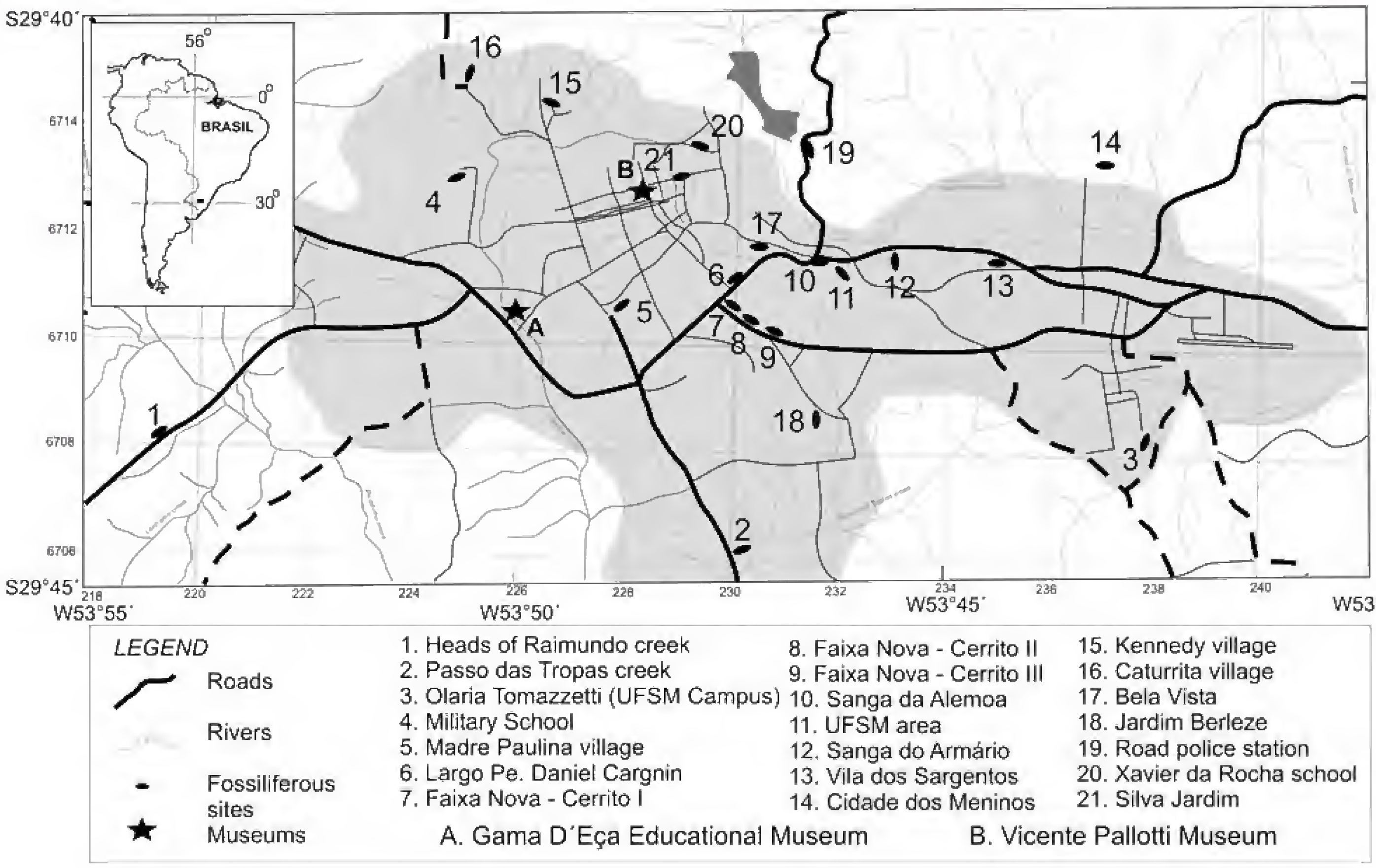

Fig.5- Urban area of the city of Santa Maria, with location of main fossiliferous sites and paleontology museums (modified from Da Rosa, 2004).

The Museu Pe. Daniel Cargnin, at Mata, has a very eclectic collection of historical, archaeological, and biological material. Thanks to the efforts of Priest Daniel Cargnin the museum houses also a rich paleontological collection. People of the city are greatly indebted to Pe. Daniel Cargnin for the preservation and exposure of the silicified logs on the streets and city squares. In the paleontological exhibit, a series of *Dinodontosaurus* skulls and an almost complete dicynodont skeleton are the most important material, collected near the city of Candelária. Aside of the museum, it can be visited the Jardim Paleobotânico de Mata, created by the partnership between the Prefeitura Municipal and UFSM. There, visitors can walk among the silicified logs preserved in the original rock.

At Faxinal do Soturno, a small museum at the district of Novo Treviso exhibits some fossil vertebrates, archaeological, and historical material. This collection is another example of the vigorous work of Pe. Daniel Cargnin, during the few years he did stay in that community.

At Candelária, the Casa Cultural of the municipality houses a paleontology room, with fossil specimens and resin casts of vertebrates found nearby, such as the dinosaur *Guaibasaurus candelariensis*.

At the region known as Quarta Colônia, fifteen municipalities gathered themselves in the named Consórcio para o Desenvolvimento Sustentável da Quarta Colônia (CONDESUS), with the aiming of building a center to support the paleontological research, as well as improving the local socio-economic development. The fossiliferous sites of São João do Polêsine, Faxinal do Soturno, Dona Francisca, and Agudo are planned take part in the Paleontological Route project.

So far, the only paleontological research lab in the region is the Laboratório de Estratigrafia e Paleobiologia (LEP), linked to the Department of Geosciences of UFSM. This lab supports the paleontological exhibit of the Museu Educativo Gama D'Eça, that is responsible for housing the paleontological collection of UFSM, and is also a center for research, teaching, and extension. This lab together with the Laboratório de Estudos e Pesquisas Arqueológicas (LEPA) of the Department of History, compose the Comissão Especial de Resgate do Patrimônio Paleontológico e Arqueológico (CERPPA), created to work together with the regional community in the preservation of its natural patrimony.

DISCUSSION AND CONCLUSIONS

The use of the paleontological patrimony for tourist purposes has been a matter of a constant worry of the academic and non-academic community. In this sense, all the present efforts to conciliate preservation of the paleontological patrimony and its socio-economic use are based on the following assumption: the paleontological tourism will only work if properly connected with educational, legislative, social, and economic activities (Fig.6).

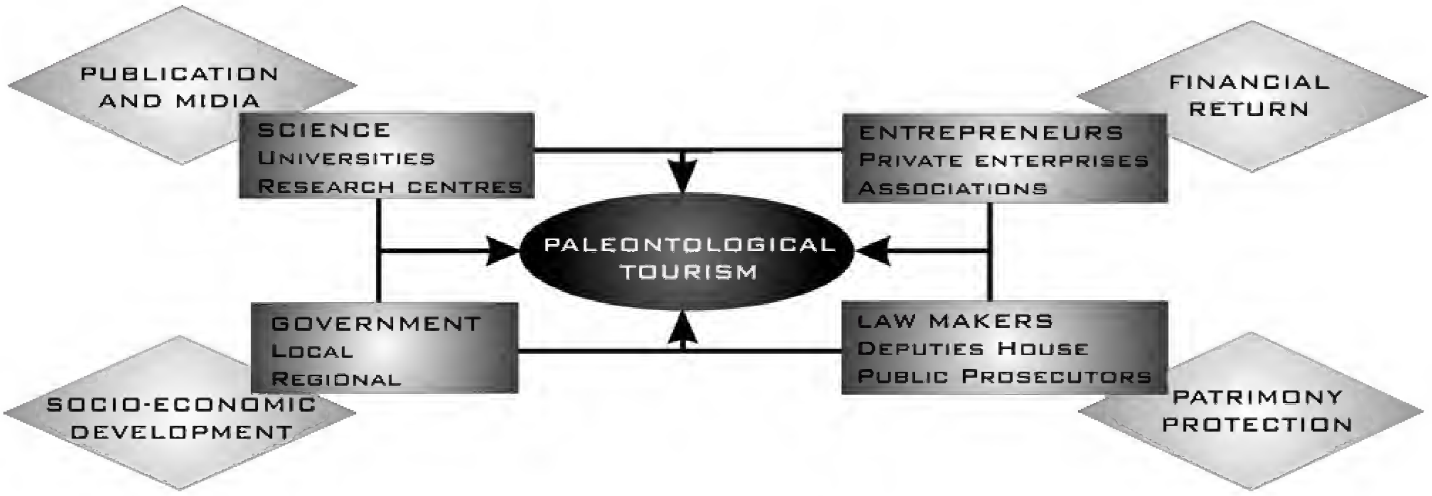

Fig.6- Schematic diagram of the relationships involved on the implementation of paleontological tourism (see discussion on text).

In the city of Santa Maria, there is an effort to legally and physically protect the fossiliferous sites at the same infrastructure for the paleontological tourism is developed. Three regional workshops were organized to specifically discuss paleontological tourism in the region (I and II Paleontur, 1st Municipal Forum on Paleontological Tourism in Santa Maria). Those meetings resulted in initiatives to protect the fossiliferous sites including in the central administrative plan (Plano Diretor) of the city. The protection and management of the fossiliferous sites is still a matter of debate, before tourism is set in the region. There are two projects for the construction of thematic paleontological parks, one located at Santa Maria and the other at São João do Polêsine, both in a preliminary phase and waiting for governmental financial support.

A project for the public developed by the UFSM is called Sítio-escola de Escavação. It aims to protect the main fossiliferous site from Santa Maria (Sanga Grande da Alemoa) and to perform educational activities with students at all levels. A protected area of 1.7ha was divided into quadrants and excavated. The site will contain an educational and tourist infrastructure, such as exhibition rooms (long term and temporary), fossil preparation lab, multimedia classrooms, mini-auditorium, cafeteria, bookstore, and souvenir store.

Notwithstanding the richness of fossil localities in RS, there is still very little infrastructure for paleontological tourism. Advertisement on the roads already point to the Paleontological Route, inviting tourists to visit the cities and local museums. However, local citizens were not prepared for this project and there is a general lack of information in foreign languages and education for environmental and paleontological protection.

The implementation of a museum of natural history in the city may boost tourist services, as well as nucleate tourism in the entire region. Whether or not all municipalities will work together, a huge increase in the tourist demand can be foreseen, leading to an expectation for a socio-economic-cultural development of the central region of the Rio Grande do Sul State.

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