Available online at www.sciencedirect.com
ScienceDirect
C. R. Palevol 7 (2008) 407–417
COMPTES RENDUS PALEVOL
http://france.elsevier.com/direct/PALEVO/

Systematic palaeontology (vertebrate paleontology)

Tooth morphology of *Notosuchus terrestris* (Notosuchia: Mesoeucrocodylia): New evidence and implications

Agustina Lecuona, Diego Pol *

CONICET, Museo Paleontológico Egidio Feruglio, Av. Fontana 140, U9100GYO, Trelew, Chubut Province, Argentina

Received 28 February 2008; accepted after revision 25 June 2008
Available online 20 August 2008

Presented by Philippe Taquet

Abstract

Notosuchia is a large and diverse group of Crocodyliforms, characterized, among other features, by a heterodont dentition. New information on the tooth anatomy of *Notosuchus terrestris* is presented, based on well-preserved specimens from the Late Cretaceous of Patagonia (southern Argentina). This allows a complete characterization of its dental anatomy (composed by incisiviform, caniniform, and molariform teeth) that includes autapomorphic features and derived features shared with *Sphagesaurus* and *Mariliasuchus*. This includes the extensive wear facets in molariforms, indicative of tooth–tooth occlusion and a sharp keel that bears rounded denticles. *Notosuchus* also shares with *Mariliasuchus* the presence of a tooth with a transitional morphology located at the premaxilla–maxilla contact and the absence of interalveolar septa in the entire premaxillary and maxillary dentition. ***To cite this article: A. Lecuona, D. Pol, C. R. Palevol 7 (2008).***

Résumé

Morphologie dentaire de *Notosuchus terrestris* (Notosuchia: Mesoeucrocodylia) : nouvelles données et implications. Notosuchia est un grand groupe diversifié de Crocodyliformes qui se distingue, entre autres caractéristiques, par une denture hétérodonte. À partir de spécimens bien conservés du Crétacé supérieur de Patagonie (Sud de l'Argentine), de nouvelles informations sur l'anatomie dentaire de *Notosuchus terrestris* sont présentées, permettant une caractérisation complète de sa morphologie dentaire (constitue de dents incisiviformes, caniniformes et molariformes) incluant des caractères autapomorphiques et dérivés partagés avec *Sphagesaurus* et *Mariliasuchus*. Il s'agit de grandes facettes d'usure sur les molariformes, qui indiquent une occlusion dent à dent et une crête aiguë avec des denticules arrondis. *Notosuchus* partage aussi avec *Mariliasuchus* la présence d'une dent avec une morphologie intermédiaire, placée au contact du prémaxillaire et du maxillaire, et l'absence de septum interalvéolaire sur l'ensemble de la denture prémaxillaire et maxillaire. ***Pour citer cet article : A. Lecuona, D. Pol, C. R. Palevol 7 (2008).***

Keywords: Teeth; *Notosuchus*; Notosuchia; Heterodoncy; Wear facets; Denticles

Mots clés : Dents ; *Notosuchus* ; Notosuchia ; Hétérodontie ; Facettes d'usure ; Denticules

1. Introduction

Notosuchia is a group of mesoeucrocodylian crocodyliforms that are mainly recorded in Cretaceous

* Corresponding author.
E-mail address: dpol@mef.org.ar (D. Pol).

1631-0683/$ – see front matter © 2008 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.
doi:10.1016/j.crpv.2008.07.001

beds of Gondwana and are particularly abundant in some Late Cretaceous deposits [18]. They have been interpreted as terrestrial organisms, given the lack of widely recognized adaptations to the aquatic environment present in other crocodyliforms [8,24]. Although most recent authors agree on the monophyly of a large clade composed by taxa traditionally classified as notosuchians and baurusuchids [14,17,22,26], the affinities of some forms are still debated (e.g., *Sebecus*, *Araripesuchus* [11,14]). In addition to the shared derived skull features that support the monophyly of Notosuchia, this clade is characterized by the presence of a heterodont dentition with a broad range of morphologies in their posterior teeth (including multicusped crowns [4,5,25]). This feature has led some authors [3,5,15,25] to infer the presence of feeding mechanisms (and possible dietary habits) that contrast with those of other groups of crocodyliforms (including living crocodylians).

Notosuchus terrestris was the first Mesozoic crocodyliform to be described from South America [24] and is the most abundant vertebrate from the Bajo de la Carpa Formation, but most specimens of *Notosuchus* are still unpublished or only briefly described. Although some recent contributions have increased our knowledge on this taxon [7,16], its dental anatomy has been briefly described based on poorly preserved materials (e.g., [3,24]). Here, we describe the specimens of *Notosuchus terrestris* that have the best-preserved dentition, allowing a characterization of its complete dentition and some relevant ontogenetic changes, and providing new anatomical information relevant both from a paleobiological and a systematic point of view.

2. Systematic paleontology

Crocodyliformes Hay, 1930

Mesoeucrocodylia Whetstone & Whybrow, 1983

Notosuchia Gasparini, 1971

Notosuchus terrestris Woodward, 1896

Lectotype. MLP 64-IV-16-5, Skull and mandible, designated by Gasparini [8].

Referred material. The two specimens described here are MACN-PV RN1038 and MACN-PV RN1127. Additional comparisons are made with MACN-PV RN1124, MACN-PV N114, which represent different ontogenetic stages. For other referred material see [7,18].

Locality, horizon and age. Paso Córdova, Río Negro Province. Bajo de la Carpa Formation. Santonian [10].

3. Materials and methods

Teeth measurements were taken following the procedures of Farlow et al. [6] with some changes given the modified morphology of posterior teeth in *Notosuchus* (Fig. 1; see description for details). The foreaft basal length (FABL) is the mesiodistal length at the crown base measured in an anteroposterior direction in the anterior conical teeth. Given that posterior teeth are obliquely oriented with respect to the anteroposterior axis (Fig. 2C), a different measure has been taken for them: the mesiodistal length (MDL; Fig. 1). We consider the MDL of *Notosuchus* as homologous to the FABL of other closely related crocodyliforms (e.g., *Mariliasuchus amarali*) because these taxa share the presence of a serrated keel along the distal edge of the posterior tooth crowns. This keel is directed posteromedially in the upper teeth of *Notosuchus* whereas it is posteriorly directed in *Mariliasuchus* ([26]: fig. 10). Consequently, the minor axis (transverse to MDL) of posterior teeth of *N. terrestris* is referred here as the buccolingual length (BLL; Fig. 1) and is oblique to the lateromedial axis of the skull.

4. Description

General Features: The dentition of *Notosuchus terrestris* is composed of three different morpholog-

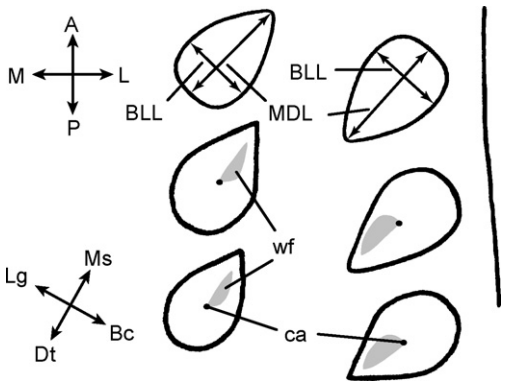

Fig. 1. Schematic drawing of lower (left) and upper (right) molariform cross section of *N. terrestris*. Abbreviations are: A, anterior; P, posterior; M, medial; L, lateral; Ms, mesial; Dt, distal; Lg, lingual; Bc, buccal; BLL, buccolingual length; MDL, mesiodistal length; ca, crown apex; wf, wear facet.

Dessin schématique des dents molariformes inférieure (gauche) et supérieure (droite) de N. terrestris en section transversale. Abréviations : A, antérieure ; P, postérieure ; M, médiale ; L, latérale ; Ms, mésiale ; Dt, distale ; Lg, linguale ; Bc, buccale ; BLL, longueur buccolinguale ; MDL, longueur mésiodistale ; ca, apex de la couronne ; wf, facette d'usure.

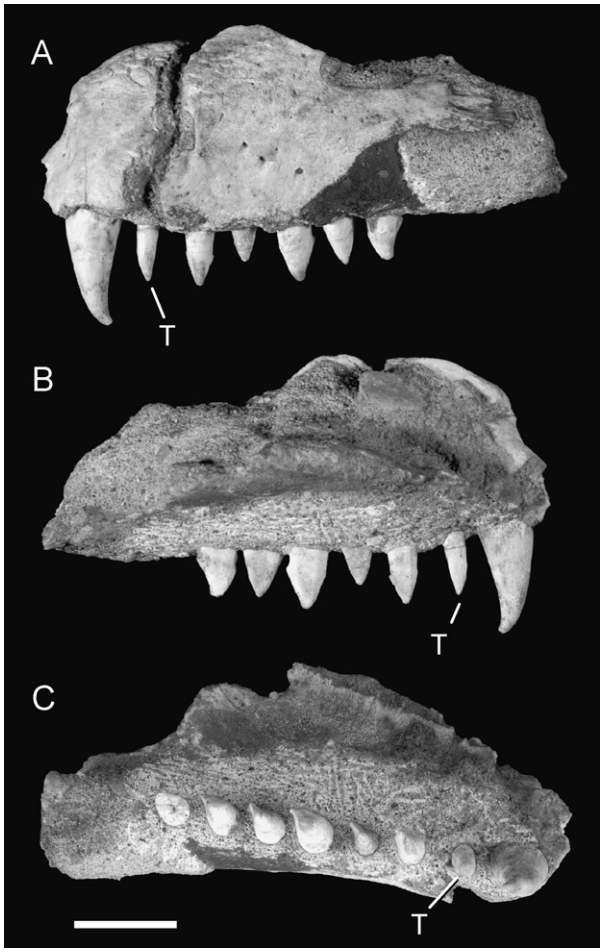

Fig. 2. Left premaxilla and maxilla of *N. terrestris* (MACN-PV RN1127) in lateral (A), medial (B) and occlusal (C) views. Abbreviation is: T, transitional tooth. Scale bar: 1 cm.
Prémaxillaire et maxillaire gauches de N. terrestris (MACN-PV RN1127) en vue latérale (A), médiale (B) et occlusale (C). Abréviation : T, dent intermédiaire. Barre d'échelle : 1 cm.

ical types: incisiviform, caniniform, and molariform. The upper toothrow is composed of three incisiviforms and one caniniform in the premaxilla, one "transitional" tooth located at the premaxilla-maxilla suture, and six maxillary molariforms. The lower toothrow is composed of three incisiviforms, one "transitional" tooth, and six molariforms. Incisiviform teeth are conical and relatively small in comparison with other tooth types. Caniniform teeth are conical, posteriorly recurved, and remarkably large in adult specimens (approximately twice as high apicobasally as the largest molariform tooth). Molariform teeth are teardrop shaped in cross section, with the major axis obliquely oriented with respect to the longitudinal axis of the skull. The acute edge of the teardrop shaped crowns is formed by an extensive sharp keel directed posteromedially in the upper toothrow and anterolaterally in the lower toothrow, as noted by previous authors [3,7]. The transitional crown morphology is intermediate between the incisiviform and molariform morphotypes and bears an incipiently developed keel. This tooth is also special because it is set at the premaxilla–maxilla suture.

PREMAXILLARY TEETH: The premaxillary dentition is composed of three incisiviform and a caniniform tooth. Additionally, the premaxilla houses the anterior half of the fifth upper tooth (see below). The incisiviforms are located in the rostral end of the premaxilla and increase gradually in size, although they all are markedly smaller than the caniniform tooth (Fig. 3B). Their FABL is between 35 and 42% of the caniniform FABL, and the apicobasal height of the incisiviform crowns varies between 37 and 43% of the caniniform

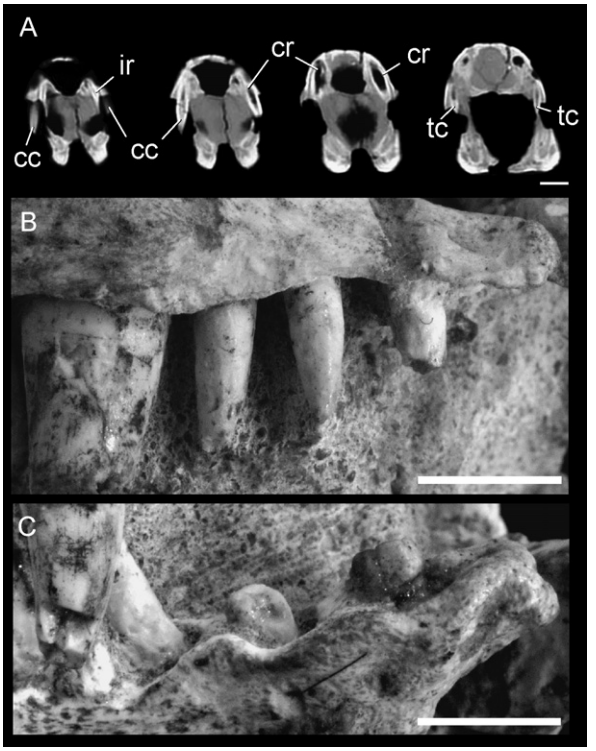

Fig. 3. Incisiviform and caniniform teeth of *N. terrestris* (MACN-PV RN1038). Coronal CT scanning at the caniniform teeth, anteriormost slice is at the left (A). Incisiviforms of rigth premaxilla (B) and rigth dentary (C). Abbreviations are: cc, caniniform crown; cr, caniniform root; ir, incisiviform root; tc, transitional crown. Scale bars: 1 cm (A), 5 mm (B, C).
Dents incisiviformes et caniniformes de N. terrestris (MACN-PV RN1038). Tomographie au niveau des caniniformes ; la région antérieure est à gauche (A). Dents incisiviformes prémaxillaires (B) et dentaires (C) droites. Abréviations : cc, couronne de la caniniforme ; cr, racine de la caniniforme ; ir, racine de l'incisiviforme ; tc, couronne de la dent intermédiaire. Barres d'échelle : 1 cm (A), 5 mm (B, C).

Table 1
Measurements (in mm) of the dentition of two specimens of *Notosuchus terrestris*. See Section 3 and Figure 1 for abbreviations. Asterisks: partially erupted teeth; "b": broken teeth. Two measures are included when left and right teeth were present
Dimensions (en mm) de la dentition de deux spécimens de Notosuchus terrestris. Voir « section 3 » et la Figure 1 pour les abréviations. Astérisques: dents en éruption partielle ; « b » : dents cassées. Deux mesures ont été incluses quand les dents gauches et droites était présentes

Measure	MACN-PV RN1127		MACN-PV RN1038	
	Upper	Lower	Upper	Lower
I^1				
FABL	–	–	2.12	–
CH	–	–	2.61[b]	–
I^2				
FABL	–	–	2.04	–
CH	–	–	4.40	–
I^3				
FABL	–	–	2.26/2.27	2.18/2.22
CH	–	–	4.75	4.4/4.2
C				
FABL	5.18/4.5	–	5.76/5.35	–
CH	9.92	–	11.81[b]/11.82	–
T				
MDL	2.58	2.68	–	–
BLL	2.20	1.59	–	–
CH	5.20	2.22	–	–
M^1				
MDL	3.08	3.51	–	–
BLL	2.32	2.01	–	–
CH	3.60	4.71	–	–
M^2				
MDL	3.64*	3.74/3.86	–	–
BLL	2.08*	2.49/1.96	–	–
CH	3.50*	5.51/3.83	–	–
M^3				
MDL	4.34	–	–	–
BLL	3.86	–	–	–
CH	4.56	–	–	–
M^4				
MDL	4.41	4.33	–	–
BLL	2.88	2.49	–	–
CH	4.86	4.24	–	–
M^5				
MDL	4.45	–	–	–
BLL	2.73	–	–	–
CH	3.90	–	–	–
M^6				
MDL	–	4.19	–	–
BLL	–	–	–	–
CH	–	4.31	–	–

crown height (MACN-PV RN1038; see Table 1). This difference, however, is affected by ontogeny as the FABL ratio between the third incisiviform and the caniniform is 50% in the juvenile material (MACN-PV N114; Fig. 4C). The incisiviforms are conical, straight, and their enamel surface is smooth and lacks apicobasal ridges. At the crown base there is a slightly marked constriction that marks the crown-root limit. The development of the roots increases in the posterior incisiviforms, being the first one implanted below the external narial opening. At this point the dorsoventral depth of the premaxilla is very low and consequently the root of the first upper incisiviform is much smaller than that of subsequent teeth (Fig. 3B). The three first premaxillary teeth are located in a continuous groove, and only the buccal edge of this groove has an incipient demarcation of the alveoli.

The single caniniform is the fourth premaxillary tooth. It has a conical shape, is vertically oriented, and is straight for most of its length, although the crown apex is posteriorly recurved in the most complete caniniform teeth (Figs. 2A, B, 5A). The cross-section of the caniniform crown is ovoid, with its major axis anteroposteriorly directed; its mesial margin is broad and rounded whereas its distal edge is slightly sharper. The distal margin, however, lacks the distinct keel present in molariform teeth (Fig. 2). The caniniform lacks well developed wear facets on its crown surface, although several specimens have a small abrasion facet at the crown's apex. The enamel surface is smooth and several striae are present on the lingual and mesial surfaces of the crown, being randomly oriented in different directions (Figs 5A and B). There is a slight constriction at the base of the crown, which is more evident in the anterior or posterior view (Fig. 5C). The exposed surface of the root bears short apicobasal grooves (Fig. 5C), probably representing the area of attachment of the periodontal ligament as in living crocodiles [13]. The caniniform root is greatly developed in adult specimens where it occupies approximately 75% of the dorsoventral extension of the premaxilla (Fig. 3A). The development of the caniniform tooth is, however, subject to marked ontogenetic change, as described above (Fig. 4). The caniniform alveolous is not completely septated, although the tooth socket is limited mesially and distally by slightly developed medial and lateral projections of the premaxilla.

Premaxillary-Maxillary Tooth: The fifth upper tooth has a transitional morphology and is located at the contact between maxilla and premaxilla, as seen in MACN-PV RN1127 (Fig. 5C). In this specimen the anterior half of the alveolar edge is formed by the premaxilla whereas the posterior half of the alveolar edge is formed by the maxilla. The root of this tooth projects dorsally along the premaxilla–maxilla suture and the anterior half of the alveolar cavity excavates the premaxilla (Fig. 5C), indicating that (at least in this adult specimen) this element is not entirely set in the maxilla. This morphology is not as clearly seen in other

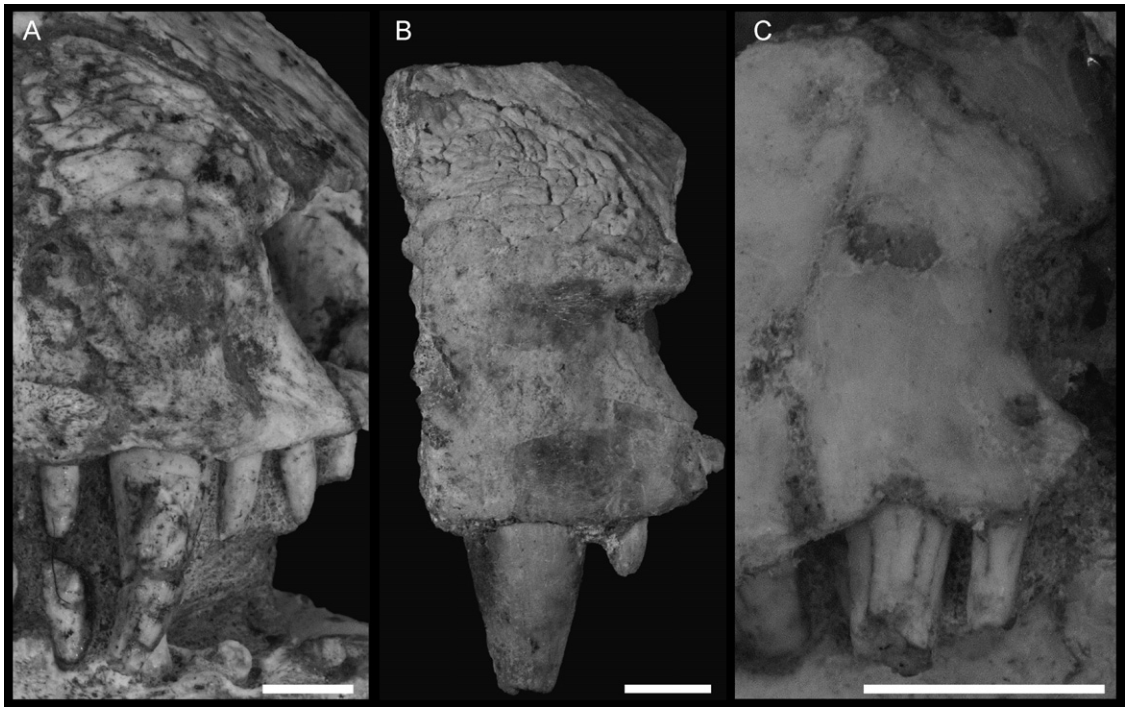

Fig. 4. Premaxillary dentition along ontogenetic series of *N. terrestris*, in right lateral view. A, MACN-PV RN1038; B, MACN-PV RN1124 (reflected for clarity in comparing); C, MACN-PV N114 (juvenile specimen). Scale bars: 5 mm.
Dentition prémaxillaire le long d'une série ontogénétique de N. terrestris, en vue latérale droite. A, MACN-PV RN1038 ; B, MACN-PV RN1124 (réfléchie pour clarifier la comparaison) ; C, MACN-PV N114 (spécimen juvénile). Barres d'échelle : 5 mm.

materials, because of their poor preservation or lack of adequate preparation (e.g., MACN-PV RN1048, MLP 64-IV-16-5, MUCPv-35). The alveolous of this tooth is not completely separated from the contiguous tooth sockets.

The crown is conical and bears an incipient distal keel, which is restricted to the apical half of the crown (Fig. 5 D and E). The distal keel extends posteromedially and therefore the tooth crown has its major axis oriented obliquely as in molariform teeth. The outer enamel surface is mostly smooth bearing only slightly developed striae, irregularly oriented as in the caniniform tooth (Fig. 5F). A distinct wear facet is present close to the tooth apex, extending lingually along the crown. This facet is small, flat, and has the dentine exposed along most of its surface (Fig. 5F). The base of the crown has a very poorly developed constriction that separates this region from the root.

Maxillary Teeth: The maxilla bear six molariform teeth in addition to the transitional tooth that is partially set in this bone. This counting is different from previously published information: seven maxillary teeth [8] or six to ten [3]. All the specimens referred to *Notosuchus* have seven upper teeth posterior to the premaxillary caniniform. Previous authors have counted the transitional tooth as the first maxillary teeth but, as noted above, this element cannot be counted as a definitive maxillary tooth. The molariform crowns are subtriangular in either the buccal or lingual views. In the buccal view, the shape of the distal margin varies depending on the development of the wear facet (see below); teeth with extensive wear facets have a slightly concave distal margin, whereas unworn crowns have a slightly convex edge.

The keels are buccolingually narrow and extend from the apex to the base of the crown (Fig. 6A, B and D). They are separated from the rest of the crown by two broadly concave apicobasal grooves, the buccal depression being more distally positioned than the lingual depression. The development of these depressions and the distinction between the keel and the rest of the crown are more developed in the posterior molariforms. The distinction of the keel and the rest of the crown also varies ontogenetically, as the molariform crowns in the most juvenile specimen (MACN-PV N114) are more bulbous, being wider on the rounded mesial margin and tapering rapidly toward the keel.

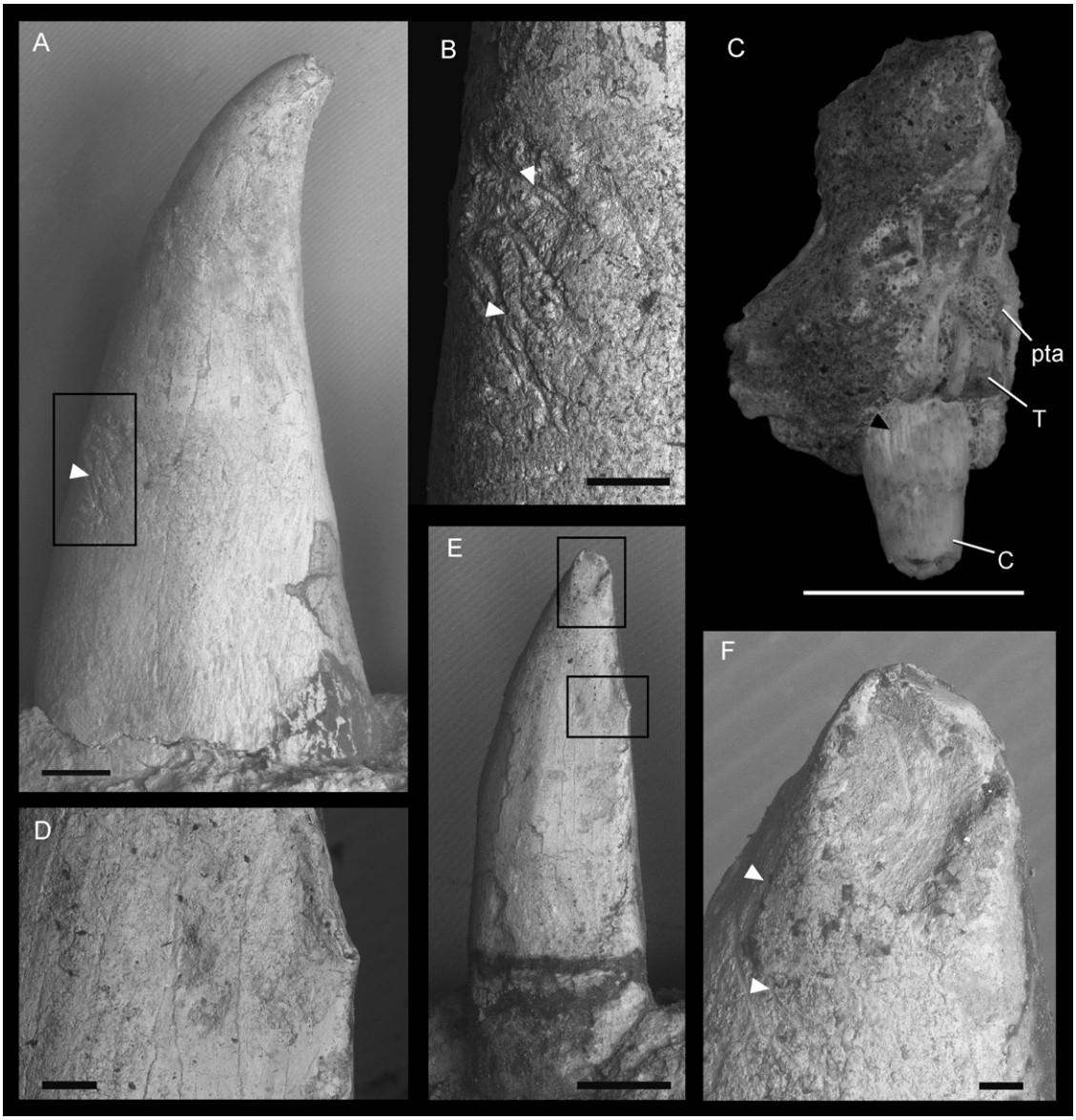

Fig. 5. Caniniform and upper transitional tooth of *N. terrestris* (MACN-PV RN1127). SEM of left caniniform in lingual view (A) and close up of its striae (B). Rigtht caniniform in posteromedial view (C). SEM of upper left transitional tooth in posterolingual view (E), close up of its small distal keel (D) and its apical wear facet (F). White arrowheads: striae, black arrowhead: periodontal ligament grooves. Boxes mark areas magnified in B, D, F. Abbreviations are: C, caniniform tooth; T, transitional tooth; pta, premaxillary transitional alveolous. Scale bars: 1 mm (A, C, E), 500 μm (B), 200 μm (D, F).

Dents caniniforme et intermédiaire supérieures de N. terrestris (MACN-PV RN1127). Photographie prise au microscope électronique à balayage (SEM) de la dent caniniforme gauche en vue linguale (A) et détail de ses striations (B). Dent caniniforme droite en vue postéromédiale (C). SEM de la dent intermédiaire supérieure gauche en vue postérolinguale (E), détail de sa petite crête distale (D) et de la portion apicale de sa facette d'usure (F). Flèches blanches : striations ; flèche noire : sillon pour le ligament périodontal. Les cadres indiquent les zones agrandies en B, D, F. Abréviations : C, dent caniniforme ; T, dent intermédiaire ; pta, alvéole de la dent prémaxillaire intermédiaire. Barres d'échelle : 1 mm (A, C, E), 500 μm (B), 200 μm (D, F).

The enamel surface is mostly smooth although some teeth have slightly developed longitudinal ridges, more distinct near the crown base (Fig. 6B and D). The basal end of the keel has an abrupt end and the crown is separated from the root through a marked constriction at the distal edge (Fig. 6A and B). The opposite edge only has a slight constriction, which progressively increases along the toothrow (Fig. 2). In the posterior-

most molariforms a shallow and narrow groove can be also distinguished along the buccal and lingual surfaces of the crown-root junction. As in the caniniform, several longitudinal grooves are present on the root, presumably for the attachment of the periodontal ligament. All the maxillary teeth are implanted in a continuous alveolar groove, being each tooth socket delimited by short and pointed bony projections that fail to form complete alveolar septa.

Some molariform teeth have distinct wear facets, which vary in development along the toothrow (Fig. 6A, B and D). The wear facets are flat and most of their surface exposes the dentine. These are remarkably extensive in some teeth (Fig. 6A and B) and extend from the tooth apex onto the lingual surface of the crown (Fig. 6A–D). The wear facets of *Notosuchus terrestris* lack striae, although in some teeth the dentine exposed within the facet has well-developed pits, mostly located along the apical region of the keeled margin (Fig. 6C).

Dentary Teeth: The lower teeth of *Notosuchus* resemble those of the upper toothrow. The first three teeth are incisiviform (Fig. 3C) and differ from the upper teeth in being slightly recurved and implanted in small (approximately 35 mm) discrete alveoli separated by bony septa. The third lower tooth seems to have been located at the level of the caniniform upper tooth, as preserved in MACN-PV RN1038.

The fourth dentary tooth is located at the level of the upper transitional tooth. Its morphology is also transitional but differs from the upper one in having a mesial keel that reaches the crown-root boundary and a well developed wear facet (Fig. 6G), as in molariform teeth. However, this element differs from molariforms in its restricted mesiodistal crown length (and therefore the development of its keel). The fourth dentary alveolous has a complete septum that divides it from the preceding tooth socket and is almost completely, if not entirely, separated from the fifth dentary alveolous.

The fifth to the tenth dentary teeth are molariform. The overall morphology of the lower molariform teeth is the same as in the upper elements, but their crowns are inversely oriented (i.e., the keel forms the anteriolaterally directed mesial edge). The apicobasal grooves of the lower molariforms are also asymmetrically located with respect to each other producing a slightly sigmoid shape of the keel in apical view (Fig. 6F). Some of the lower molariform crowns are relatively unworn and have preserved denticles on their mesial keel (Fig. 6H). The denticles have convex edges in buccal view and are irregularly spaced, separated by rounded interdenticular slits and broad cellae (Fig. 6H). The basal width and height of the denticles are also highly variable, approximately ranging between 74 and 318 μm (approximately three to 13 denticles per mm) and 65 and 270 μm, respectively. The mesial surface of the denticles is rounded as in the denticles of *Mariliasuchus* [2] and *Sphagesaurus* [20], instead of having the sharp cutting edge present in the denticles of ziphodont forms [9,12,19]. The worn dentary molariforms bear wear facets that extend onto their buccal surface (Fig. 6F and I) and therefore match those of the opposite upper molariforms. The roots of the three posteriormost lower molariforms are exposed in MACN-PV RN1038. They are relatively long, ranging approximately between 55 and 71% of the total tooth height. The lower molariforms are implanted in a continuous alveolar groove and the incipient interalveolar septa are formed by projections of the dentary (buccal side) and the splenial, which forms the entire lingual margin of the alveolar groove.

5. Discussion

The new information of *Notosuchus terrestris* contains dental characters that are relevant for providing evidence on its phylogenetic affinities among notosuchians, identifying a diagnostic combination of dental characters for this taxon (including autapomorphies), and inferring functional aspects of this taxon.

Phylogenetic Information: The teeth of *Notosuchus* share three derived characters with *Mariliasuchus amarali* and *Sphagesaurus huenei* from the Late Cretaceous of Brazil, providing support to recent suggestions that depict these three taxa as more closely related to each other than to other crocodyliforms [1]. First, these three taxa have similar rounded and tuberous denticles [2,20,26] on the margins of posterior teeth that differ from those of other crocodyliforms (including those with ziphodont dentition such as sebecosuchians and peirosaurids). Andrade and Bertini [2] described the denticulated carinae of *Mariliasuchus* as ziphomorph, although it is not clear if the two other taxa have all the characters that define the ziphomorph condition (i.e., anisomorph and well spaced denticles with ornamented enamel non extending onto the carina). Second, the enamel surface of posterior teeth of *Notosuchus* bear slightly developed ridges at the base of their crowns (Fig. 6B and D). *Mariliasuchus* and *Sphagesaurus* also have these ridges, although more prominently developed [2,15,20,26]. Although these ridges occur in other crocodyliforms, they are absent in all other notosuchians. Third, the posterior teeth of *Notosuchus* bear extensive wear facets that resemble, in their general morphology and disposition, those of *Sphagesaurus* [15] and *Mariliasuchus* [2,26], which have been interpreted as caused

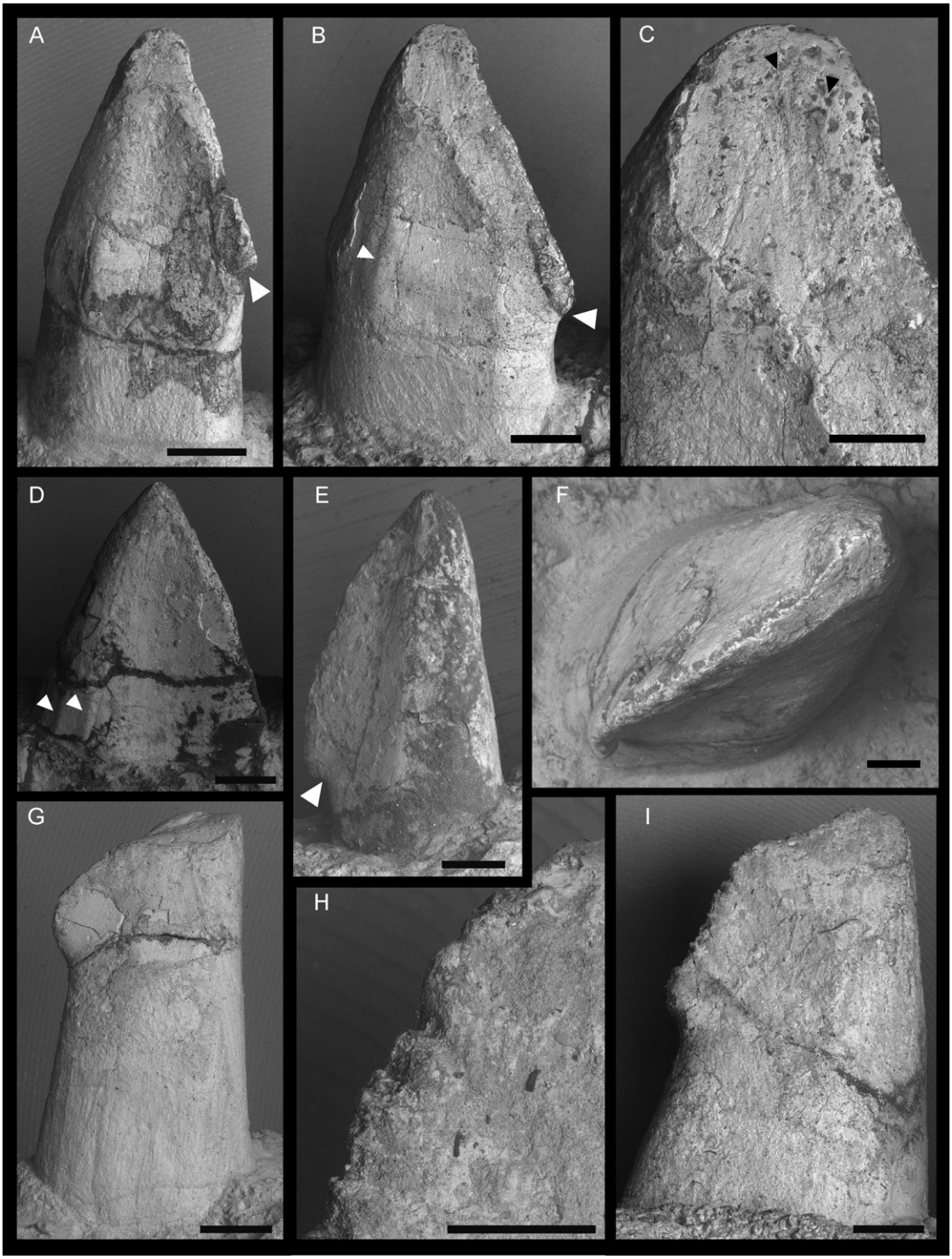

Fig. 6. SEM of molariform and lower transitional teeth of *N. terrestris* (MACN-PV RN1127). Left maxillary teeth in lingual view (A-D): first tooth (A), third tooth (B) with close up of its wear facet (C), fourth tooth (D). Left mandibular teeth in buccal (E, G-I) and occlusal view (F): sixth tooth (E, F), transitional (fourth) tooth (G), eigth tooth (I) and close up of denticles on mesial keel (H). Large white arrowheads: constriction at the crown base, small white arrowheads: longitudinal ridges, black arrowheads: pits on the wear facet. Scale bars: 1 mm (A, B, D, E, G, I), 500 μm (C, H, F). *SEM des dents molariformes et intermédiaires de N. terrestris (MACN-PV RN1127). Dents maxillaires gauches en vue linguale (A-D) : première dent (A), troisième dent (B) et détail de sa facette d'usure (C), quatrième dent (D). Dents mandibulaires gauches en vue buccale (E, G-I) et occlusale*

by tooth–tooth occlusion [15]. This type of wear facets is unknown to occur in other crocodyliforms.

Furthermore, the teeth of *Notosuchus* have an additional set of three characters exclusively shared with *Mariliasuchus*, providing further support for the close relationships proposed for these taxa [1]. First, both taxa lack interalveolar septa in the entire premaxillary and maxillary dentition, contrasting with the presence of discrete alveoli in (at least part of) upper toothrow of other notosuchians (including *Sphagesaurus*). Second, both taxa bear a single large caniniform in the premaxilla [2,26], in contrast to the absence of an enlarged premaxillary caniniform in other notosuchians (e.g., *Araripesuchus*, *Uruguaysuchus*, *Malawisuchus*, *Comahuesuchus*, *Anatosuchus*) or the presence of two large caniniforms in *Chimaerasuchus* [25] and *Sphagesaurus* [15]. Third, the transitional tooth located at premaxilla-maxilla contact in *Notosuchus* is also present in *Mariliasuchus* (MZSP-PV 51) but is absent in other notosuchians, including in those with highly modified molariform teeth (e.g., *Chimaerasuchus*, *Sphagesaurus*).

Interestingly, *Notosuchus* also shares with *Sphagesaurus* two characters absent in other forms, including *Mariliasuchus*. First, *Notosuchus* and *Sphagesaurus* [15] have six molariform teeth in the maxilla and the dentary. This condition differs from the derived reduction of maxillary teeth present in some notosuchians (e.g., *Comahuesuchus* [3], *Baurusuchus* [21], *Mariliasuchus* [26]) and from the larger tooth-count present in all crocodyliforms including other notosuchians (i.e., *Uruguaysuchus*, *Lybicosuchus*, *Araripesuchus*, *Simosuchus, Anatosuchus*). Second, as previously noted [15], the upper and lower molariform teeth of these two taxa are teardrop shaped in cross section and obliquely oriented with respect to the longitudinal axis of the skull.

Diagnostic Characters: The teeth of *Notosuchus* also bear a unique combination of characters that distinguish this taxon from other notosuchian crocodyliforms. First, *Notosuchus* has three anterior incisiviforms in the premaxilla, contrasting with the two premaxillary incisiviforms of *Mariliasuchus* [26] and the absence of upper incisiviforms in *Sphagesaurus* [15]. Other notosuchians have four or five premaxillary incisiviforms (e.g., *Araripesuchus*, *Uruguaysuchus*), which is the generalized crocodyliform condition. Second, the base of the distal keel of *Notosuchus* is slightly curved and is separated from the root by a well-developed constriction (Fig. 6E and F), a combination of characters that is autapomorphic of this taxon. Some notosuchians have a marked constriction between the root and crown, but are different from that of *Notosuchus* because the constriction is evenly developed around the entire tooth surface (e.g., *Mariliasuchus*, *Uruguaysuchus*, *Simosuchus*, *Malawisuchus*).

In comparison with *Mariliasuchus* and *Sphagesaurus*, the dentition of *Notosuchus* has a very thin and smooth enamel coat in comparison with the thick layer of enamel with well-developed wrinkles and tubercles of these two taxa. More specifically, the posterior teeth of *Notosuchus* differ from those of *Mariliasuchus* in having a larger ratio of crown height (CH) to the mesiodistal length (MDL). Finally, *Notosuchus* has three small and vertically oriented dentary incisiviforms, differing the procumbent anterior dentary teeth of *Mariliasuchus* [26] and other notosuchians (e.g., *Comahuesuchus*, *Anatosuchus* [22]).

Functional Implications: The wear facets described here provide new information and allow a better understanding of the tooth occlusion in *Notosuchus*. The wear facet orientation is subparallel to the mesiodistal axis of the tooth (i.e., oblique to the longitudinal axis of the skull). This contrast with the anteroposterior orientation mentioned and figured in previous studies of *Notosuchus* (e.g., [3]: fig. 5), in which the wear facets of adjacent teeth were depicted as forming a continuous wear surface oriented parasagittally. The new material shows that wear facets of adjacent teeth are parallel to each other but located on different planes given that they follow the orientation and disposition of the molariform tooth crowns (see Figs. 1 and 2). Each upper wear facet, lingually located, matches a complementary facet from the lower toothrow, buccally located, forming a precise tooth-tooth contact during occlusion, as in *Sphagesaurus* [15] and *Mariliasuchus* [2]. Thus, these taxa share a common occlusal pattern in addition to the characters noted above.

The wear facets of *Notosuchus* bear small subcircular pits and lack the numerous and parallel obliquely oriented striae present in *Mariliasuchus* and *Sphagesaurus* [15,26]. The alternative presence of pits and striae in microwear facets of mammals has been interpreted as related to the intake of soft or hard food items (e.g., [23]). Although further research and sampling is needed,

(H) : sixième dent (E, F), dent intermédiaire (quatrième) (G), huitième dent (I) et détail des denticules de sa carène mésiale (H). Grandes flèches blanches : constriction à la base de la couronne, petites flèches : crêtes longitudinales, flèches noires : petites dépressions dans la facette d'usure. Barres d'échelle : 1 mm (A, B, D, E, G, I), 500 μm (C, H, F).

the highly developed striae in *Sphagesaurus* (and *Mariliasuchus*) and the pitted wear facet of *Notosuchus* may reflect differences in their diet, matching the noted differences in the thickness and wrinkling of their enamel and other dental characters of the incisiviform and caniniform teeth.

The absence of striation in the wear facets of *Notosuchus* (or a step in the enamel-dentine boundary of the wear facets) precludes testing if the jaw movements included a large anteroposterior component as suggested by the elongated glenoid facet of the articular for the quadrate condyles [3]. However, the orientation and disposition of the wear facets on the maxillary teeth are compatible with this hypothesis of jaw motion during occlusion.

6. Conclusions

This study results in a full characterization of the dentition of *Notosuchus terrestris*, which clarified previous disagreements on its tooth-count, as well as adding new information on the morphological diversity within its toothrow, its ontogenetic changes, and the orientation of its wear facets.

Furthermore, this study provides dental characters supporting the proposed close affinities of *Notosuchus* with *Sphagesaurus* and *Mariliasuchus* from the Late Cretaceous of Brazil [1]. This new data needs to be tested by character congruence as the relationships of notosuchians are still debated, but it underscores the phylogenetic informativeness of dental characters, which have not been fully explored in current phylogenetic analyses of Crocodyliforms. Finally, the morphology of the wear facets are indicative of precise tooth-tooth occlusion and matches those described for *Sphagesaurus* and *Mariliasuchus*, suggesting that a common derived occlusal pattern would also characterize these notosuchians from the Late Cretaceous of South America.

Acknowledgements

We would like to specially thank Aluar Aluminio Argentino SAIC for access to the SEM lab as well as the valuable help of Mr. Jaime Groizard. Thanks are also extensive to Instituto del Diagnóstico del Este del Chubut, Dr. Daniel Villegas, Mr. Dante Lopez, and Mr. Leonardo Ponce for access to the CT scan lab. P. Puerta and L. Canessa are thanked for the final preparation of the specimens. A. Kramarz (MACN) is thanked for allowing specimen access and loans.

References

[1] M.B. Andrade, R.J. Bertini, Morphological and anatomical observations about *Mariliasuchus amarili* and *Notosuchus terrestris* (Mesoeucrocodylia), and their phylogenetical relationships with other "notosuchians" from South America. Boletim de Resumos II Congreso Latino-Americano de Paleontología de Vertebrados (2005) 23–24.

[2] M.B. Andrade, R.J. Bertini, Morphology of the dental carinae in *Mariliasuchus amarili* (Mesoeucrocodylia: Archosauria) and the pattern variation among fossil Crocodylomorpha, Arquivos do Museu Nacional, Rio de Janeiro (in press).

[3] J.F. Bonaparte, Los vertebrados fósiles de la Formación Río Colorado, de la ciudad de Neuquén y cercanías, Cretácico superior, Argentina, Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" – Paleontología 4 (1991) 17–123.

[4] G.A. Buckley, C.A. Brochu, D.W. Krause, D. Pol, A pug-nosed crocodyliform from the Late Cretaceous of Madagascar, Nature 405 (2000) 941–944.

[5] J.M. Clark, L.L. Jacobs, W.R. Downs, Mammal-like dentition in a Mesozoic crocodilian, Science 244 (1989) 1064–1065.

[6] J.O. Farlow, D.L. Brinkman, W.L. Abler, P.H. Currie, Size, shape, and serration density of theropod dinosaur lateral teeth, Mod. Geol. 16 (1991) 161–198.

[7] L. Fiorelli, J. Calvo, New Remains of *Notosuchus terrestris* Woodward, 1896 (Crocodyliforms: Mesoeucrocodylia) from Late Cretaceous (Santonian) of Neuquén, Patagonia, Argentina, Arquivos do Museu Nacional, Rio de Janeiro (in press).

[8] Z. Gasparini, Los Notosuchia del Cretácico de América del Sur como un nuevo infraorden de Mesosuchia (Crocodilia), Ameghiniana 8 (1971) 83–103.

[9] Z. Gasparini, D. Pol, L.A. Spalletti, An unusual marine Crocodyliform from the Jurassic-Cretaceous boundary of Patagonia, Science 311 (2006) 70–73.

[10] C.A. Hugo, H.A. Leanza, Hoja Geológica 3969-IV, General Roca, Provincias de Neuquén y Río Negro, Instituto de Geología y Recursos Naturales, SEGEMAR 308 (2001) 1–71.

[11] H.C.E. Larsson, H.-D. Sues, Cranial osteology and phylogenetic relationships of *Hamadasuchus rebouli* (Crocodyliforms: Mesoeucrocodylia) from the Cretaceous of Morocco, Zool. J. Linn. Soc.-Lond. 149 (2007) 533–567.

[12] O. Legasa, A.D. Buscalioni, Z. Gasparini, The serrated teeth of *Sebecus* and the Iberoccitanian crocodile, a morphological and ultrastructural comparison, Stud. Geol. Salm. 29 (1994) 127–144.

[13] J.E. McIntosh, X. Anderton, L. Flores-de-Jacoby, D.S. Carlson, C.F. Shuler, T.G.H. Diekwisch, *Caiman* periodontium as an intermediate between basal Vertebrate ankylosis-type attachment and mammalian "true" periodontium, Microsc. Res. Tech. 59 (2002) 449–459.

[14] F. Ortega, Z.B. Gasparini, A.D. Buscalioni, J.O. Calvo, A new species of *Araripesuchus* (Crocodylomorpha: Mesoeucrocodylia) from the Lower Cretaceous of Patagonia (Argentina), J. Vertebr. Paleontol. 20 (2000) 57–76.

[15] D. Pol, New remains of *Sphagesaurus huenei* (Crocodylomorpha: Mesoeucrocodylia) from the Late Cretaceous of Brazil, J. Vertebr. Paleontol. 23 (2003) 817–831.

[16] D. Pol, Postcranial remains of *Notosuchus terrestris* (Archosauria: Crocodyliformes) from the Upper Cretaceous of Patagonia, Argentina, Ameghiniana 42 (2005) 21–38.

[17] D. Pol, S. Apesteguía, New *Araripesuchus* remains from the early Late Cretaceous (Cenomanian-Turonian) of Patagonia, Am. Mus. Novit. 3490 (2005) 1–38.
[18] D. Pol, Z. Gasparini, Crocodyliforms, in: Z. Gasparini, R. Coria, L. Salgado (Eds.), Patagonian Mesozoic Reptiles, Indiana University Press, Bloomington, 2007, pp. 116–142.
[19] G.V.R. Prasad, F.L. de Broin, Late Cretaceous crocodile remains from Naskal (India): comparisons and biogeographic affinities, Ann. Paleontol. 88 (2002) 19–71.
[20] L.I. Price, On a new crocodilian, *Sphagesaurus*, from the Cretaceous of the State of São Paulo, Brazil, An. Acad. Bras. Cienc. 22 (1950) 77–83.
[21] D. Riff, A.W.A. Kellner, On the dentition of *Baurusuchus pachecoi* Price (Crocodyliforms, Metasuchia) from the Upper Cretaceous of Brazil, Boletim do Museu Nacional, Rio de Janeiro, Brasil, Geologia 59 (2001) 1–15.
[22] P.C. Sereno, C.A. Sidor, H.C.E. Larsson, B. Gado, A new notosuchian from the Early Cretaceous of Niger, J. Vertebr. Paleontol. 23 (2003) 477–482.
[23] N. Solounias, M. Teaford, A. Walker, Interpreting the diet of extinct rumiants: the case of a non-browsing giraffid, Paleobiology 14 (1988) 287–300.
[24] A.S. Woodward, On two Mesozoic crocodilians *Notosuchus* (genus novum) and *Cynodontosuchus* (genus novum) from the Red Sandstones of the Territory of Neuquén (Argentina Republic), Anales del Museo de La Plata, Paleontología 4 (1896) 1–20.
[25] X.-C. Wu, H.-D. Sues, A. Sun, A plant-eating crocodyliform reptile from the Cretaceous of China, Nature 376 (1995) 678–680.
[26] H. Zaher, D. Pol, A.B. Carvalho, C. Riccomini, D. Campos, W. Nava, Redescription of the Cranial Morphology of *Mariliasuchus amarili*, and its phylogenetic affinities (Crocodyliforms, Notosuchia), Am. Mus. Novit. 3512 (2006) 1–40.