PROVENANCE AND ANATOMY OF *GENYODECTES SERUS*, A LARGE-TOOTHED CERATOSAUR (DINOSAURIA: THEROPODA) FROM PATAGONIA

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ABSTRACT—The type material of *Genyodectes serus*, the first unquestionable non-avian theropod dinosaur to be described from South America, is redescribed in detail and its provenance and systematic position are discussed. Although no detailed information about the provenance of the specimen exists, it is probably derived from the lower part of the Cerro Barcino Formation (Chubut Group; Aptian-Albian) at Cañadón Grande, central Chubut Province, Argentina. *Genyodectes* is characterized by closely-spaced premaxillary teeth that are arranged in an overlapping en-echelon pattern and extremely transversely compressed maxillary teeth, the longest of which exceed the minimal height of the dentary in apicobasal length. Although systematic information is limited by the fragmentary nature of the material, the combination of fused interdental plates, maxillary and dentary teeth with a pronounced flat or even slightly concave area adjacent to the serrated carinae, premaxillary teeth that are considerably shorter than the maxillary teeth and strongly compressed and very long maxillary teeth indicates neoceratosaurian and, more specifically, ceratosaurid affinities for *Genyodectes*. Thus, this taxon adds a further lineage of neoceratosaurs to the already diverse South American record of this group.

INTRODUCTION

In 1901, A. S. Woodward [1] described a partial snout of a theropod dinosaur from Chubut Province, Argentina, as a new genus and species, *Genyodectes serus*. With the possible exception of a probable theropod tooth included in the type material of *Loncosaurus* (Ameghino, 1899; Coria and Salgado, 1996), this was the first unquestionable non-avian theropod described from South America. Up to the late 1970s, it remained the most complete theropod specimen known from this continent (Bonaparte 1978), with the exception of the probably theropodan herrerasaurids (Reig, 1963; Benedetto, 1973; Novas, 1993; Sereno and Novas 1993). This specimen is thus of considerable historical interest, but its systematic position and phylogenetic relationships have remained enigmatic, mainly due to the fragmentary nature of the type and only known specimen. Originally thought to be a megalosaurid (Huene, 1929), von Huene later (1932) tentatively referred *Genyodectes* to the Dinodontidae (= Tyrannosauridae), and this view was accepted by most of the few other authors who took this genus into consideration (e.g. Maleev, 1974). However, Molnar (1990) argued that *Genyodectes* does not show any tyrannosaur synapomorphies and thus considered it Theropoda incertae sedis. Paul (1988) noted that Genyodectes probably represents an abelisaurid and tentatively suggested that it might be the same as *Abelisaurus*, but gave no detailed justification for this. Similarly, Bonaparte (1996) noted some similarities between the snout of *Genyodectes* and abelisaurids, but concluded that the material "provides limited information to attempt a serious interpretation of the systematics" (p. 93) of this taxon.

In the last twenty years, our knowledge of South American theropod faunas has increased dramatically. One of the most important results of the work on Cretaceous theropods from South America is the recognition of a highly diverse group of basal theropods, the neoceratosaurs, as one of the most important Cretaceous theropod groups in the Southern Hemisphere (e.g. Bonaparte, 1991, 1996; Novas, 1997; Coria and Salgado, 2000; Coria et al., 2002).

The type material of *Genyodectes* has recently been removed from the artificial matrix in which it was exhibited at the Museo de La Plata and reprepared. This has revealed new information regarding the internal surfaces of the jaws, which were previously still largely covered in matrix. Thus, the holotype of this first South American theropod is here redescribed and its geographic provenance, stratigraphic age, and systematic position are discussed in the light of our much improved knowledge of South American theropods and theropods in general.

PROVENANCE OF THE MATERIAL

An important and so far unsolved problem concerning *Genyodectes* is the exact geographic and especially stratigraphic provenance of the specimen. Woodward (1901: 179) noted that the material came from a "red sandstone in the Cañadón Grande, Chubut". Huene (1929) gave more precise, but partially contradictory information. On p. 5 he stated, referring to the locality: "Cañadón Grande of the Río Chubut, not very far from Gaiman" (translated by OR). However, no Mesozoic sediments crop out within some 50 km of the town of Gaiman, and this information is not in accordance with other accounts of the provenance of the specimen. On a later page, Huene (pp. 17–18) discussed the provenance of *Genyodectes* in more detail and even gave approximate coordinates for the locality (44°30′ S, slightly east of 70° W), which is within the area between the Río Senguer and the Río Chubut, where Santiago Roth, who collected the specimen sometime between 1896 and 1898, mainly worked (Reguero, pers. com. 2002). This is also in accordance with other information on the locality that the material came from (Roth, 1908; Ameghino and Torcelli, 1934:fig. 22). It thus seems most likely that *Genyodectes* was found in the area between Laguna del Mate and Manantial Pelado, some 70 km southwest of the town of Paso de Indios. In fact, a valley with the name Cañadón Grande is situated only some 20 km to the east of the Laguna del Mate, and it seems very likely that the material is derived from this location (Fig. 1). Unfortunately, no detailed geological map of this area exists, but according to the general geological map of the province of Chubut (Lizuaín et al., 1995), the only Mesozoic sedimentary unit cropping out in this area is the Chubut Group (Hauterivian-Cenomanian; Fig. 1), and no uppermost Cretaceous units are found in this part of the province (Lizuaín et al., 1995; Page et al., 1999; Puerta, pers. comm.
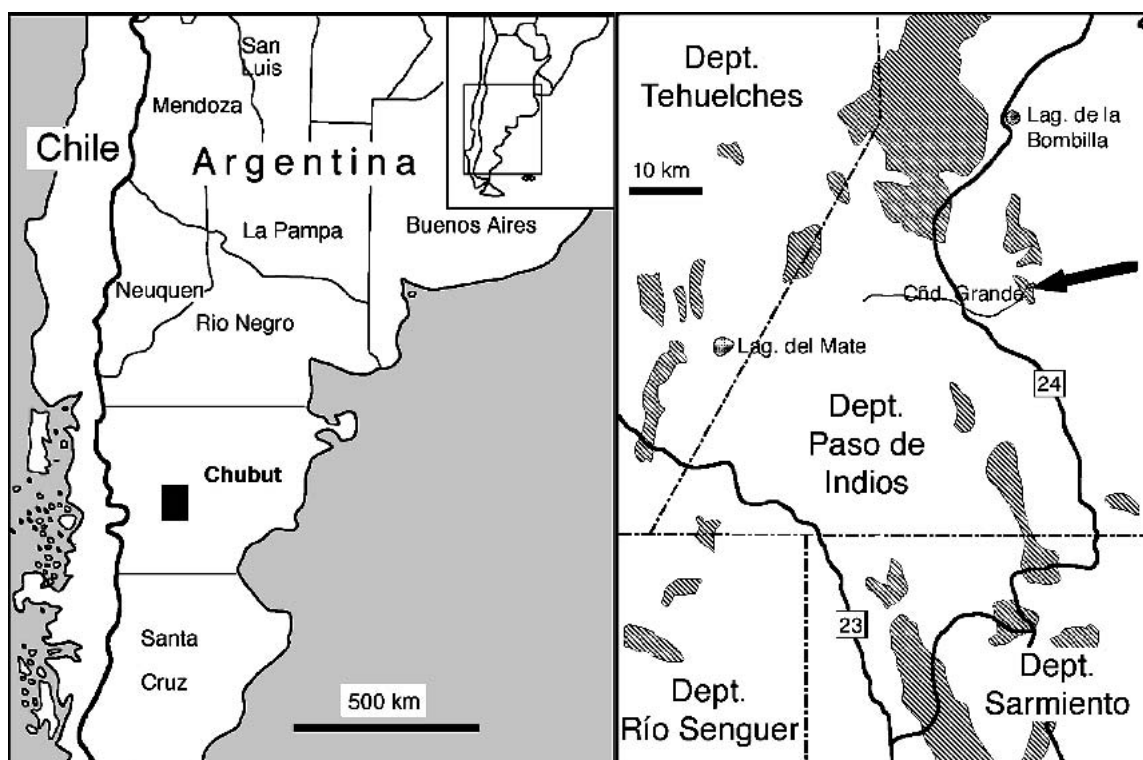
FIGURE 1. Probable locality of the type specimen of *Genyodectes serus*. Hatched areas indicate outcrops of the Chubut Group.

2002). Just northwest of the Cañadón Grande, in the Sierra del Cerro Negro, the outcropping units of the Chubut Group include the lowermost Los Adobes Formation (Hauterivian-Barremian) and the lower two units of the Cerro Barcino Formation, the Puesto la Paloma (Barremian-Aptian) and Cerro Castaño (Aptian-Albian) members (Nullo, 1983). It is thus very likely that the type locality of *Genyodectes* is located in one of these units. Within these units, the Cerro Castaño Member of the Cerro Barcino Formation is the most likely candidate to have yielded the material, because it is the most fossiliferous unit within the lower parts of the Chubut Group and contains frequent red sandstones (pers. obs.). Furthermore, no vertebrate fossils have been reported from the Los Adobes Formation so far and the La Paloma Member of the Cerro Barcino Formation in the area of Paso de Indios is dominated by gray to greenish sediments. The interpretation of the fossil coming from the Cerro Castaño Member is also in accordance with information from Roth (1908), who noted that the specimen came from a "dinosaur sandstone". Some of his illustrations of this dinosaur sandstone in the province of Chubut (Roth, 1908:pl. 11, 12, 13) show sections of the Cerro Barcino Formation along the Chubut river between the towns of Los Altares and Paso de Indios (pers. obs.), which are now considered to belong to the Cerro Castaño Member (Page et al., 1999; Manassero et al., 2000). Thus, an Aptian-Albian age for this fossil is likely (Page et al., 1999).

It might be noted that, according to Huene (1929, p. 17), Roth (1908) provided a photograph of the locality on his pl. 14, but this is not obvious from Roth's text. However, the general aspect of the "dinosaur sandstone" on this photograph is in general accordance with the Cerro Castaño Member of the Cerro Barcino Formation.

Institutional Abbreviations—**BM**, Museum für Naturkunde der Humboldt Universität, Berlin, Germany; **BSP**, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany; **MACN**, Museo Argentino de Ciencias Natu-

rales, Buenos Aires, Argentina; **MLP**, Museo de La Plata, La Plata, Argentina; **MWC**, Museum of Western Colorado, Fruita, Colorado, U.S.A.; **QG**, National Museum of Natural History, Harare, Zimbabwe.

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842
SAURISCHIA Seeley, 1887
THEROPODA Marsh, 1881
CERATOSAURIA Marsh, 1884
?CERATOSAURIDAE Marsh, 1884

Comment—The Ceratosauridae–created by Marsh (1884) to include *Ceratosaurus* and potentially its closest relatives–has not been formally defined phylogenetically yet. Although it is premature to give such a formal definition at present, the name is used here for a clade containing all ceratosaurs that are more closely related to *Ceratosaurus* than to abelisaurids.

GENYODECTES SERUS Woodward, 1901

Holotype—MLP 26–39, partial snout, including both nearly complete premaxillae, fragments of both maxillae, both dentaries, all with teeth, parts of both supradentaries, and fragments of the left splenial.

Locality and Horizon—Cañadón Grande, Departamento Paso de Indios, Chubut Province, Argentina. ?Cerro Castaño Member, Cerro Barcino Formation; Aptian-Albian, Lower Cretaceous.

Diagnosis—Differs from all theropods with the possible exception of *Ceratosaurus* in that the premaxillary teeth are arranged in an overlapping *en-echelon* pattern and the longest maxillary tooth crowns are longer apicobasally than the minimal

dorsoventral depth of the mandible. Differs from *Ceratosaurus* in the presence of four, as opposed to three, premaxillary teeth.

DESCRIPTION

Preservation—Generally, the snout elements of *Genyodectes* are rather poorly preserved, although the semi-articulated state in which the material was obviously found, and the fact that most of the teeth are still in place, indicate that this is due to recent erosion rather than to taphonomic processes. Both premaxillae were preserved in articulation, but were not fused in life, as indicated by a slight anteroventral displacement of the right premaxilla. Likewise, the maxillae were found in articulation with the premaxilla, but were affixed to the latter only by matrix. In the lower jaw, the supradentaries are only very slightly displaced, and, as far as can be made out, the fragments of the left splenial seem to be in their original position relative to the dentary. All the elements of the right side of the skull show signs of slight deformation, whereas the left side seems to be undeformed.

The left premaxilla is almost complete, lacking only the nasal process and the subnarial process. The right premaxilla is missing both processes and parts of its posterodorsal border. It is furthermore slightly compressed, making the inturn along the narial fossa less marked than on the left side. Both maxillae are only represented by their anterior alveolar borders, and neither the ascending process nor the rim of the antorbital fenestra are preserved. Both dentaries lack only their thin posteriormost portion,

although parts of this are preserved on the left side. Of the supradentaries, only short sections of the posterior parts are preserved. The left splenial is represented only by scattered fragments affixed to the inner side of the dentary by matrix.

Premaxillae—The premaxillae (Fig. 2) are massive and meet each other along a symphysis in their anterior third to form a tip of the snout that is broadly U-shaped in ventral view. The subnarial premaxillary body is approximately as high as long (ca. 75 mm) and bears four teeth (Fig. 2A, B, D). The lateral side is pierced by several large foramina above the alveolar border and along the anterior margin (Fig. 2A, C, D). Dorsally, the lateral side bends medially to form an anteroventral shelf of the narial fossa (Fig. 2A, C). The broken base of the nasal process is anteroposteriorly long but transversely narrow, with a broader anterior edge and a posterior, plate-like portion. The posterior process was obviously rather small, but nothing can be said about its exact size or shape because it is missing and the region of its connection with the premaxillary body is damaged on both sides.

Medially, the interdental plates are fused without any visible suture, forming a medial alveolar border that is only slightly lower than the lateral border (Fig. 2B). The paradental groove delimiting the interdental plates from the premaxillary body is developed only as a faint step that curves down abruptly anteriorly behind the premaxillary symphysis (Fig. 2B). Vertical striations on the interdental plates, as are found in abelisaurids (Sampson et al., 1996), are not present. Dorsally, directly below this paradental shelf, one small, round foramen is present over
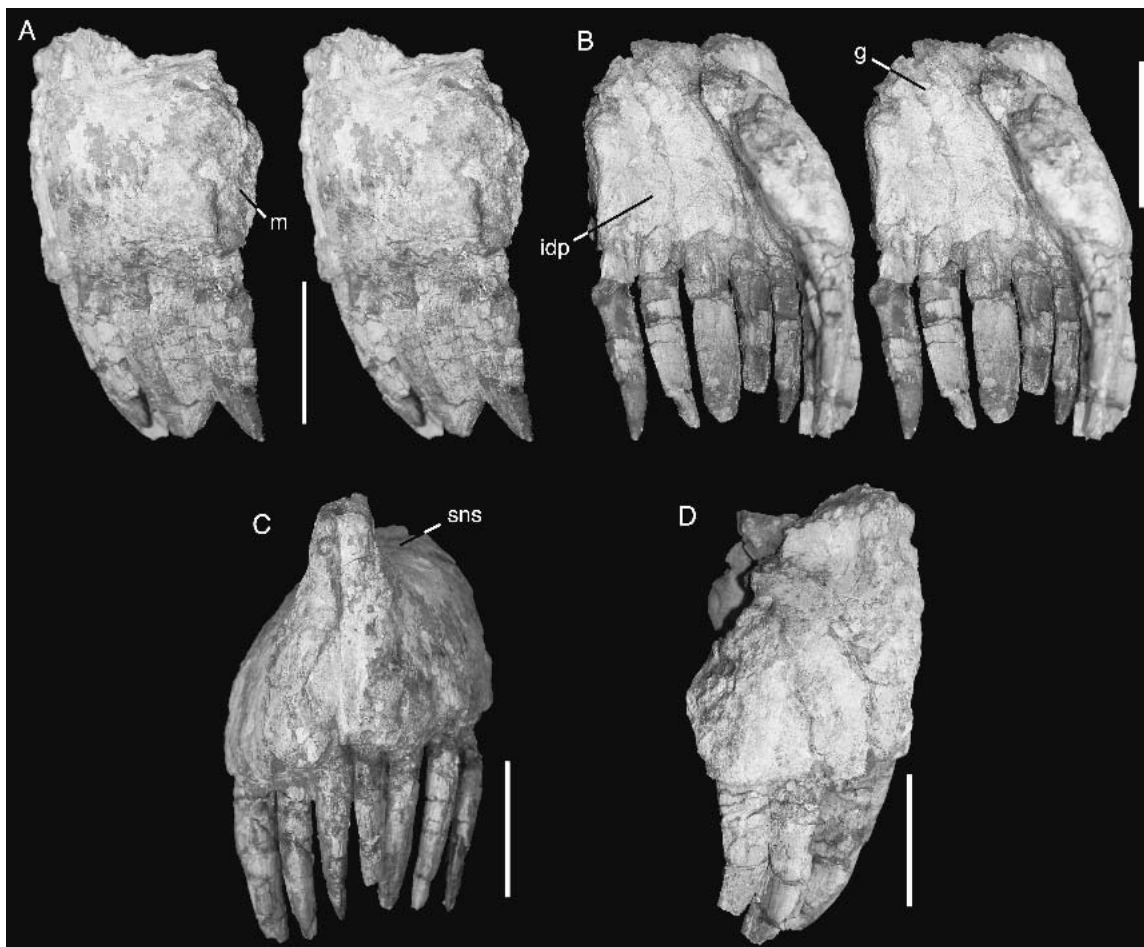

FIGURE 2. *Genyodectes serus*, holotype, MLP 26–39. Articulated premaxillae in **A**, left lateral view (stereopair), **B**, medial view of the left side (stereopair), **C**, anterior view, and **D**, right lateral view. **Abbreviations**: **g**, groove; **idp**, interdental plates; **m**, contact with maxilla; **sns**, subnarial shelf. Scale bars equal 5 cm.

each tooth. In the posterodorsal part of the medial side, just below the narial shelf, a short, broad, anteroventrally inclined groove seems to be present, although it might merely be an artifact of preservation (Fig. 2B).

The suture with the maxilla is developed as a broad, flat, slightly rugose surface that faces posterolaterally (Fig. 2A). Whereas this surface blends into the lateral side along a smooth curve dorsally, it is set off from the latter ventrally by a pronounced rounded step.

Maxillae—Not much can be said about the maxillae, owing to their fragmentary preservation. Of the left maxilla, 190 mm of the alveolar border, containing 5 1/2 alveoli and 225 mm of the right maxilla, containing 6 1/2 alveoli, are preserved.

The lateral side of the maxilla seems to be smooth, with only few small foramina above the alveolar border (Fig. 3A, C). No sign of the border of the antorbital fossa is present on the preserved parts, indicating that this border was placed rather high above the alveolar border. Medially, the interdental plates are fused (Fig. 3B, D), as in the premaxillae. The paradental shelf (Madsen, 1976), which is only preserved on a very small area in the anterior end of the left maxilla (Fig. 3D), is some 35 mm above the medial alveolar border. The contact with the premaxilla consists of a broad medial surface, which is slightly rugose anteriorly and very slightly medially directed, and a robust anteriorly directed lateral lip (Fig. 3D). The maxillae diverge slightly from their articulation with the premaxillae, and are not parallel, as is the case in some theropods (e.g., *Allosaurus*; Madsen, 1976).

Dentary—As is the case with the bones of the skull, the dentaries are rather massive (Fig. 4). In dorsal view, the better-preserved left dentary is slightly flexed medially, although less so

than in *Carnotaurus* (MACN CH 894). The anterior end of the dentary is slightly expanded dorsally, so that the tooth row is notably concave behind the third dentary tooth, whereas the portion containing the anteriormost three teeth dips very slightly anteriorly (Fig. 4A, C, D). The ventral border is straight over most of its length and gradually curves dorsally anteriorly to meet the dorsal border at nearly a right angle. In the left dentary, the ventral margin flexes ventrally towards the posterior end of the tooth row, and thus the dentary expands posteriorly (Fig. 4A, B). Posteriorly, both dentaries are too damaged to determine the nature of the mandibular fenestra.

The lateral side of the dentary is very slightly convex dorsoventrally, with the exception of the posteriormost expanded part, which is planar. Anteriorly, several large foramina are found (Fig. 4A, C). Beginning at the 5th alveolus, a notable longitudinal groove runs over the bone posteriorly, at approximately one-third of the height of the bone from the alveolar border (Fig. 4A). This groove is deeper and more sharply bordered ventrally, but gradually shallows dorsally. Several large, slit-like foramina seem to be placed along its ventral border, slightly more widely spaced than the teeth.

Medially, a shallow and very gradually posteriorly widening Meckelian groove is present, placed just below the mid-height of the bone (Fig. 4B, D). This groove narrows and becomes slightly deeper in its anteriormost part, and its tip bends sharply ventrally (Fig. 4B). Although this area is not well preserved in either element, it seems that the groove widens considerably dorsoventrally towards the posterior end of the tooth row and here thus leaves only a thin lateral wall of the bone below the dorsal alveolar part. As in the upper jaw, the interdental plates are fused without any visible suture and only set off from the main body by
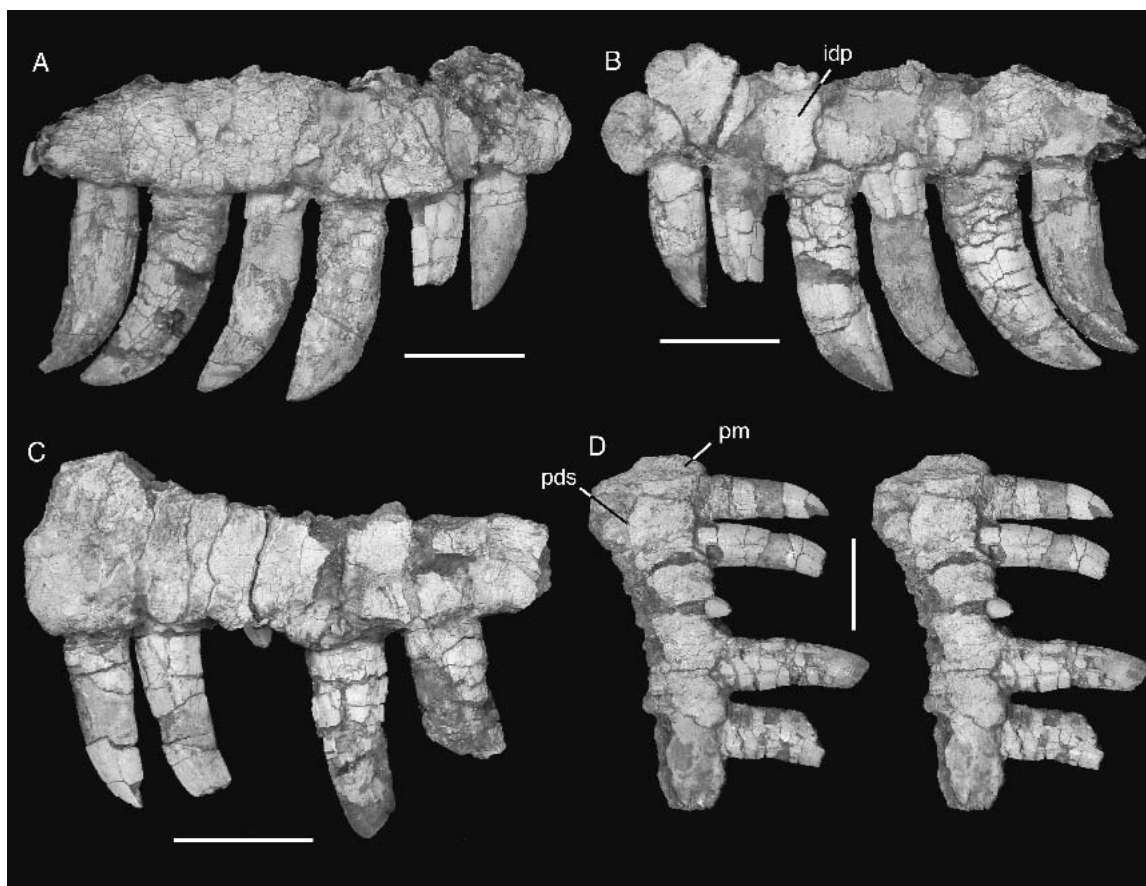

FIGURE 3. *Genyodectes serus*, holotype, MLP 26–39. Right maxilla in **A**, lateral and **B**, medial view. Left maxilla in **C**, lateral and **D**, medial view (stereopair). **Abbreviations**: **idp**, interdental plates; **pds**, paradental shelf; **pm**, contact with the premaxilla. Scale bars equal 5 cm.
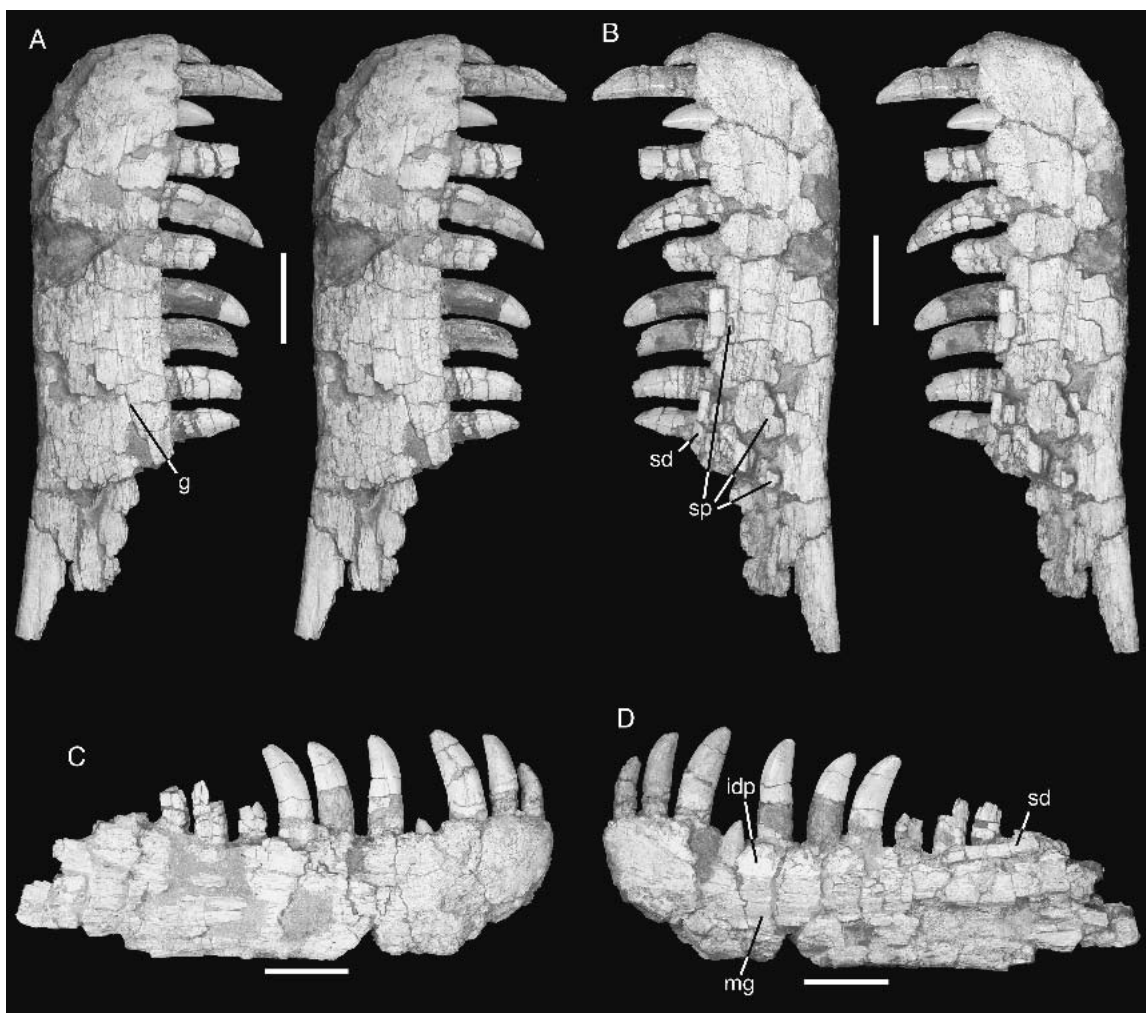
FIGURE 4.   *Genyodectes serus*, holotype, MLP 26–39. Left dentary in **A**, lateral (stereopair) and **B**, medial view (stereopair). Right dentary in **C**, lateral and **D**, medial view. **Abbreviations**: **g**, groove; **idp**, interdental plates; **mg**, Meckelian groove; **sd**, supradentary; **sp**, splenial. Scale bars equal 5 cm.

a low paradental shelf (Fig. 4B, D). Anteriorly, this shelf rises in a smooth curve to meet the alveolar border just at the posterior end of the first alveolus. No foramina are visible at the base of this shelf below the alveoli. With a maximum height of 22 mm in the anterior mid-part of the bone, the dentary interdental plates are considerably lower than those in the maxilla. As noted by Woodward (1901), no clearly defined symphyseal facet is present on the anterior part of the medial side of the dentary, but it seems most probable that the symphysis was restricted to a narrow vertical zone at the slightly oblique anteriormost margin of the dentary.

The preserved length of the more complete left dentary is ca. 335 mm, its maximum anterior height is ca. 76 mm and its minimal height ca. 67 mm. The left dentary preserves 10 alveoli over a preserved alveolar border of 230 mm, whereas the right dentary exhibits 11 tooth position over a length of 260 mm. Given the morphology towards the posterior break of the dentary, it is very likely that the total number of teeth did not exceed 14.

Supradentary—The supradentary is a long, slender rod of bone, about half the height of the dentary interdental plates (Fig. 4B, D). It covers the upper half of the interdental plates medi-

ally. Its anterior extent cannot be ascertained because only small parts are preserved on both sides.

Splenial—Not much can be said about this bone. It was apparently a thin plate of bone that ended anterodorsally in a sharp tip just below the supradentary behind the seventh tooth position (Fig. 4B). From this tip it seems to have expanded rapidly posteriorly and probably covered most of the large posterior part of the Meckelian groove medially.

Dentition—Although the exact number of teeth can only be ascertained for the premaxillae (4), in comparison with other theropods and based on the estimation of the number of teeth in the dentary, it seems likely that the maxillary tooth count did not exceed 15. As noted above, there were probably no more than 14 teeth in the dentary. The teeth do not show the alternating pattern of fully and partially erupted teeth seen in other theropods (e.g. *Tyrannosaurus*; Molnar, 1991), but largely seem to represent the same tooth generation (Figs. 2–4). Clearly erupting teeth without a larger functional tooth laterally are only found in the second alveolus of the right maxilla, the third alveolus of the left, and possibly the fourth alveolus of the right dentary (although in the latter, the larger tooth might simply be missing). In addition,

erupting teeth with the functional tooth lateral to them are present in the third alveolus of the left premaxilla (Fig. 2B) and the third alveolus in the left maxilla (although here the larger tooth is missing, its presence is indicated by a large alveolus lateral to the erupting tooth).

The premaxillary teeth are very closely spaced and even overlap each other considerably in labial view (Fig. 2A, D). All four teeth on either side seem to be of subequal length, although parts of the tip are missing in all but one (in which the tip has been glued on the wrong way round). The premaxillary tooth crowns are considerably shorter (ca. 65–75 mm) and stouter than those of the maxillary teeth. They are slightly asymmetrical, with their distal carina being displaced labially, especially in the anteriormost two teeth.

The maxillary crowns are considerably larger than the premaxillary crowns, although their exact size is hard to ascertain since many teeth are missing the tip or are reconstructed in some part. However, the size of the tooth crowns seems to be real, and not an artifact of loosening and displacement of the teeth within their alveoli. Although the crowns are badly fractured, making interpretations difficult, serrations on the distal carina reach down to almost the alveolar border in the third and fourth tooth of the right maxilla and the crown-root boundary is not visible in any of the preserved crowns, indicating that it was placed at, or directly below the alveolar border. Another indication that the

teeth have at least not experienced any major displacement is the fact that their roots fit their respective alveoli at the eroded dorsal surface of the maxillary fragments.

The tooth crowns seem to increase in size from the first to the third maxillary tooth and then remain subequal in size to at least the fifth or sixth maxillary tooth (Fig. 3A, C). The first crown of the left maxilla is approximately 70–75 mm long, whereas the longest preserved crown, the fifth of the right maxilla, is more than 80 mm long; as reconstructed, this crown is 95 mm long, which seems a reasonable estimate for its total length. Thus, the longest maxillary tooth crowns are longer than the height of the corresponding part of the dentary. The maxillary crowns are symmetrical and very strongly compressed labiolingually (Fig. 5A), more so than the premaxillary teeth or the maxillary teeth of most theropods. Unfortunately, the fact that the bases of all teeth are damaged, probably by expansion of mineral infillings of the pulpa cavity, makes a quantification of this labio-lingual flattening and a comparison with published measurements (Farlow et al., 1991) impossible. In most crowns, an unusual flat area is present adjacent to the mesial and distal carinae (Fig. 5A), an area that is usually convex in most theropods. The maxillary teeth are also rather tightly spaced, with less than half the mesiodistal length of a tooth separating two subsequent teeth.

In all crowns of the upper jaw, both the apical half of the mesial and all of the distal carinae are serrated. There are ap-
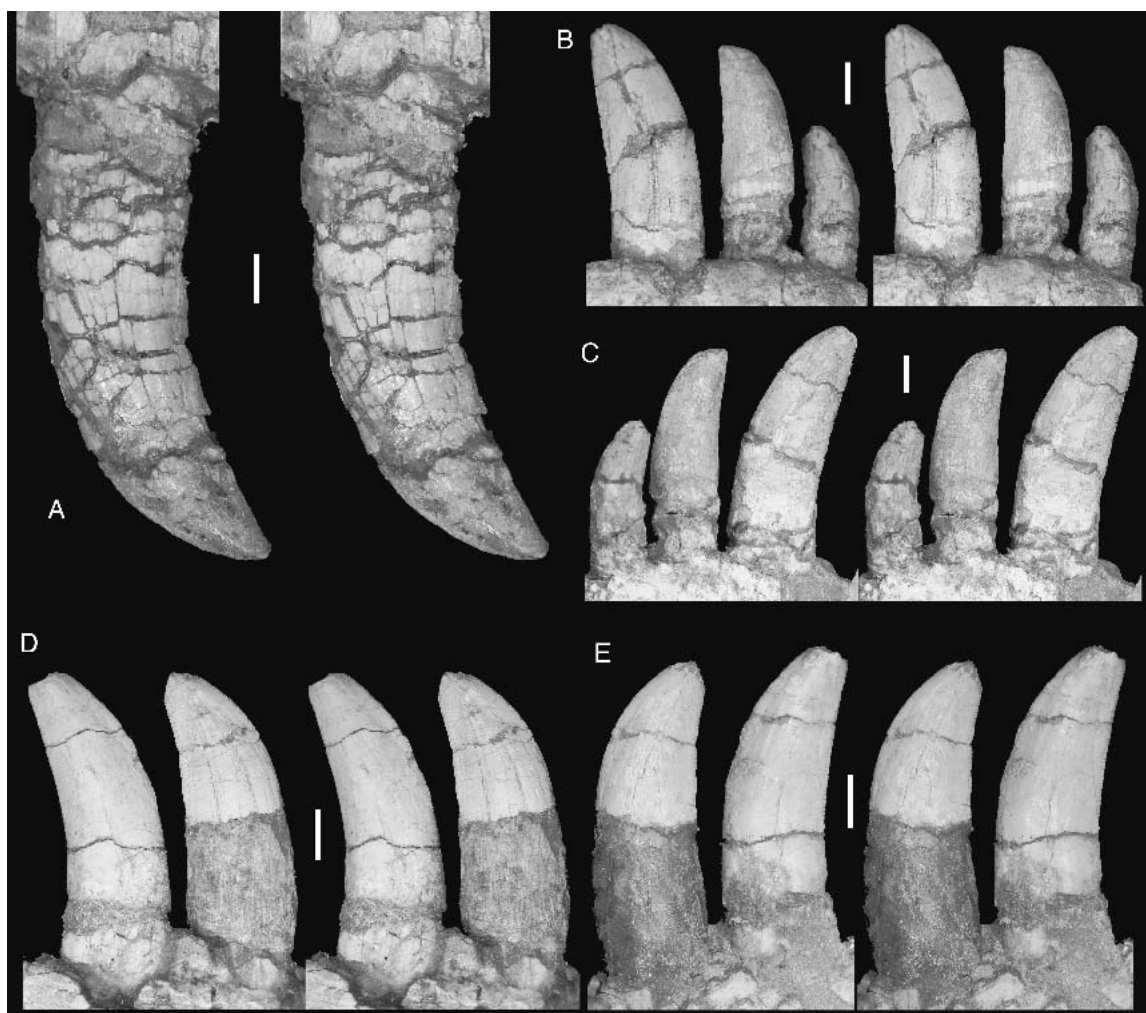

FIGURE 5. *Genyodectes serus*, holotype, MLP 26–39. Dentition. **A**, medial view of the 5th right maxillary tooth (stereopair). **B**, **C**, anteriormost three teeth of the right dentary in B, lateral and C, medial view (stereopairs). **D**, **E**, sixth and seventh right dentary teeth in D, lateral and E, medial view (stereopairs). Scale bars equal 1 cm.

proximately 12 denticles per 5 mm mesially and distally. The denticles are chisel-shaped, perpendicular to the long axis of the carina and do not show any grooves extending from their bases onto the crown.

The dentary tooth crowns are considerably shorter than those of the maxillary teeth. They rapidly increase in size from the small first (ca. 40 mm in the right dentary) to the third crown (Figs. 4, 5B, C) and then remain of subequal size (approximately 60 mm) up to at least the seventh tooth. Only the two anterior-most crowns are asymmetrical, similar to those in the premaxilla (Fig. 5B, C). The third crown seems to be transitional, and from the fourth onwards, the teeth are more or less symmetrical. The dentary crowns are less strongly compressed transversely than the maxillary crowns, but show the same flat areas adjacent to the carinae (Fig. 5D, E). Denticle density and morphology are as in the upper teeth.

DISCUSSION

On the basis of the above description, it is clear that *Genyodectes* differs from all other theropod dinosaurs from South America for which cranial material is known. Furthermore, based on the characters given in the diagnosis, it can currently be distinguished from all other theropods and thus should be considered a valid taxon, despite the poor preservation of the holotype. However, determining its systematic position is much more problematic. Unfortunately, the extremely fragmentary nature of the type of *Genyodectes* prohibits a formal phylogenetic analysis, and so this discussion will focus on an evaluation of previously proposed affinities and the distribution of important characters seen in *Genyodectes* within theropods.

Huene (1932:243, translated by OR) referred *Genyodectes* to the Dinodontidae (= Tyrannosauridae) simply on the basis that "according to the teeth and size, it fits with the dinodontids". This assignment was accepted by several other authors (e.g., Maleev, 1974), although no detailed justification has ever been published. *Genyodectes* shows premaxillary tooth crowns that are considerably smaller than the maxillary crowns, a tyrannosaurid synapomorphy (Holtz, 2001). However, as pointed out by Molnar (1990), the premaxillary crowns are not D-shaped in cross-section, which is another tyrannosaurid synapomorphy (Holtz, 2001). More importantly, a considerable size difference between the premaxillary and maxillary crowns is also found in *Ceratosaurus*. In the type of *Ceratosaurus dentisulcatus*, the longest premaxillary crown is an estimated 63 mm in length (the longest completely preserved crown only 49 mm), whereas the longest preserved maxillary crown is 93 mm long (Madsen and Welles, 2000). Likewise, an isolated premaxillary tooth of the type of *Ceratosaurus magnicornis* (MWC 1) has an estimated crown length of ca. 50 mm, while the maxillary crowns measure up to 80 mm. Furthermore, the strongly transversely compressed maxillary crowns of *Genyodectes* are very unlike the rather stout crowns of tyrannosaurids (Currie et al., 1990). Thus, there is no convincing evidence for referring *Genyodectes* to the Tyrannosauridae.

Little evidence has been brought forward for the proposed abelisaurid relationships of *Genyodectes* as well. Paul (1988:283) noted that "the teeth have the long length and slender build characteristic of abelisaurs" and Bonaparte (1996:93) stated that "the distance between the alveolar border and the lower rim of the narial opening is rather large and resembles the abelisaurid snout condition". However, the teeth in *Carnotaurus* (MACN Ch 894; Bonaparte et al., 1990), *Majungatholus* (FMNH PR 2100; Sampson et al., 1998), and at least some other abelisaurids (Lamanna et al., 2002) are rather short and not as flattened transversely as is the case in *Genyodectes*; the teeth of *Abelisaurus* are unknown (Bonaparte and Novas, 1985). Likewise, although the premaxillary body below the nares in *Genyodectes* is

high, it is almost as long as high and thus differs from the premaxillae in abelisaurids, which are higher than long (Bonaparte and Novas, 1985; Bonaparte et al., 1990; Sampson et al., 1998). Furthermore, *Genyodectes* lacks several abelisaurid synapomorphies, such as the strong external sculpturing of the external skull bones (Sampson et al., 1998) and the presence of longitudinal striations on the interdental plates (Sampson et al., 1996; Carrano et al., 2002). One derived character that *Genyodectes* shares with abelisaurids is the presence of a longitudinal groove that is deeper ventrally than dorsally on the dentary. However, the distribution of this character needs further elucidation before its systematic value can be evaluated.

Nevertheless, several characters indicate neoceratosaurian and, more precisely, ceratosaurid relationships. First, the presence of a flat or even slightly concave area adjacent to the marginal carinae in the lateral teeth is a character shared with both *Ceratosaurus* (USNM 4735, MWC 1, UMNH V 5278) and at least some abelisaurids (*Majungatholus*: FMNH PR 2100). In other theropods, this area is usually slightly to strongly mesiodistally convex, especially at the anterior carina, and thus this character seems to represent a neoceratosaurian synapomorphy.

Completely fused interdental plates are found in *Ceratosaurus* (Gilmore, 1920; Madsen and Welles, 2000) and abelisauroids (Bonaparte, 1991; Sampson et al., 1998; Carrano et al., 2002), whereas they are separate in basal sauropodomorphs (*Plateosaurus*: MB R. 1937), basal theropods (e.g. *Syntarsus*: QG 193; *Dilophosaurus*: Welles, 1984), basal tetanurans (e.g. Buckland, 1824; Currie and Zhao, 1993; Zhao and Currie, 1993; Allain, 2002) and basal coelurosaurs (*Compsognathus*: BSP AS.I. 563; Ostrom, 1978). Although fused interdental plates are not uncommon in theropods, being also present in *Torvosaurus* (Britt, 1991), advanced allosauroids (Stromer, 1931; Madsen, 1976), and some coelurosaurs (Currie, 1995), the distribution of unfused interdental plates indicates that this is the plesiomorphic character state. Thus, in the light of all available evidence, the presence of fused interdental plates in *Genyodectes* is most parsimoniously explained as a synapomorphy shared with neoceratosaurs.

Another noteworthy character in the teeth of *Genyodectes* is the extreme transverse flattening of the lateral maxillary crowns. Similarly flattened teeth are only found in *Ceratosaurus* (USNM 4735, MWC 1, UMNH V 5278) and advanced carcharodontosaurids (Stromer, 1931; Sereno et al., 1996). However, the teeth of carcharodontosaurids differ from those of *Genyodectes* in the presence of downpointing grooves at the bases of the marginal denticles (Stromer, 1931) and the presence of pronounced enamel wrinkles on the crown (Sereno et al., 1996).

Another character shared with *Ceratosaurus* is the extreme length of the maxillary tooth crowns. In *Ceratosaurus dentisulcatus*, the longest maxillary crown is 93 mm long, which corresponds to the minimal height of the dentary (Madsen and Welles, 2000). Likewise, in the type of *Ceratosaurus nasicornis* (USNM 4735; Gilmore, 1920), with a length of approximately 70 mm, the longest preserved crown in the maxilla exceeds the minimal height of the mandible, given as 63 mm at the fifth dentary tooth by Gilmore (1920). Thus, only in *Genyodectes* and *Ceratosaurus*, does the length of the longest maxillary crowns exceed the minimal height of the dentary, and this character might represent a synapomorphy of these two taxa.

Thus, although the information is limited, and most possible synapomorphies are ambiguous, the character combination exhibited by the jaws of *Genyodectes* indicates ceratosaurid relationships for this taxon. Possible ceratosaurid synapomorphies include strongly labiolingually compressed maxillary tooth crowns, maxillary crowns that exceed the minimal height of the dentary in length, and a significant size difference between the premaxillary and maxillary crowns (with the possible exception of the anteriormost maxillary teeth).

Thus, *Genyodectes* adds a further lineage of neoceratosaurs to

the already diverse Cretaceous record of this group in South America. Our knowledge of Early Cretaceous theropod faunas of South America is still poor, and thus this record of a basal neoceratosaur from most probably Lower Cretaceous sediments is of significance. Together with the possible abelisaur *Ligabueno* from the Hauterivian-Barremian La Amarga Formation of Neuquén (Bonaparte, 1996) and fragmentary abelisaurid remains from the Barremian La Paloma member of the Cerro Barcino Formation (Rauhut et al., 2003), this record hints at an early diversification of neoceratosaurs in South America, well before the Late Cretaceous (see also Lamanna et al., 2002).

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