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A NEW SPECIES OF THE TRAVERSODONTID CYNODONT *EXAERETODON* FROM THE SANTA MARIA FORMATION (MIDDLE/LATE TRIASSIC) OF SOUTHERN BRAZIL

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ABSTRACT—The skull of the traversodontid cynodont *Exaeretodon riograndensis*, sp. nov. from the Santa Maria Formation, Rio Grande do Sul State, Brazil is described. The excellent preservation of one specimen reveals new cranial information about the genus. The presence of prootic crests in the extensive lateral flange, anterior to the fenestra ovalis, is a noteworthy basicranial trait, unique to this new taxon among non-mammalian cynodonts. These crests are interpreted as related to the origin of the posterior pterygoid muscle representing the first evidence, among non-mammalian cynodonts to mammals transition, of the attachment of this muscle onto the prootic bone. The new species is most similar to *Exaeretodon frenguellii* from the Ischigualasto Formation of Argentina. Small differences in the posterior projections of the jugal onto the squamosal and in the shape of prefrontals distinguish the two species. Additionally, the number of postcanines seems to be ontogenetically less variable in the Brazilian species. The postcanine number decreases from six plus one erupting in a small individual (preorbital length: 82.9 mm) to five plus one erupting in the largest specimen (pl. 121.5 mm).

INTRODUCTION

Traversodontidae is a heterogeneous group of non-mammalian cynodonts characterized principally by the morphology of their postcanine teeth. The upper ones are transversely wide, with a rectangular outline, whereas the lower ones have a quadrangular shape in occlusal view. This particular structure ensures a crown-to-crown occlusion comparable, in some way, to that developed later by mammals (Hopson, 1984).

They are a cosmopolitan Triassic family, being represented in South America (Kemp, 1982), North America (Hopson, 1984; Sues and Olsen, 1990), India (Chatterjee, 1982), Europe (Hahn et al., 1988; Godefroit and Battail, 1997), Southern and East Africa (Kemp, 1982) and, most recently, Madagascar (Flynn et al., 1999, 2000). This group is highly diversified in South America, being frequently dominant in faunas of Argentina (Bonaparte, 1982; Rogers et al., 1993). In the Ladinian to Norian-age Santa Maria Formation in southern Brazil, dicynodonts and rhynchosaurs are, by far, the dominant groups (Barberena et al., 1985; Azevedo et al., 1990), although the number of traversodontid cynodonts has been increasing steadily with new discoveries over the last few years (Abdala et al., 1999).

The Ladinian to Norian-age faunas of Argentina and Brazil are highly similar, sharing at least eight tetrapod genera (Barberena et al., 1985). Among these, the traversodontid *Exaeretodon* is particularly abundant in Argentina's Ischigualasto Formation (Bonaparte, 1982; Rogers et al., 1993). The genus was also recognized in the Santa Maria Formation, Brazil by Barberena (1974) who reassigned a maxillary fragment, without teeth, originally considered as *Traversodon*? *major* by Huene (1935–1942) to the new combination *Exaeretodon major*.

Exaeretodon has proven to be especially significant for the phylogenetic studies in the last decade (e.g., Rowe, 1988, 1993; Wible, 1991) because of the completeness of the available cranial and postcranial materials, including an endocranial cast (Bonaparte, 1962, 1963a, 1966a). However, the relationships of traversodontids, and in a wider context, that of gomphodonts, are part of an unresolved debate centered on the still uncertain monophyly of the family and on the interrelationships with tritylodontids (Hopson and Barghusen, 1986; Rowe, 1986, 1993; Hopson, 1991, 1994; Wible, 1991; Abdala, 1996a, 1998). Thus, new morphological information on those groups could be particularly important for attempting a clarification of their phylogenetic interrelationships.

In 1985, three skulls of *Exaeretodon* were recovered from outcrops located in the Candelaria District, Rio Grande do Sul State, Brazil (Fig. 1). The material comes from the same outcrops that yielded the skull of *Proterochampsa nodosa* described by Barberena (1982) and a fragmentary lower jaw of a sectorial toothed cynodont (Abdala and Ribeiro, 2000). Particularly remarkable is the excellent preservation of the specimen MCP 1522 PV, providing new morphological information on the genus.

A description of these cynodont findings, widely reported in biostratigraphic works (e.g., Barberena et al., 1985; Schultz, 1995), is presented herein. A comparison is made with the Argentine (Ischigualasto Formation) representative of the genus. The presence of a small-referred specimen allows us to propose an ontogenetic sequence for the dentition.

Both Traversodontidae, and the more inclusive group Cynognathia (as Hopson, 1994:fig. 6, but excluding Tritylodontidae) are supported by ambiguous synapomorphies in eucynodont cladistic analysis by Abdala (1996a). Thus, Traversodontidae, is provisionally considered as monophyletic, including all the non-mammalian cynodonts with bucco-lingually-expanded postcanines, which are subquadrate and/or trapezoidal shaped in occlusal view. Differently from hypotheses by Sues (1985) and Hopson (1994), Tritylodontidae is not sister group of Traversodontidae but is instead, closely related with Mammaliaformes.

Institutional Abbreviation—**MACN**, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires; **MCP**, Laboratório de Paleontologia, Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil; **MCZ**, Museum of Comparartive Zoology, Harvard University; **MLP**, Museo de La Plata, Argentina; **PVL**,

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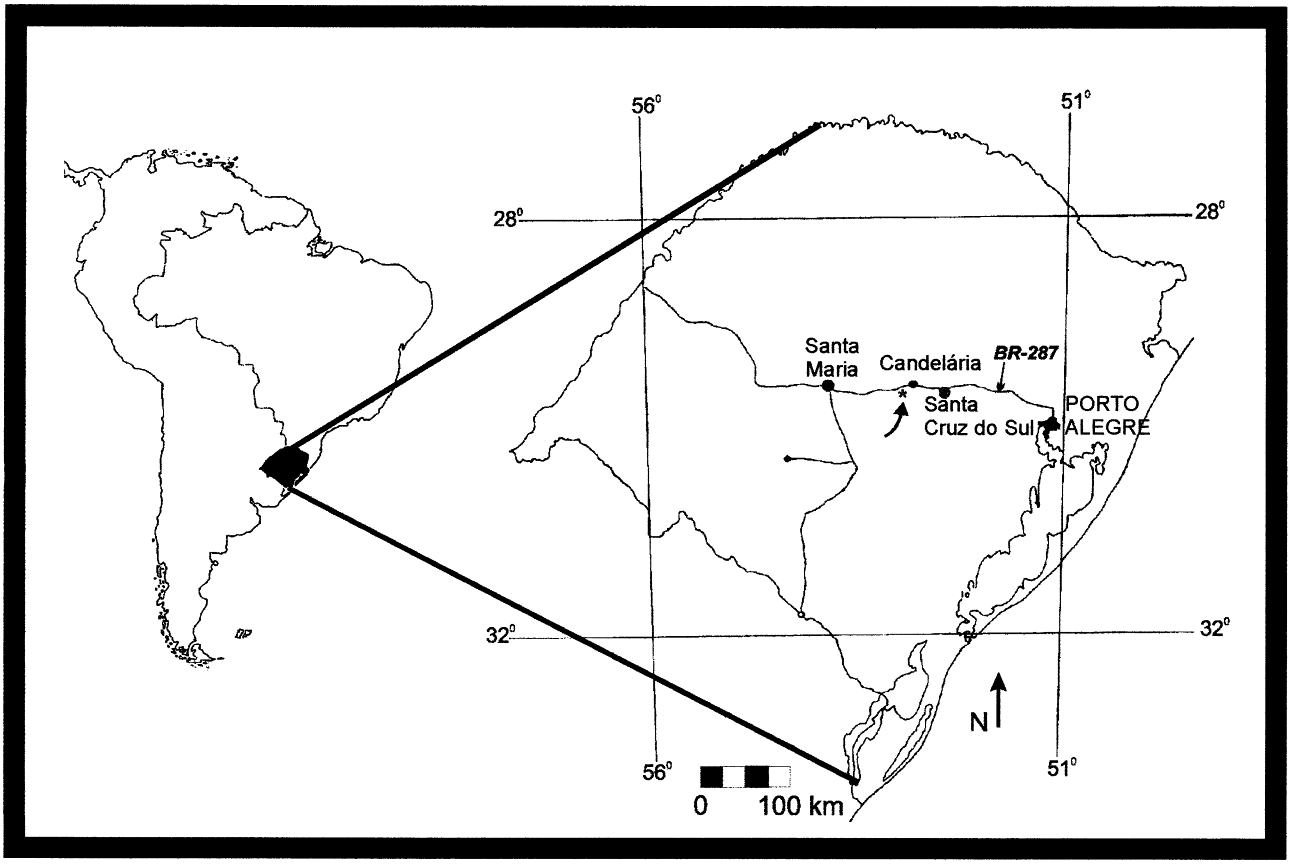

FIGURE 1. Map of the collection locality (*) of *Exaeretodon riograndensis* in the Rio Grande do Sul State, southern Brazil.

Paleontologia de Vertebrados Lillo, Universidad Nacional de Tucumán, Argentina; **PVSJ**, Museo de Ciencias Naturales, Universidad Nacional de San Juan, Argentina.

SYSTEMATIC PALEONTOLOGY

SYNAPSIDA
THERAPSIDA
THERIODONTIA
EUCYNODONTIA
TRAVERSODONTIDAE
EXAERETODON (Cabrera, 1943)
EXAERETODON RIOGRANDENSIS, sp. nov.

Etymology—Referred to the State of Rio Grande do Sul, Brazil, where the Santa Maria Formation crops out.

Holotype—MCP 1522 PV: complete skull plus proatlas and atlas arches on the occiput, dislocated from their anatomical position.

Referred Material—MCP 2361 PV: skull, lacking the anterior portion of the rostrum; MCP 3843 PV: skull and lower jaw in occlusion, lacking the right temporal region, right dentary also incomplete.

Horizon and Locality—Santa Maria Formation, Middle to Upper Triassic; km 136 of the railroad Br 287, six km west of the Botucarai hill, in the Candelaria district, Rio Grande do Sul State, Brazil (Fig. 1). Based on its occurrence in the same outcrop where *Proterochampsa* comes from, a Carnian age is suggested for this level of the Santa Maria Formation.

Diagnosis—Presence of a series of crests in the lateral flange of the prootic anterior to the fenestra ovalis; number of postcanines less variable in ontogeny than in *E. frenguellii.*

Comparative Material—Specimens of *Exaeretodon frenguellii* from the Ischigualasto Formation, at the collections of the Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires; Museum of Comparative Zoology, Harvard University, Cambridge, MA; Museo de La Plata, Argentina; Paleontología de Vertebrados Lillo, Universidad Nacional de Tucumán, Argentina and Museo de Ciencias Naturales, Universidad Nacional de San Juan, Argentina, were also examined by one of the authors (FA). The list of the specimens is the following: MACN 18114, 18125; MCZ 111-64A, 334-58M, 377-58M, 4074, 4468, 4469, 4470, 4480, 4482, 4483, 4486, 4493, 4500, 4502, 4510, 4781; MLP 43-VII-14-2, 43-VII-14-3; PVL 2056, 2079, 2082, 2083, 2094, 2473, 2554, 2565, 2750; PVSJ 157.

DESCRIPTION

We present a brief description of this new species based mainly on the holotype MCP 1522 PV. The genus morphology is well known from the Argentine species (Bonaparte, 1962; Chatterjee, 1982; Hopson, 1984; Goñi and Goin, 1990); therefore, only peculiarities or differences of the new species will be pointed out here. Traits concerning other non-mammalian cynodonts and basal mammals serve as the basis for additional commentary.

Facial Region (Figs. 2, 3 and 4)

The rostrum is short and wide, with the premaxilla ending as a conical prominence. The internasal process is lacking in MCP 1522 PV, considering the absence of the dorsal tip of this process between the anterior portion of the nasals (Fig. 2A).

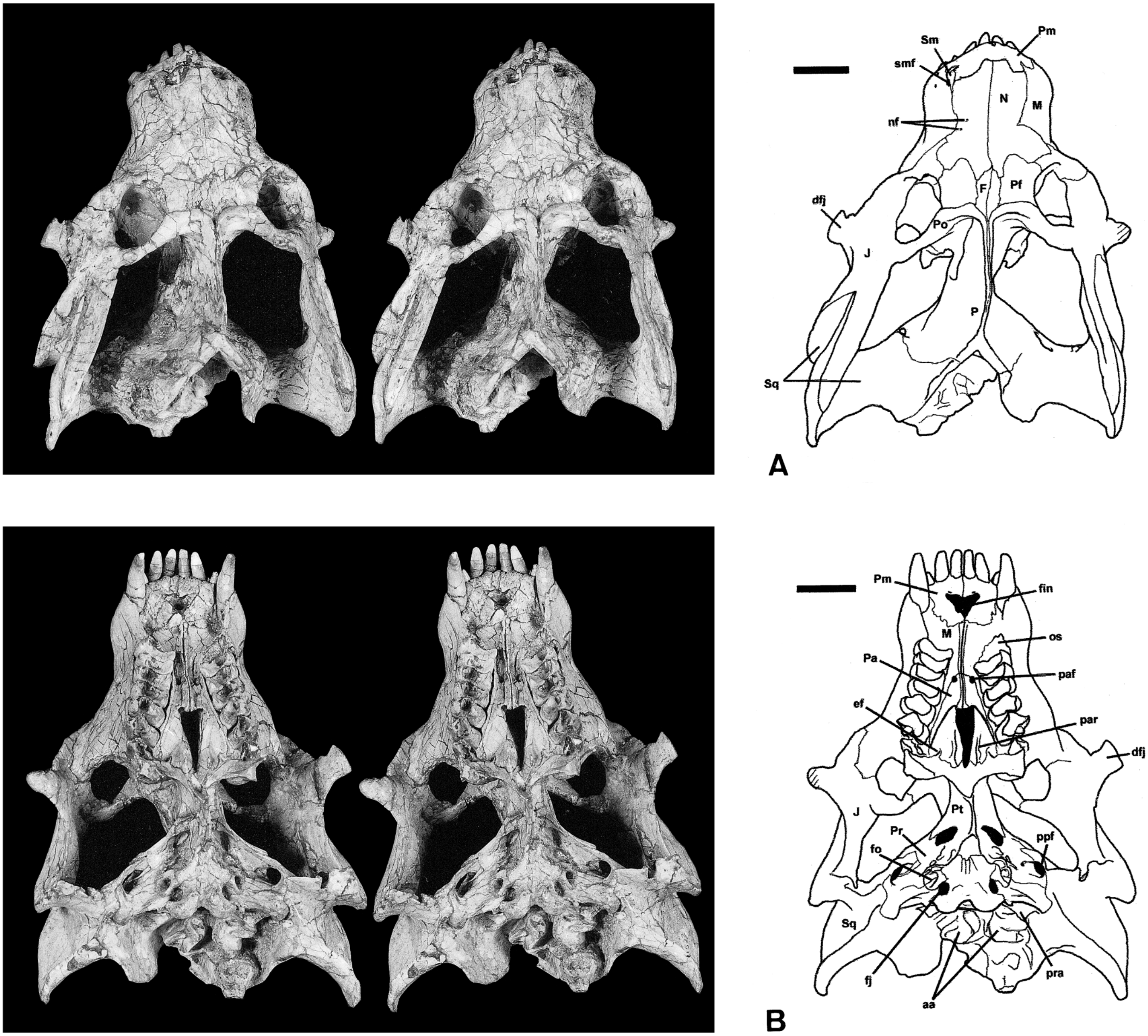

FIGURE 2. Stereo pair and line drawing of the skull of *Exaeretodon riograndensis* (MCP 1522 PV) in (**A**) dorsal and (**B**) ventral view. **Abbreviations**: **aa**, atlas arches; **dfj**, descending flange of jugal; **ef**, ectopterygoid foramen; **F**, frontal; **fin**, incisive foramen; **fo**, fenestra ovalis; **fj**, foramen jugulare; **J**, jugal; **M**, maxilla; **N**, nasal; **nf**, nasal foramina; **os**, osseous scar in the first left alveolus; **P**, parietal; **paf**, posterior palatal foramen; **par**, palatine ridges; **Pf**, prefrontal; **Pm**, premaxilla; **Po**, postorbital; **ppf**, pterygo–paroccipital foramen; **Pr**, prootic; **pra**, proatlas; **Pt**, pterygoid; **Sm**, septomaxilla; **smf**, septomaxillary foramen; **Sq**, squamosal. Scale bar equals 4 cm.

Bonaparte (1962) reported this condition for *Exaeretodon frenguellii*, contrasting to its suggested presence in the phylogenetic analyses by Rowe (1988) and Wible (1991). A tip of the premaxilla dorsal process however, seems to be present between the nasals in the muzzle of the small specimen MCP 3843 PV, but this region is somewhat distorted with numerous cracks on the bone. The basal process of the septomaxilla, above the premaxilla, is larger than the medial transverse shelf. The well developed septomaxillary foramen is situated between the posterodorsal process of the septomaxilla dorsally, and the maxilla ventrally (Fig. 3).

There are two infraorbital foramina; the small anterior one, subdivided on the right side, lies at the anterior edge of the postcanine series. The large posterior foramen is positioned at the level of postcanines two and three. The same condition is present in the referred specimen MCP 3843 PV (Fig. 4). One large or two small infraorbital foramina were described in specimens of *Exaeretodon frenguellii* (Bonaparte, 1962); they also occur at the level of the second and third postcanines (see also Hopson, 1984:fig. 2A).

In the dorsalmost portion of the maxilla, near to the nasal suture, is a wide depression, the naso-maxillary fossa. This depression was also reported for the Argentine species (Bonaparte, 1962). This fossa is much shallower in *Exaeretodon* than in *Cynognathus* (Broili and Schröder, 1935; Abdala, 1996b), *Diademodon* (Brink, 1955) and in the traversodontid *Pascualgnathus* (Bonaparte, 1966b).

The nasal is wide at its contact with the lacrimal, becoming

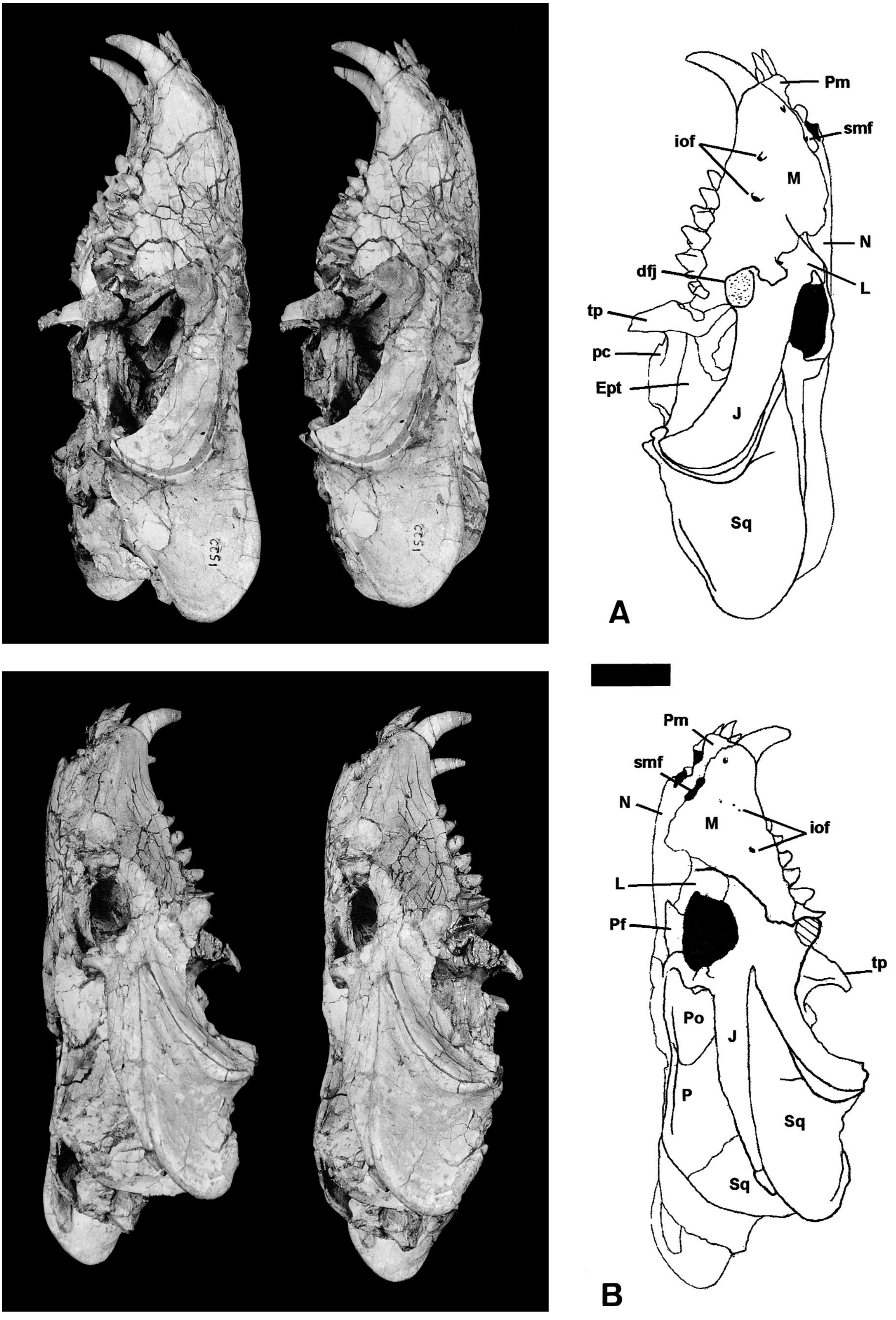

FIGURE 3. Stereo pair and line drawing of the skull of *Exaeretodon riograndensis* (MCP 1522 PV) in (**A**) left lateral and (**B**) right lateral view. **Abbreviations**: **dfj**, descending flange of jugal; **Ept**, epipterygoid; **iof**, infraorbital foramen; **J**, jugal; **L**, lacrimal; **M**, maxilla; **N**, nasal; **P**, parietal; **Pf**, prefrontal; **Pm**, premaxilla; **Po**, postorbital; **Sm**, septomaxilla; **smf**, septomaxillary foramen; **Sq**, squamosal; **tp**, transverse process. Scale bar equals 4 cm.

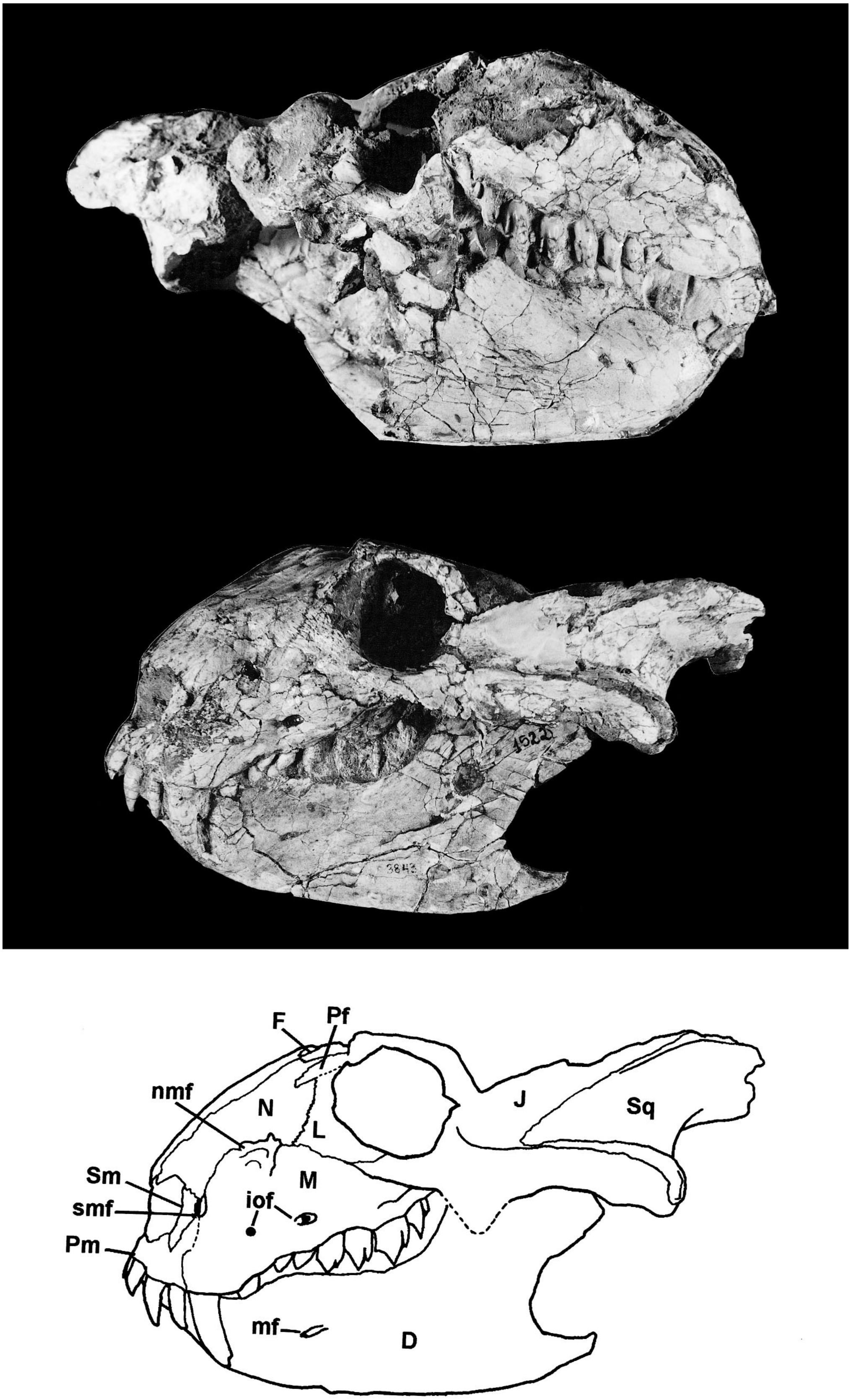

FIGURE 4. Right and left lateral view with line drawing of left lateral view of *Exaeretodon riograndensis* (MCP 3843 PV). The upper tooth details in the line drawing are from the right side of the specimen. **Abbreviations**: **D**, dentary; **F**, frontal; **iof**, infraorbital foramen; **J**, jugal; **L**, lacrimal; **M**, maxilla; **mf**, mental foramen; **N**, nasal; **nmf**, naso–maxillary fossa; **Pf**, prefrontal; **Pm**, premaxilla; **Sm**, septomaxilla; **smf**, septomaxillary foramen; **Sq**, squamosal. Scale bar equals 4 cm.

remarkably narrow distally, in contact with the prefrontal and frontal. The anterior border produces a medial process extended anteriorly. Although illustrated differently by Bonaparte (1962: fig. 3), the nasals are similar in specimens from Argentina notably in MCZ 377-58M. There are three foramina on the nasal. The large posterior one is close the naso–maxillary depression and opens antero-laterally. The two smaller foramina, which open anteriorly, are slightly medial to the large one. These foramina are also known in chiniquodontids (Abdala, pers. obs.), *Morganucodon* (Kermack et al., 1981) and the docodont *Haldanodon* (''nasal foramina,'' Lillegraven and Krusat, 1991).

Palate (Figs. 2B, 8A)

The posteriorly confluent incisive foramina are circumscribed entirely by the premaxilla. There is a small foramen anterior to the incisive foramina, elliptical in outline with the major axis aligned lateromedially. A similar structure occurs in *Thrinaxodon* (Fourie, 1974:fig. 1, FNNG?), chiniquodontids (Abdala, 1996a), *Oligokyphus* (Kühne, 1956), *Morganucodon* (Kermack et al., 1981) and *Haldanodon* (Lillegraven and Krusat, 1991: ventral premaxillary foramen). In these taxa this opening is round and smaller than in *Exaeretodon*.

As in *E. frenguellii*, the paracanine fossa, made up principally by the maxilla, occurs postero-medial to the upper canine. This condition is shared by *Scalenodontoides macrodontes* (Gow and Hancox, 1993) and *Boreogomphodon* (Sues, pers. comm.).

The palatal section of the maxilla extends posteriorly to the well-developed palatal foramen, between the second and third right postcanines and the first and second left. Palatine conforms a third of the palate length reaching up the level of the fourth postcanine. This bone shows a distinct medial boss and a crest at the end of the osseous palate for the attachment of the soft palate (Barghusen, 1986). Different of *Cynognathus* and *Diademodon* (Barghusen, 1986), and of the traversodontidae *Massetognathus* and chiniquodontids (Abdala, pers. obs.), this crest is not extended into the pterygoid bone. In this respect, the end of the osseous palate in *Exaeretodon* is more similar to the condition of typical therian (Barghusen, 1986). There is no vestige of an ectopterygoid; the foramen usually present in that bone (i.e., ectopterygoid foramen; suborbitario of Bonaparte, 1962) is instead limited anteriorly by the palatine and posteriorly by the pterygoid.

As stated by Bonaparte (1962), there is a vestige of the jugal, clasped by the maxilla, in contact with the pterygoids at the base of the pterygoid flange. This portion of bone is isolated from the rest of the jugal by the posterior extension of the maxilla.

The internal choana has distinct palatine and pterygoid ridges, the latter embracing the cultriform process of the parasphenoid. The palatine ridge divides the nasopharynx into a median and lateral passages. In the choanae, the palatine–pterygoid sutures are visible, but not that of palatine–vomer.

Orbital Region and Zygomatic Arch (Figs. 2, 3 and 4)

Behind the orbit, the well developed descending flange of the jugal is directed downwards and outwards. In the external surface, it bears prominent scars of the tendinous attachment of the superficial masseter muscle. On the zygomatic arch, the jugal has two portions separated by the anterior projection of the squamosal. The ventral part is strong, especially its dorsal border which is in contact with the squamosal. The dorsal portion extends posteriorly beyond the distal tip of the ventral one, nearly reaching the posterior border of the squamosal. Both processes are subequal in length in *E. frenguellii* (Bonaparte, 1962; Hopson, 1984:fig. 2). The zygomatic process of the squamosal extends further anteriorly in the Brazilian form, reaching the level of the base of the postorbital process.

The prefrontal is a wide element, square in outline. Bonaparte (1962:fig. 3) illustrates it as a rectangular element in *E. frenguellii*, but in some specimens (e.g., MCZ 377-58M) it is square. As in *E. frenguellii*, the postorbital overlies the prefrontal giving rise to a conspicuous protuberance (''rodete oseo'' of Bonaparte, 1962). The posterior projection of the postorbitals over the parietals is well developed and high, extending to the middle of the parietal crest. This projection is noticeably more anterior in the Argentine form (Bonaparte, 1962:fig. 3). The frontal extends below the inferior edge of the postorbitals overlying the orbitosphenoid and reaching the anterodorsal border of the epipterygoid. The fused parietals make up the parietal crest. There is no vestiges of parietal foramen.

The orbitosphenoid is a thin element, being crushed and distorted in both MCP 1522 PV and MCP 2361 PV. It is overlaid by frontal and by a small portion of the epipterygoid. In specimens MCP 1522 PV and especially in MCP 2361 PV there is evidence of a thin osseous septum in the midline of the interorbital vacuity, composed, partially, by the palatine.

Lateral Wall of the Braincase

The lateral wall of the braincase is not well preserved. A large trigeminal foramen is placed between the prootic and the epipterygoid. The fragile anterior lamina of the prootic is broken and distorted on both sides of the skull. The dorsal ascending groove between parietal and prootic follows the opening of the posttemporal canal. There is no evidence of an external orbitotemporal groove, possibly as consequence of the poor preservation of the anterior lamina of the prootic and the dorsal edge of the epipterygoid.

The anterodorsal projection of the epipterygoid lies medial to the lower border of the parietal and contacts the frontal anteriorly. The epipterygoid–parietal suture is visible only anteriorly, being the epipterygoid covered by the parietal.

Basicranium (Figs. 6 and 7)

The basicranial girder is conspicuously shorter and wide in relation to most of the non-mammalian cynodonts including traversodontids, except *Scalenodontoides* (Gow and Hancox, 1993:fig. 2). Similar condition in the basicranial girder is known in tritylodontids [Sues, 1986:fig. 6; sometimes extremely short and wide as in *Bienotheroides* (Sun, 1984:fig. 4)], and in tritheledontids and mammaliaformes (Hopson and Barghusen, 1986).

In ventral view, medial to the fossa for the quadrate, the squamosal has a well-developed anteromedially directed projection. It delimits the pterygo–paroccipital foramen and contacts the quadrate ramus of the epipterygoid anteriorly and the lateral flange of the prootic medially. This condition is also known in *Massetognathus* (Rougier et al., 1992; Luo and Crompton, 1994:fig. 8), but not to the extent that it is developed in *Exaeretodon*.

The squamosal bears a wide medial notch for reception of the quadrate. On the left side of the MCP 1522 PV, there is a pronounced crest between the notches for the quadrate and the small lateral one for the quadratojugal. A conspicuous crest delimits the medial border of the quadrate attachment (Fig. 5). The quadrate and quadratojugal are not preserved.

The paroccipital process is well developed, contacting the squamosal laterally. There is a visible suture between this process and the prootic. In ventral view, the paroccipital process presents a well-developed protuberance nearly contacting the lateral border of the occipital condyles. Lateral to it, some scars seem to be muscle insertion sites.

The fenestra ovalis is formed by the opisthotic posteriorly

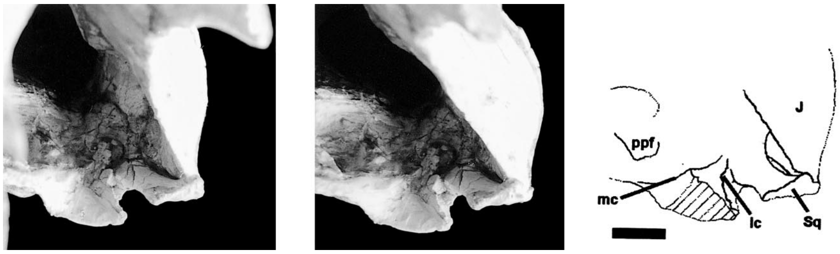

FIGURE 5. Stereo pair and line drawing of the quadrate–quadratojugale attachment in the squamosal of *Exaeretodon riograndensis* (MCP 1522 PV). Scale bar equals 1 cm. **Abbreviations: j**, jugal; **lc**, lateral crest; **mc**, medial crest; **ppf**, pterygo–paraoccipital foramen; **Sq**, squamosal.

and the prootic anteriorly and medially. The basisphenoid wing is well developed but is excluded from the fenestra ovalis by the opisthotic.

In the lateral flange of the prootic, close to the anterior margin of the pterygoparaoccipital foramen, there is a wide tympanic opening for the prootic vein directed posteriorly. This is also known in *Massetognathus*, *Probainognathus* (Rougier et al., 1992; Wible and Hopson, 1995) and chiniquodontids (Abdala, 1996a). The prootic makes up an extensive floor of the cavum epiptericum anterior to the prootic opening. Both features, the tympanic opening of the prootic canal and the extensive floor of the cavum epiptericum, also occurs in MACN 18125 from the Ischigualasto Formation.

Anterior to the fenestra ovalis is the primary facial foramen, nearly closed by a well-developed crest on the lateral flange of the prootic (Fig. 6, arrow). A notch, probably for the facial nerve passageway, interrupts this crest. A second crest is between the fenestra ovalis and the primary facial foramen, delimiting two shallow depressions. In addition, there is a rudimentary projection of the prootic close to the basisphenoid wing. Both crests and projection are unknown in other cynodonts.

The paraoccipital process possesses a posterior ridge that extends obliquely forward reaching the margin between the fenestra ovalis and the foramen jugulare (Fig. 7). Behind this ridge, there is a very shallow depression, located in the same place where the levator hyoidei muscle fossa (or stapedial muscle fossa) is developed in tritylodontids (Kuhne, 1956:text–fig. 13; Luo, 1994:fig. 6.3D). This fossa is also present in many early Mammaliaformes as *Morganucodon* (Kermack et al., 1981:fig. 98), *Sinoconodon* (Crompton and Luo, 1993:fig. 4.10), *Megazostrodon* (Gow, 1986:fig. 4) and *Haldanodon* (Lillegraven and Krusat, 1991:fig. 8, ventrolateral petrosal pit).

Occipital Plate

In occipital view, the squamosal extends to the dorsal anterior third of the lambdoidal crest. The occipital condyles are well developed, with an odontoid notch between them. There are swellings on both sides of the dorsal portion of the foramen magnum, in position similar to those interpreted as proatlas articulations in *Probelesodon* (Romer, 1969). Internal to the foramen magnum two foramina for the hypoglossal nerve are visible, both connected to the jugular foramen. The major portion of the occipital plate is obscured by the proatlas and atlas arches, and other vertebral fragments attached to the plate (Fig. 2B).

Lower Jaw (Fig. 4)

The lower jaw is only present in the juvenile MCP 3843 PV. Dentaries are broken at the symphysis, being extremely thin bones with the anterior mental foramen at the level of the sec-

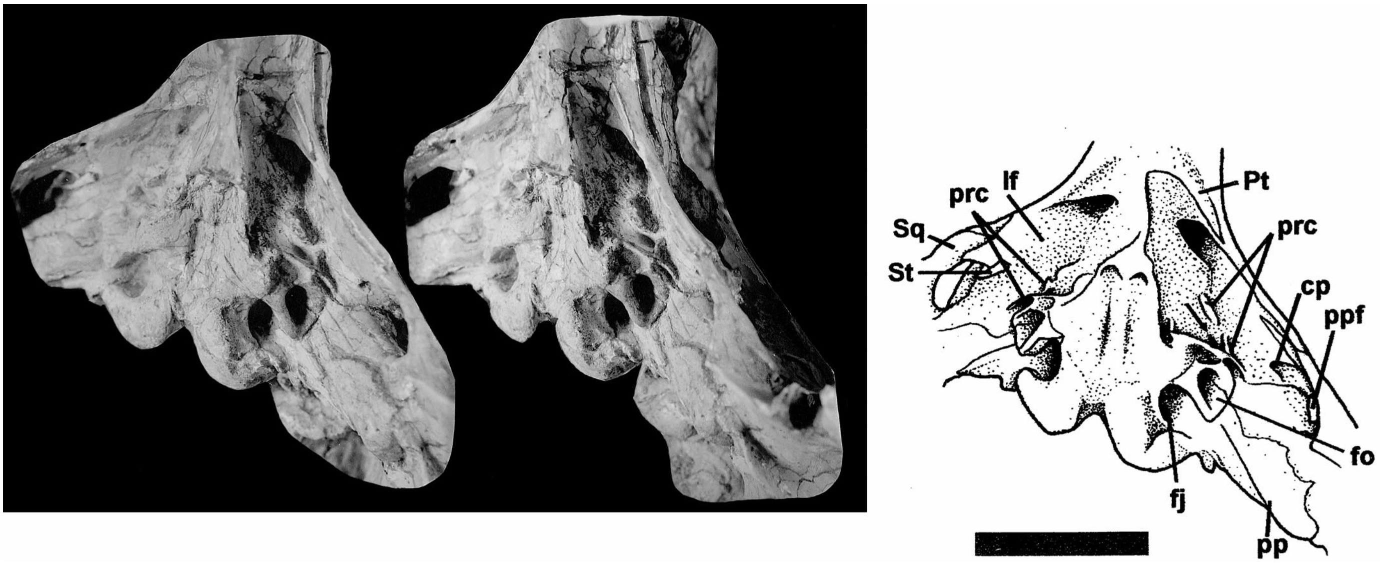

FIGURE 6. Stereo pair and line drawing of the basicranium of *Exaeretodon riograndensis* (MCP 1522 PV). The crest and projection anterior to the fenestra ovalis are shown. **Abbreviations**: **cp**, prootic canal; **fo**, fenestra ovalis; **fj**, foramen jugulare; **lf**, lateral flange of the prootic; **pop**, paraoccipital process; **ppf**, pterygo–paraoccipital foramen; **Pr**, prootic; **prc**, prootic crests; **Pt**, pterygoid; **Sq**, squamosal; **St**, portion of the stapes. Arrow indicates primary facial foramen. Scale bar equals 4 cm.

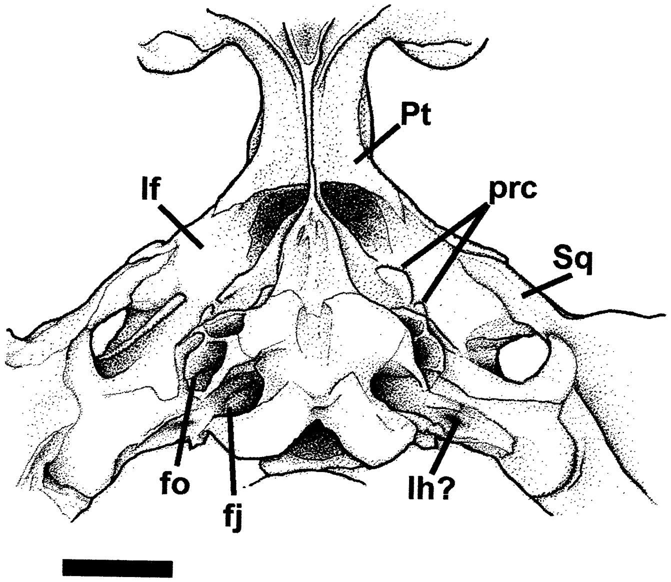

FIGURE 7. Basicranial reconstruction of *Exaeretodon riograndensis* (MCP 1522 PV). **Abbreviations**: **fo**, fenestra ovalis; **fj**, foramen jugulare; **lh?**, levator hyoidei? pit; **lf**, lateral flange of the prootic; **prc**, prootic crests; **Pt**, pterygoid; **Sq**, squamosal. Scale bar equals 2 cm.

ond lower postcanine. There is a shallow masseteric fossa extending a little in advance of the mental foramen, at the level of the first lower postcanine. The angular process, as typical in *Exaeretodon*, is backwardly projected, a trait shared with the new Malagasy traversodontid *Menadon besairiei* (Flynn et al., 2000). The coronoid process, even though incomplete on both sides, is tall. The postdentary bones are not preserved.

Dentition (Figs. 8 and 9)

The dental formula in the largest specimen is three incisors, one canine, and six/five postcanines plus one in eruption. The smallest specimen (MCP 3843 PV) has three upper and lower incisors, one canine and six plus one in eruption upper and lower postcanines.

The upper incisors are somewhat procumbent. The first two are larger and spatulate, with wear facets in their lingual edges. The third one is considerably smaller, showing no wear facet. In the juvenile MCP 3843 PV there are three lower incisors, the last one less developed. As stated by Chatterjee (1982) for *Exaeretodon statisticae*, enamel layer on the incisor is only developed in the labial face.

The upper canine is large, somewhat anteriorly directed. The enamel layer is also restricted to the labial side of the tooth in the MCP 1522-PV, with a clear wear facet at its anterior edge, in front of the anterior margin of the enamel layer. The vertically oriented lower canine in MCP 3843-PV is distinctively smaller than the upper. It takes a posterior position in relation to the upper canine when the jaw is closed.

The postcanine crown is similar to those described for the Argentine specimens (Bonaparte, 1962). In unworn teeth, the labial posterior accessory cusp is completely isolated from the crest that descends from the main labial cusp (Fig. 9). Thus, two basins characterize the unworn postcanine: the principal one formed by the anterior accessory labial cusp and the main labial cusp, and a posterior small one formed only by the posterior accessory labial cusp. This implies that the posterior transverse crest extends from the posterior lingual cusp to the main labial cusp, a condition also observed in unworn postcanines of Argentine specimens (Crompton, 1972; Chatterjee, 1982; contra Goñi and Goin, 1990). The crown in these elements looks narrow, especially the lingual lobe, and there is a remarkable angulation between the lingual and labial lobes of the tooth (Fig. 9; see Chatterjee, 1982:text–fig. 4G). With slight wear in the postcanines, the posterior accessory cusp is ultimately incorporated into the principal basin.

The erupting last postcanine in MCP 2361 PV shows the labial lobe of the tooth folded upon the lingual, giving the impression of a recent separation of both. Gow and Hancox (1993) pointed out a similar condition for *Scalenodontoides macrodontes*. However, in the material described here, only two cusps are observed in the sectorial border of the postcanine, with the anterior accessory cusp unexpectedly absent. The posterior accessory cusp appears isolated from the principal basin of the tooth and the posterior transverse crest is clearly disposed between the labial main cusp and the posterior lingual cusp.

Proatlas and Atlas Archs (Fig. 2B)

Both proatlas and atlas arches, along with other cervical elements are preserved in MCP 1522 PV. These elements are displaced from their original position and are firmly attached to the occiput. The proatlas possesses the concave articulation facet for the atlas and a long transverse process. The atlas arch is visible in medial view with the articular facet for the occipital condyle slightly concave and a little smaller than the facet for the atlas centrum. The transverse process is well developed. Both elements are similar, in the features observed, with those from Argentina (Bonaparte, 1963a; MACN 18125).

DISCUSSION

Exaeretodon frenguellii from the Ischigualasto Formation, Argentina has been thoroughly described and illustrated (e.g., skull, Bonaparte, 1962; Chatterjee, 1982; Hopson, 1984; middle ear, Allin, 1975, 1986; postcanine dentition, Bonaparte, 1962; Crompton, 1972; Chatterjee, 1982; Hopson, 1984; Goñi and Goin, 1990; postcranium, Bonaparte, 1963a; and endocranium, Bonaparte, 1966a). The skull of the form described herein differs from *E. frenguellii* in the extension of some bones (i.e., the posterodorsal projection of the jugal behind of the posteroventral; prefrontal relatively wide). Two features are remarkably different from the Argentine species, however. The first is the striking presence of a series of crests on the prootic, not observed in specimens from Argentina with the basicranium well preserved (e.g., MACN 18125). The second is that the number of postcanines appears less variable ontogenetically in the limited skull size sample of the Brazilian species. Other features that could look at first sight as differences compared with Bonaparte's (1962) description were also found to occur in additional material from Argentina at the MACN, MCZ and PVL collections. Another species, *Exaeretodon major* (Huene), was established previously on the basis of a fragmentary maxilla from the Santa Maria Formation, that lacks teeth but preserves 7 alveoli with angulations similar to those seen in *Exaeretodon frenguellii* (Barberena, 1974). The size of the holotype and only known specimen agrees with those of the larger skulls of *E. riograndensis*. However, it exhibits a conspicuous difference in size between the anterior and posterior alveoli, contrasting with the small size variation of postcanines in the new species here proposed. Although traits such as the difference in tooth size of the same postcanine series are not definitely diagnostic for traversodontid species (see discussion below and Abdala and Giannini, 2000), we favor recognizing *E. major* as a distinct species. However, additional and more informative material will be necessary to confirm this species unquestionably. The holotype of *E. major* was collected in the Chiniqua outcrop ''Baum Sanga'' that also produced the dicynodonts *Dinodon-*

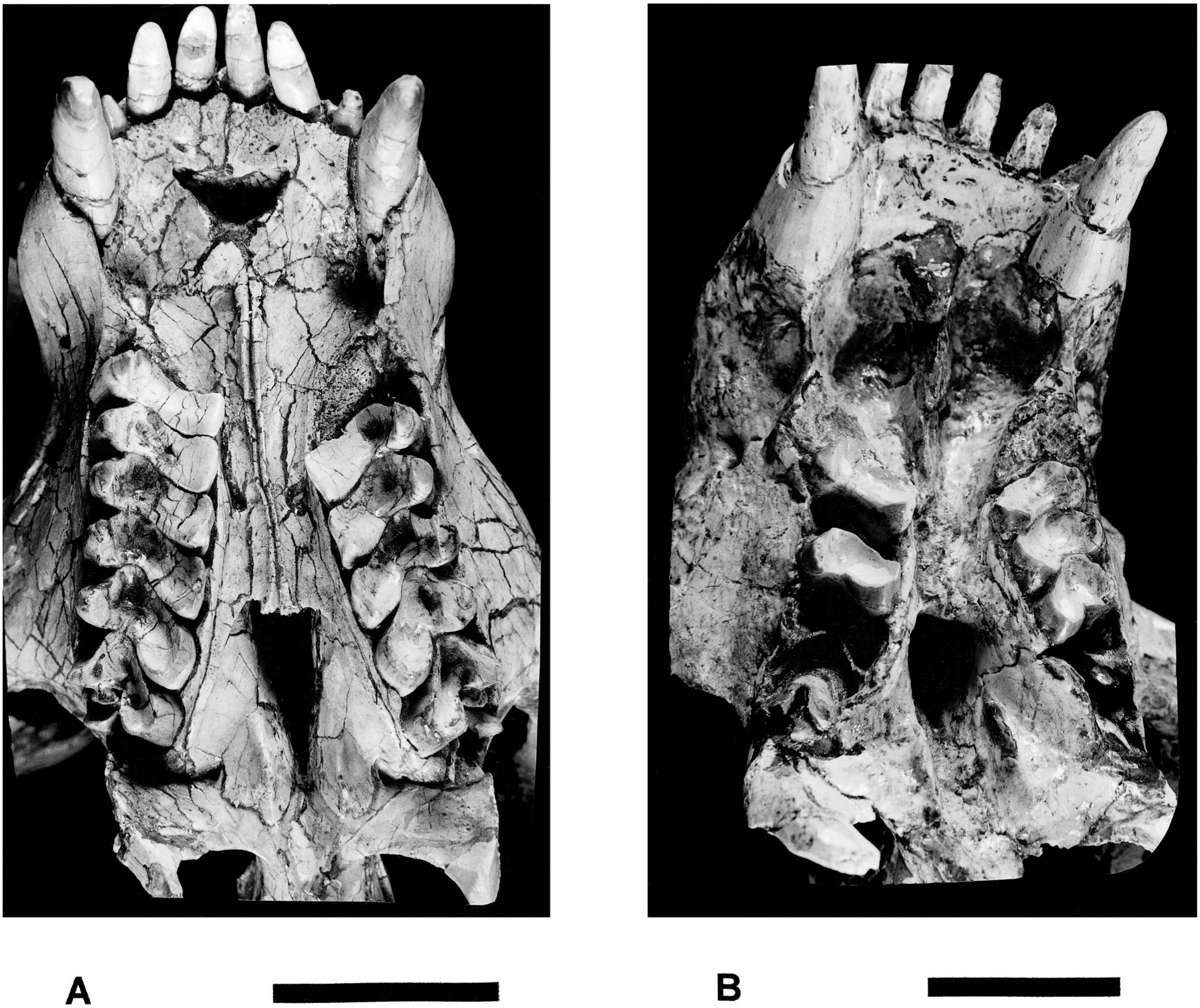

FIGURE 8. Postcanine series of *Exaeretodon riograndensis* (**A**) specimen MCP 1522 PV and (**B**) specimen MCP 2361 PV. Scale bar equals 4 cm.

tosaurus and *Stahleckeria* (Huene, 1935–42:148). This implies a Ladinian age for *E. major*, thus representing the oldest record for *Exaeretodon*.

The well-preserved basicranium of the MCP 1522 PV clarifies our understanding of this region in *Exaeretodon*. Unfused prootic and opisthotic is a symplesiomorphy shared with many non-mammalian cynodonts (Rowe, 1993), but features, such as the prominent basisphenoid wing not forming the periphery of the fenestra ovalis, the tympanic opening for the prootic sinus, and the well developed incipient floor of the cavum epiptericum suggest a derived position for *Exaeretodon* among eucynodonts. Luo (1994:character 74) recognizes the same derived condition for the basisphenoid wing in *Massetognathus*, *Probainognathus*, tritylodontids, and tritheledontids. The opening for the prootic canal is also present in *Massetognathus*, *Probainognathus* (Rougier et al., 1992; Luo, 1994; Luo and Crompton, 1994), and chiniquodontids (Abdala, 1996a). Thus, this feature appears more widely distributed among non-mammalian cynodonts than previously thought (Wible and Hopson, 1995). The floor of the cavum epiptericum in *Exaeretodon* is remarkably more developed than in other late cynodonts, being presumably further developed than in the carnivorous cynodont *Ecteninion lunensis* (Martinez et al., 1996:fig. 3B), and closer to the condition seen in *Morganucodon* (Luo and Crompton, 1994:figs. 13A, B).

The most striking feature in the basicranium of the new species is the presence of well-developed prootic crests in the lateral flange, close to the origin of the basisphenoid wing and anterior to the fenestra ovalis. A possible function for these crests is attachment for the posterior pterygoid muscle. The origin of this muscle in non-mammalian cynodonts as *Thrinaxodon* extended, as in extant reptiles, from the posterior edge of the transverse process, reaching the medial pterygoid crest and the quadrate ramus (Barghusen, 1986). *Exaeretodon* presents the basicranial girder shorter and wider than in *Thrinaxodon* and most of the non-mammalian cynodonts. This condition of the basicranial girder is also interpreted as suggesting that part of the posterior pterygoid origin extended onto the prootic. Additionally, the fossa for the tensor tympani muscle in a similar location of the prootic crests, is known in triconodontidae and

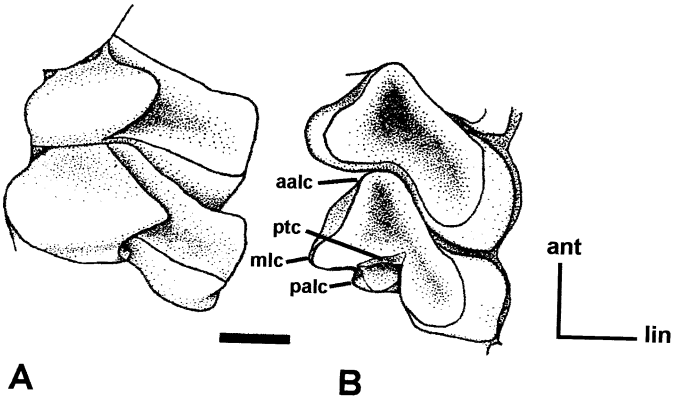

FIGURE 9. Last two postcanines of *Exaeretodon riograndensis* (MCP 1522 PV) in (**A**) crown and (**B**) lingual view. **Abbreviations**: **aalc**, anterior accessory labial cusp; **mlc**, main labial cusp; **palc**, posterior accessory labial cusp; **ptc**, posterior transverse crest. Scale bar equals 1 cm.

multituberculata (Wible and Hopson, 1993). The presence of this muscle in *Exaeretodon* is unlikely, considering the lack of fossa for the tensor tympani in tritheledontids, tritylodontids, and most of early mammaliaformes. However, crests and the basicranial girder structure could be interpreted as evidence of change in the attachment of the posterior pterygoide muscle. In *Exaeretodon*, the origin of the muscle extended onto the prootic (and probably onto alisphenoid) but without a significantly reduction in size of posterior pterygoid muscle, when compared with *Thrinaxodon*.

Considering the skull size range of the new species (Table 1), and a larger sample of *E. frenguellii*, some aspects of postcanine replacement become apparent. The number of postcanines decreases slightly from the smaller to the larger specimen. Six teeth plus one in eruption are present in MCP 3843 PV; in the next larger specimen MCP 1522 PV six teeth plus one in eruption are present on the right side and five plus one on the left, where the anteriormost postcanine is absent and its alveolus filled by bone. The largest specimen MCP 2361 PV features five postcanine teeth plus one in eruption on both sides, with left and right first alveoli filled by bone. The evidence suggests a trend in which postcanines become reduced in number towards adulthood and agrees with our observations on a sample of *E. frenguellii* (contra Bonaparte, 1962; Hopson, 1985; but see Bonaparte, 1963b:fig. 4). Small specimens of the Argentinean species have eight to nine postcanines and there is a reduction to six in larger specimens (Table 2). Note that specimens MCZ 4480 and PVL 2565 (holotype of *Proexaeretodon vincei*), which are of similar size, show a strikingly high number of postcanines. Additionally, a huge specimen, PVL 2079, only preserved as an upper postcanine series, shows 10 plus 1 in eruption. In all these cases, the three or four first elements are remarkably smaller than the rest of the series. We regard the presence of such teeth as an anomalous retention, taking into account the fewer number of these elements observed in most of the larger specimens of the Argentinean sample (Table 2). The anteriormost two or three postcanines of MCP 1522 PV are highly worn, almost without vestige of the original shape of the crown, and virtually without any enamel. The crowns of the following two teeth, have a typical posterior inflection that separates the sectorial border of the tooth, and in both teeth, the sectorial cusps are badly worn out. The posteriormost members of the series retain the original crown morphology.

The evidence in *Exaeretodon* partially agrees with the general pattern of tooth replacement proposed for traversodontids and *Sinoconodon*, with the loss of the anterior postcanines, and addition of new ones at the end of the series (Crompton, 1955; Goñi, 1986; Goñi and Goin, 1990; Crompton and Luo, 1993). However, the number of postcanines in *Exaeretodon* decreases in larger (presumably adults) specimens, a development that

TABLE 1. Measurements of the skulls of *Exaeretodon riograndensis* (in mm). *Estimated.

	MCP 3843 PV	MCP 1522 PV	MCP 2361 PV
Basal skull length (bl)	170.0*	223.0	263.0*
Middle dorsal length	–	223.7	262.0*
Preorbital length (pl)	82.9	96.9	121.0*
Nasal length	77.6	91.0	132.0*
Orbital length	–	44.3	46.4
Interorbital width	31.0*	60.5	69.8
Orbital diameter	37.9	32.4	45.3
Palate length	70.1	102.0	109.0*
Upper canine width	46.8	83.5	87.6
Anterior postcanine distance	–	16.3	21.9
Posterior postcanine distance	–	51.5	58.5
Transverse process width	42.3	71.8	–
Upper postcanine series length	57.7	79.4/71.6	64.1
Maximum width of the skull	–	193.7	254.5
Maximum height of jugal	56.6	80.4	90.2
Temporal region length	–	83.0	109.5
Temporal fossa length	–	158.5	164.8
Basicranial girder width	–	23.4	22.9
Length from the occipital condyle to end of the cultriform process	–	70.9	94.0
Basicranial length	–	49.3	58.6
Occipital plate height	–	82.3	108.1
Occipital plate base width	–	–	111.2
Mandibular length	153.2	–	–
Dentary height at level of the first postcanine	35.2	–	–
Angle to back of the canine	98.9	–	–

TABLE 2. Postcanine numbers paired with basal skull length in *Exaeretodon*. Specimens of *E. riograndensis* are in bold. Estimated measurements (*); +1: plus last postcanine in eruption. A question mark indicates uncertainty (possibly plus one element).

Specimen	Basal length of the skull (in mm)	Upper Postcanine number
PVSJ 157	150	9,8
MCZ 4781	160	9
PVL 2563	168	10
MCZ 4470	170	8 + 1
MCP 3843 PV	**170***	**6 + 1**
PVL 2056	178*	6–7
MCZ 4469	210	8(?)
MCZ 111-64A	219	7
MCZ 4510	220	7 + 1
MCP 1522 PV	**223**	**6 + 1/5 + 1**
PVL 2565	230	10
MCZ 4480	240	9 + 1
MCP 2361 PV	**260***	**5 + 1**
PVL 2082	265*	6 + 1
PVL 2750	280	7 + 1
MCZ 4074	290	7
MCZ 4500	300*	7 + 1
MCZ 4483	320	6 + 1
PVL 2473	322	6(?)
MCZ 377-58M	329	6
PVL 2554	330*	5(?)
MACN 18125	330	5 + 1
MCZ 4468	330	6
PVL 2094	335	5 + 1(?)
MCZ 2083	380	6
MCZ 4486	400*	5(?)

contrasts with the ontogenetic increase in postcanine number described for *Scalenodon* (Crompton, 1955) and *Massetognathus* (Abdala and Giannini, 2000). In this context, it is interesting to note the existence of an odontogenetic phase of the dental lamina in larger (and thus possibly adults) specimens, which shows the last postcanine in eruption at the base of the pterygoid flange. The crown of this element shows the lingual lobe folded on the labial portion, a condition also reported for *Scalenodontoides macrodontes* (Gow and Hancox, 1993). This condition implies conspicuous differences in tooth morphology in the recently emerged postcanine and the preceding one, which is completely unfolded and in its regular position in the tooth row. These differences could be linked to wear on the labial crests and on the lingual surface in fully erupted teeth to ‘‘open up’’ the crown.

CONCLUSION

Traversodontid cynodonts are a highly diversified group, particularly in South America, where they span the whole of the Triassic. The new species *Exaeretodon riograndensis* from the Santa Maria Formation of southern Brazil is remarkably similar to *E. frenguellii* from the Ischigualasto Formation of Argentina, differing in the presence of a series of prootic crests on the basicranium and a less marked ontogenetic reduction in the number of postcanines. Considering evidence from *Exaeretodon frenguellii* and *E. riograndensis*, a reduction in the number of postcanines towards adulthood is proposed for both species, a trend unrecorded previously for any non-mammalian cynodont.

The presence of the prootic crests is an autapomorphy for *Exaeretodon riograndensis* and as such, does not modify phylogenetic relationships among taxa. But, if our functional interpretation is correct, they represent the first evidence in the non-mammalian cynodont-to-mammal transition, of the origin of the posterior pterygoid muscle onto the prootic. This condition is present in many late mammaliaformes, including therian, in which the tensor timpany and the tensor veli palatini muscles, both attached onto the petrosal, are allegedly originated from the posterior pterygoid muscle (Barghusen, 1986; Allin and Hopson, 1992). Indeed, this interpretation will have some implications on phylogeny, because even if prootic crests like those of *Exaeretodon* are lacking in tritheledontids, tritylodontids, and early mammaliaformes, all of them, as *Exaeretodon*, have a short and wide basicranial girder. This condition also suggests a shift of the attachment site of the posterior pterygoids muscle onto the prootic and alisphenoid. In some phylogenetic hypotheses (e.g., Abdala, 1996a; Allin and Hopson, 1992), the attachment of posterior pterygoid muscle onto the prootic would be an independent acquisition in late traversodontids and Mammaliamorpha. Contrary, in Rowe’s hypothesis (1988, 1993) the origin of the pterygoid muscle on the prootic would be a synapomorphy uniting *Exaeretodon* and Mammaliamorpha.

As already demonstrated to be fairly common in studies on non-mammalian cynodonts to mammals transition, the evidence of major changes towards ‘‘mammalness’’ is widespread in different clades of this lineage, with similar changes appearing, at times, independently in several branches (Allin and Hopson, 1992; Martinez et al., 1996). Features found in *Exaeretodon*, as the extensive floor of the cavum epiptericum with a similar extension to these of *Morganucodon*, are more difficult for understanding in a phylogenetic context, because independently of the preferred hypothesis, the minimum of two unconnected changes are necessary to explain its distribution in the late non-mammalian cynodonts and mammaliaformes. In conclusion, the most relevant anatomical traits here introduced for *Exaeretodon*, (e.g., the extensive epipteric floor mentioned above, the presence of the prootic canal, and the crest at the end of the osseous palate not extended into the pterygoid bone) seem to set up yet more ambiguity in poorly resolved groups of eucynodonts (i.e., Cynognathia, Probainognathia, and Gomphodontia). But, the analysis of this information in a cladistic framework, including a wide array of non-mammalian cynodonts (in progress by Abdala) would reveal the actual incidence of these features in the phylogeny of non-mammalian cynodonts and early mammaliaformes.

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