

DIADEMODON TETRAGONUS SEELEY, 1894 (THERAPSIDA: CYNODONTIA) IN THE TRIASSIC OF SOUTH AMERICA AND ITS BIOSTRATIGRAPHIC IMPLICATIONS

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ABSTRACT—We report for the first time the presence of the cynodont *Diademodon tetragonus* Seeley, 1894 in the South American Triassic. The specimen, represented by a fragmented skull and lower jaws, was found in levels of the Río Seco de la Quebrada Formation (Puesto Viejo Group), Mendoza Province, Argentina. It is assigned to *D. tetragonus* based on its overall skull shape (narrow and elongated snout with a concave outline in dorsal view), the morphology of the jugal that forms most of the dorsoventral depth of the zygoma and shows a well-excavated external auditory meatus, and a postcanine series including circular outlined anterior teeth, ovoid gomphodont teeth in the middle, and posterior sectorial teeth. The association of this taxon with the cynodonts *Cynognathus crateronotus* and *Pascualgnathus polanskii*, along with comparisons to African Triassic assemblages, suggest an Early to Late Anisian age for the Río Seco de la Quebrada Formation. These levels are most likely correlated to the subzones B and C of the South African *Cynognathus* Assemblage Zone, where both *Cynognathus* and *Diademodon* are known. This discovery represents the fourth report of shared cynodont genera between allegedly Lower to Middle Triassic African and South American terrestrial faunas.

INTRODUCTION

Herbivorous/omnivorous diademodontid cynodonts are among the most abundant tetrapods represented in the *Cynognathus* Assemblage Zone (AZ; Late Olenekian to Late Anisian) of the Beaufort Group of South Africa (Kitching, 1977; Hancox, 2000; Hancox and Rubidge, 2001; Abdala et al., 2005). In addition, remains of this family have been discovered in the Ntawere, Manda, and Omingonde formations of Zambia, Tanzania and Namibia respectively (Crompton, 1955; Brink, 1963a; Keyser, 1973a, 1973b), and in the Upper Fremouw Formation of Antarctica (Hammer, 1995), all equivalent to the *Cynognathus* AZ.

Representatives of this group were first described during the 1800s (Owen, 1859; Seeley, 1894, 1895) and several aspects of their anatomy, morphological variation, and paleobiology have been studied in detail since then (e.g., Broom, 1911, 1919; Watson, 1911, 1913; Broili and Schröder, 1935; Brink, 1955a, 1956, 1963b; Fourie, 1963; Hopson, 1971; Crompton, 1972; Osborn, 1974; Grine, 1977; Grine and Hahn, 1978; Grine et al., 1978, 1979; Botha and Chinsamy, 2000). More than twenty species of diademodontids have been named, especially through Seeley and Broom's contributions. In the most recent taxonomic reviews of the group, opinions have differed. Brink (1979) considered *Cragievarus* and *Diademodon* (from the Karoo Basin) and *Titanogomphodon* (from Namibia) valid genera. In addition, he recognized four species within the genus *Diademodon*, three for South Africa, namely *D. tetragonus*, *D. mastacus*, and *D. grossarthi*, and one, *D. rhodesiensis*, for Zambia. On the other hand, Grine and collaborators (Grine, 1978, 1981; Grine and Hahn, 1978; Grine et al., 1978; Bradu and Grine, 1979; see also Hopson and Kitching, 1972) recognized *Diademodon tetragonus* as the only valid taxon. They attributed variations recognized by

Brink (1979) as being of taxonomic value to sexual and age differences and preservation artifacts. Both Brink (1979) and Grine et al. (1978) included the Chinese *Ordosiodon lincheyuensis* from the Lower Ermaying Formation in diademodontids, but it was subsequently demonstrated that taxon is a therocephalian (see Sun et al., 1992). An isolated partial lower jaw recently described from the Lower Elliot Formation of South Africa has been tentatively assigned to Diademodontidae, suggesting the survival of this family as a relict into the Norian (Abdala et al., 2007a).

In this contribution we report for the first time the presence of the cynodont *Diademodon tetragonus* in the South American Triassic. The new specimen, represented by a fragmented skull and lower jaws, was discovered in outcrops of the Río Seco de la Quebrada Formation, Puesto Viejo Group (Stipanovic et al., 2007) about 40 km southwest of San Rafael, Mendoza Province, Argentina (Fig. 1). This finding represents the fourth report of shared cynodont genera between allegedly Lower to Middle Triassic African and South American terrestrial faunas. Moreover two cynodont species (the taxon reported here and *Cynognathus crateronotus*; Abdala, 1996) are currently known to be common to these continents in the Triassic. A description of the new material from the Puesto Viejo Group and the biostratigraphic implications of the findings are discussed below.

Cynodonts from the Puesto Viejo Group—Two cynodonts have been previously described in this unit: *Pascualgnathus polanskii* and *Cynognathus crateronotus* (Bonaparte, 1966a, b, 1969a; Abdala, 1996, 1999), both coming from the Río Seco de la Quebrada Formation (Bonaparte, 1982).

Pascualgnathus was originally considered a diademodontid with strong affinities to the African genera *Trirachodon* and *Diademodon* (Bonaparte, 1966b, 1967), but was later reinterpreted as a basal traversodontid (e.g., Hopson and Kitching, 1972; Barberena, 1974). *Pascualgnathus* is known from the holotype described by Bonaparte (1966b) and two additional undescribed specimens (see Abdala, 2000). This taxon exhibits a

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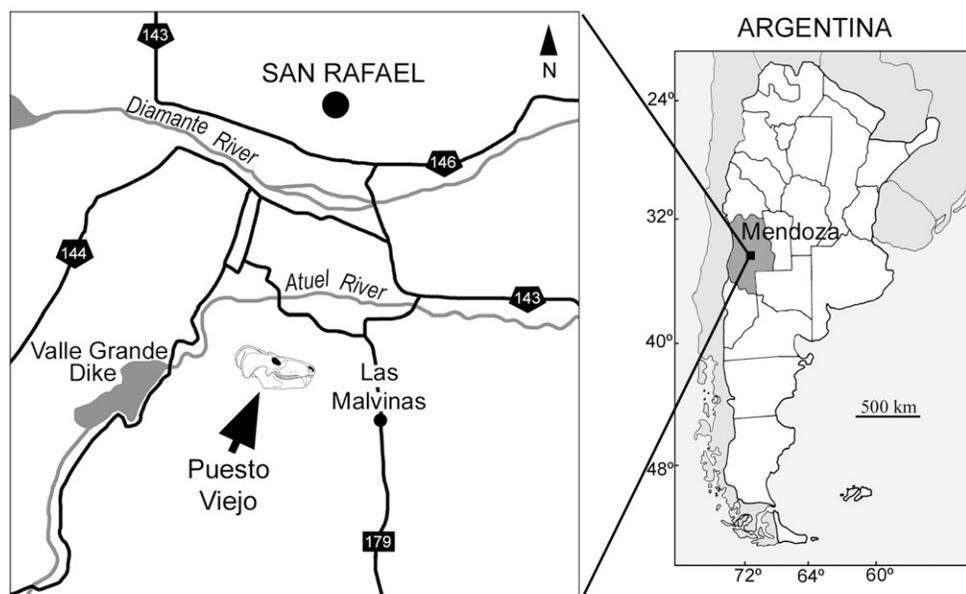


FIGURE 1. Map showing the locality where MHNSR–Pv 357 was discovered (arrow) in the Mendoza Province (highlighted in dark grey in the map of Argentina on the right).

mixture of primitive and derived traversodontid features in its skeleton, and displays traits that are reminiscent of trirachodontids (see discussion). A forthcoming contribution on this taxon is currently in preparation.

The only known South American specimen of *Cynognathus* includes a skull with lower jaws, right humerus, and one thoracic vertebra and was first described as the new species, *C. minor* (Bonaparte, 1969a). Further preparation of the specimen, comparison with South African specimens, and an analysis of individual variation in the extensive sample of South African *Cynognathus crateronotus* supports the conclusion (previously proposed by Hopson and Kitching, 1972), that the South American and South African taxa are the same species (Abdala, 1996). *Cynognathus* is a key carnivorous cynodont of the *Cynognathus* AZ of South Africa and represents one of the larger non-mammalian cynodonts. The postcanines of *Cynognathus* are sectorial, with a main cusp curved slightly backward, sometimes with serrated margins, and accessory mesial and distal cusps, lacking any cingulum. The skull of *Cynognathus* exhibits a long snout representing approximately half of the skull length, an extremely robust postorbital bar and zygomatic arch, and a reduced temporal opening that has a morphology significantly different from that known in other cynodonts (see Broili and Schröder, 1934; Brink, 1955b; Hopson and Barghusen, 1986; Hopson and Kitching, 2001). The presence of this taxon in the Puesto Viejo Group was crucial for the biostratigraphic correlation of this unit with African faunas (Bonaparte, 1969a).

Institutional Abbreviations—BP, Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa; GSN, Geological Survey, Windhoek, Namibia; MHNSR–Pv, Museo de Historia Natural de San Rafael, Mendoza, Argentina; UCMP, Museum of Paleontology, University of California, Berkeley.

Anatomical Abbreviations—c, canine; cr, canine root; d, dentary; eam, external auditory meatus; f, frontal; j, jugal; i, incisor; la, lachrymal; m, maxilla; mf, masseteric fossa; n, nasal; ob, orbit; pcf, paracanine fossa; pf, prefrontal; pl, palatine; pa, parietal; pm, premaxilla; po, postorbital; pt, postdentary trough; sm, septomaxilla; sq, squamosal; wf, wear facet.

SYSTEMATIC PALEONTOLOGY

THERAPSIDA Broom, 1905

CYNODONTIA Owen, 1861

EUCYNODONTIA Kemp, 1982

GOMPHODONTIA Seeley, 1894 (sensu Abdala and Ribeiro, 2003)

DIADEMODON TETRAGONUS Seeley, 1894
(Figs. 2–5)

Referred Specimen—MHNSR–Pv 357, skull fragments of a single individual including partial lateral right portion of the skull (snout and temporal regions), a fragment of the left snout with dentition, left zygomatic arch, small portion of skull roof with a fragment of the occipital plate and the lateral wall of the braincase, and fused dentaries with partial dentition lacking postdentary bones (Figs. 2–5).

Locality and Horizon—MHNSR–Pv 357 was found in the vicinity of the Puesto Viejo farm house, about 40 km southwest of San Rafael, Mendoza Province, Argentina (Fig. 1). The outcrops correspond to the recently named Río Seco de la Quebrada Formation, the upper unit of the Puesto Viejo Group (Stipanovic et al., 2007). Earliest Middle Triassic (González Díaz, 1964, 1966, 1972; Bonaparte, 1967).

DESCRIPTION

Skull—The skull is fragmented in four pieces (see measurements in the Table). The bones are riddled with fractures, making clear recognition of the sutures difficult. The estimated anteroposterior length of the skull is 280 mm. The two snout fragments have no clear contact between them. The left side includes the facial portion of the maxilla with teeth, whereas the right side includes the snout (i.e., a portion of the septomaxilla, part of the premaxilla and maxilla with teeth, and a portion of the palatine), part of the orbit, and the zygomatic arch. A relatively long and narrow snout with a prominent constriction posterior to the level of the canines can be inferred from the preserved fragments.

TABLE. Cranial measurement of *Diademodon tetragonus* MHNSR-Pv 357 (in mm)

Total skull length	290*
Snout length (from the anterior edge of the orbit to the tip of the snout)	142*
Greatest snout width	55*
Maximum height of the zygomatic arch	111
Maximum height of the jugal	87
Upper postcanines series length	99
Maximum dentary length preserved	215
Height of horizontal ramus at mid tooth row	41
Symphysial width at the level of canines	42
Symphysial width at the level of diastema between canine/postcanine	38
Lower teeth series length	148
Lower postcanine series length	107

*Estimated.

The right portion of the snout is poorly preserved (Fig. 2). The maxilla bears a canine alveolus at its anterior end. There are numerous small vascular foramina above and in front of the canine alveolus and two infraorbital foramina. The anterior foramen is placed above the socket of the first postcanine, while the posterior one is slightly larger and located above the seventh postcanine. The premaxilla-maxilla suture is posterior to the last incisor preserved, running anterodorsally up to the point where the maxilla contacts the ascending process of the septomaxilla. A relatively large vascular foramen opens on the premaxilla-maxilla suture, close to the alveolar level. A fragment of septomaxilla is preserved. In ventral view, the maxilla has a deep paracanine fossa, placed on the internal wall of the premaxilla-maxilla suture, a little anterior to the alveolus of the canine. Only a small portion of the palatine is preserved; the suture with the maxilla is only evident at the level of the posterior portion of the tooth row (Fig. 2). There is a groove parallel to the posterior portion and on the lingual side of the tooth row. The palatine forms the medial wall of the groove parallel to the posterior portion of the tooth row. On this groove two large foramina open anteriorly. Parallel to the tooth row there is a longitudinal broken ridge that indicates the lateral base of the secondary osseous palate. Medially, there is a concave medial projection of the palatine that corresponds to the wall of the choanal row (Fig. 2).

The lateral suture between jugal and maxilla is not clear. In ventral view, the jugal contacts the maxilla and the palatine. The orbit is strongly deformed by compression; the jugal forms the ventral and posterior borders whereas the postorbital forms the dorsal border. The anterodorsal border is broken. Below the orbit there is a significant shelf on the jugal that runs almost horizontally, and below it at least two foramina that open anteriorly (Fig. 2). Medial to this shelf, the jugal exhibits a sharp crest that forms part of the posteroventral rim of the orbit. The ventral edge of the jugal below the orbit is broken, exhibiting only the eroded base of the suborbital process.

The left maxilla preserves a small portion of the palatal process at the level of the canine root that forms the posterior edge of the paracanine fossa (Fig. 3). This maxillary fragment has a more substantial lateral concave surface which appears to be less affected by compression than the surface on the right side.

The right zygomatic arch is articulated with the remaining right portion of the skull (Fig. 2), whereas the left one is isolated. The right arch includes part of the postorbital, jugal and squamosal (Figs. 2 and 4). The jugal is massive and tall, being the dominant bone (about 90%) of the zygomatic arch and showing a subtle ridge on the ventral edge. This bone extends from the edge of the orbit to reach the posteroventral edge of the zygomatic arch, extending beyond the level of the craniomandibular joint. The ventral edge descends abruptly forming a significant

posteroventral projection of the zygomatic arch. In lateral view the squamosal forms only the posterodorsal border of the zygomatic arch, and has a short anterior process that forms a small portion of the zygomatic arch depth and wedges between the dorsal portions of the jugal (Figs. 2 and 4). Medially, the squamosal is broken, having no apparent contact with the area of the craniomandibular joint of the skull. The beginning of a prominent external auditory meatus is evidenced in the posterodorsal margin of the squamosal (Fig. 4).

The preserved portion of skull roof includes nasals, left lachrymal, frontals, prefrontals, and parietals (Fig. 4). All these bones are incomplete. The nasal is slightly convex dorsally, showing small, shallow grooves. Posteriorly it makes contact with the frontal through an interdigitated, irregular suture, laterally with the lachrymal, and posterolaterally with the prefrontal (Fig. 4). The suture between nasals forms a median elevation that is continued backward by the median suture between the frontals. Only small fragments of lachrymal and prefrontal are preserved. The frontals are anteroposteriorly elongated, with an acute posterior process that enters between the parietals. There is no evidence of a pineal foramen. The parietals overlap the frontals forming two elevated rims that converge posteriorly to form the parietal crest. Most of this crest is broken off and posteriorly the lambdoidal crests (incomplete on both sides) diverge to form an angle of less than 90° (Fig. 4). In Figure 4, an estimation of the placement of the right zygomatic arch in relation to the skull roof is shown, suggesting the presence of a relatively large and wide temporal region. The skull portion which includes the occipital plate, the lateral wall of the braincase, and the basicranium is poorly preserved and does not provide additional information.

Lower Jaw—Only the dentaries are preserved. These are massive and tall in relation to the height of the postcanine crowns (see measurements in the Table). The lower edge of the lower jaw is straight, and the symphyseal region curves gently. In contrast, the alveolar margin shows a stronger curvature (Fig. 5). In lateral view, the masseteric fossa extends well forward, until the level of the sixth postcanine. The fused symphysis is anteroposteriorly elongated, reaching posteriorly the level of the first postcanines (Fig. 5). A transverse constriction is present at the symphysis, followed by the divergence of the mandibular rami. The coronoid processes and the angular processes of the dentaries are not preserved. In medial view, a relatively reduced postdentary trough and the meckelian groove is observed. No postdentary bones are preserved.

Upper Dentition—The upper dental formula is ?I/1C/13-14PC. Details of the tooth crowns of most teeth are not available, as several teeth are broken off while others are extensively worn. There is a large diastema between the incisors and the canine, but not as large as the diastema between the canine and first postcanine.

Only the last right (possibly fourth) incisor is preserved, with the crown broken. It is drop-shaped in cross section.

The upper canine is prominent, slightly curved, transversely narrowed, and oval in cross section (Fig. 3). The tip of the crown is broken, and on the mesiolingual and distal borders there is a worn vertical carina. In the most basal section of the mesiolingual carina there are very shallow serrations. The crown is covered with an irregular layer of enamel. The base of the right canine is widely exposed out of the alveolus, increasing in size upward and ending in a convex base. The left canine preserves only its robust root.

The postcanine tooth rows diverge posteriorly and end in advance of the anterior border of the subtemporal fenestra (Fig. 2). Three types of postcanines are present in the rows: anterior conical teeth, gomphodont teeth in the middle, and sectorial teeth at the back. The right and left postcanine series exhibit a few differences and they are therefore described separately.

On the right side, postcanine 1 is missing and its alveolus seems to be filled by bone. Crowns of postcanines 2 to 4 are missing but their roots indicate that they are smaller than the following teeth and have a circular cross section. These postca-

nines constitute the simple conical teeth. The fifth postcanine is broken but its cross section is slightly oval, and remarkably larger than the preceding tooth. The sixth tooth is subrectangular in shape and transversely widened. The crown of this tooth is

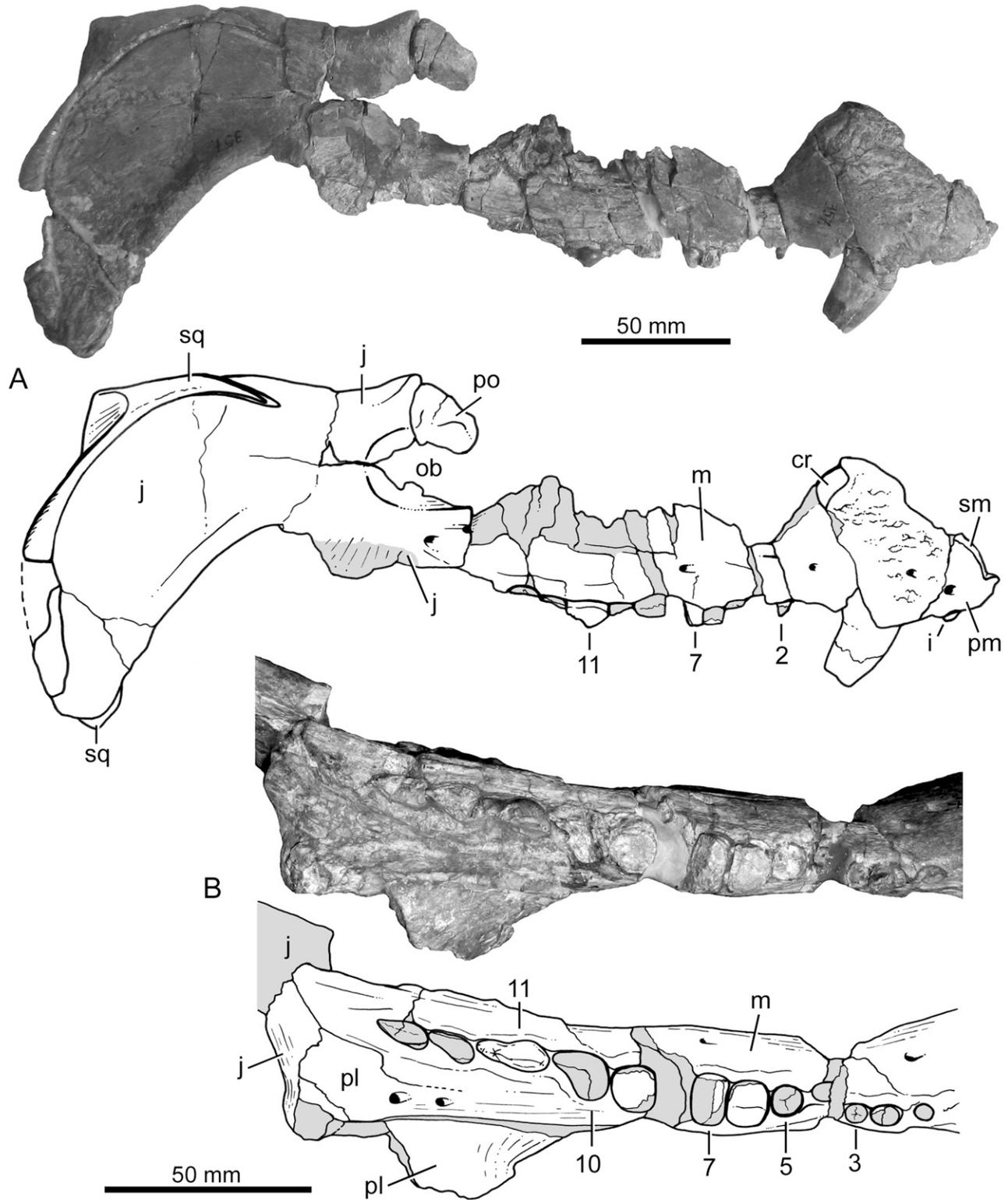


FIGURE 2. *Diademodon tetragonus* MHNSR-Pv 357 from the Río Seco de la Quebrada Formation (Puesto Viejo Group; Argentina). **A**, lateral view of the right side of the skull; **B**, detail of the postcanine tooth row in ventral view. Grey areas indicate broken surfaces. Arabic numbers refer to the positions of the postcanines.

fully worn, with a slightly concave wear facet on the labial side and an oblique straight facet on the lingual side, slightly narrower than the labial. Postcanines 7 and 9 are broken off, whereas the eighth tooth and its alveolus are entirely missing. The transversely wide crowns of postcanine 6 to 9 increase slightly in size posteriorly. The cross section of postcanine 7 is slightly

broader transversely and shorter mesiodistally than postcanines 6 and 9. Postcanine 10 is also broken but besides being transversely widened in section as in the previous gomphodont teeth, it presents a posterior projection on its distolabial corner. This is a transitional tooth with elements between gomphodont and sectorial morphologies (i.e., 'intermediate gomphodont' tooth

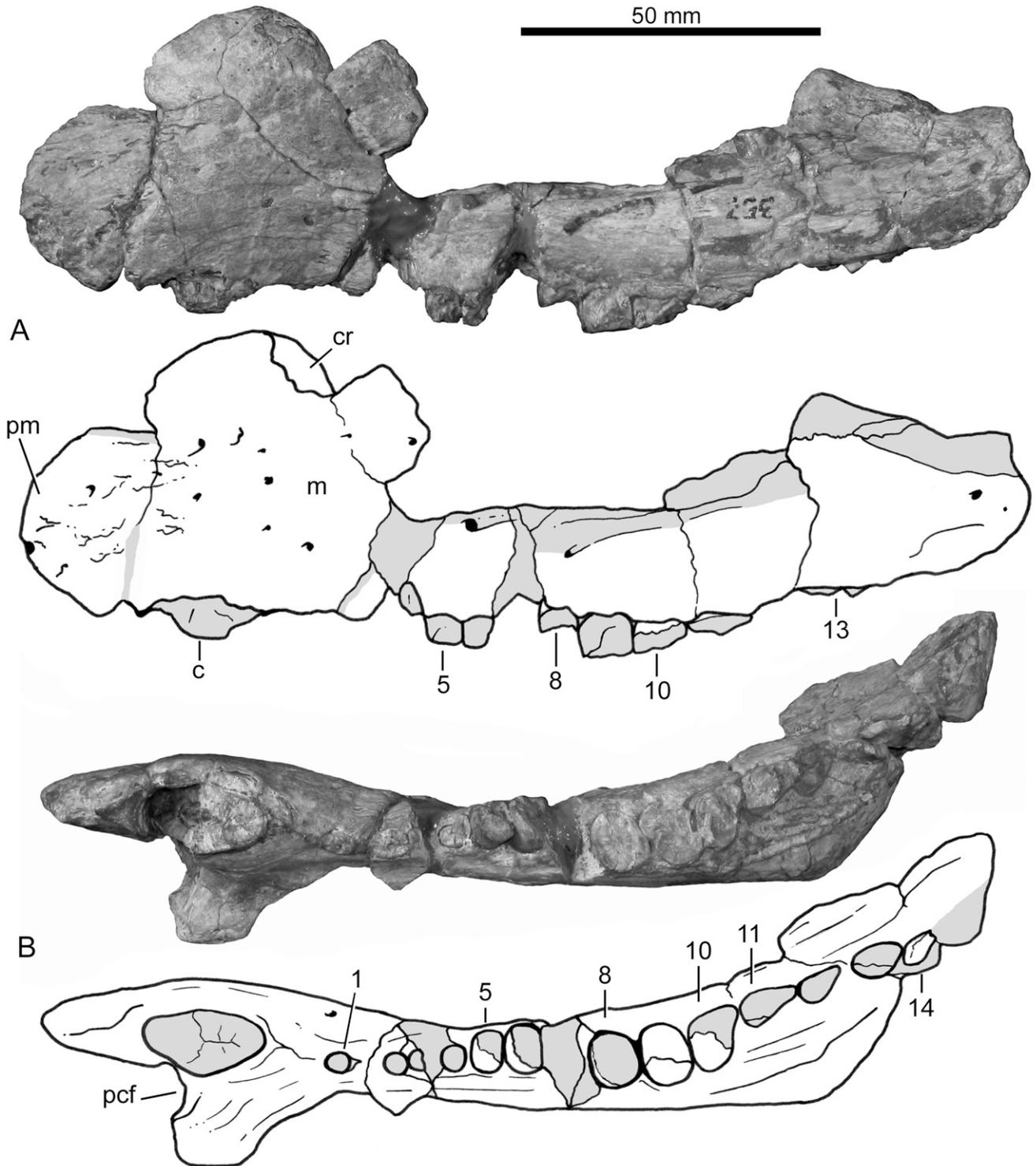


FIGURE 3. *Diademodon tetragonus* MHNSR-Pv 357 from the Río Seco de la Quebrada Formation (Puesto Viejo Group; Argentina). Left maxilla in lateral (A) and ventral (B) views. Grey areas indicate broken surfaces. Arabic numbers refer to the positions of the postcanines.

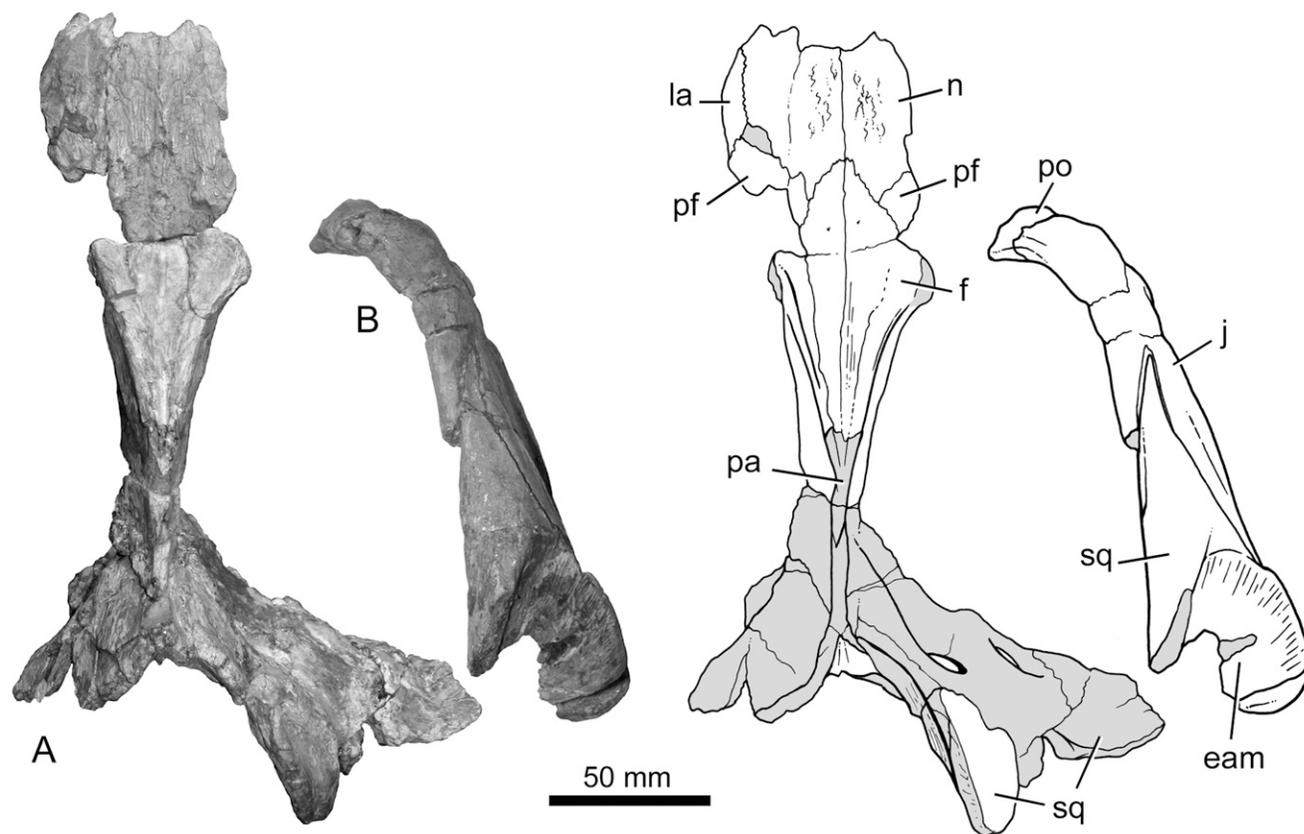


FIGURE 4. *Diademodon tetragonus* MHNSR-Pv 357 from the Río Seco de la Quebrada Formation (Puesto Viejo Group; Argentina). **A**, portion of the skull roof and occiput in dorsal view; **B**, detail of the zygoma in dorsal view, in its expected natural placement with regard to the skull roof. Grey areas indicate broken surfaces.

sensu Fourie, 1963). Postcanine 11 is transversely narrow with a main prominent cusp occupying most of the crown (Fig. 2). The main cusp has a strongly convex labial surface and a straight to slightly concave lingual surface, with a poorly preserved faint cingulum at the base. On the mesiolingual edge of the main cusp there is a small cusp and on the distal edge there are two small cusps with serrated carinae. Postcanines 12 and 13 are broken and their cross sections are drop-shaped, indicating they were also sectorial teeth.

Differing from the right side, the left postcanine 1 has preserved its root within the alveolus (Fig. 3), and the partially preserved postcanine 5, that shows an oblique lingual wear facet, is subrectangular in cross section. Finally, a last sectorial postcanine 14 is erupting, showing a curved backward main cusp, and mesial and distal cutting edges with tiny cusps. The concave lingual side presents a mesial and a distal groove at the sides of the tip of the main cusp. The size of the crown of this last postcanine is slightly smaller than the anterior tooth. In summary, MHNSR-Pv 357 has four conical, six gomphodont, and three/four sectorial upper postcanines (Figs. 2 and 3).

Lower Dentition—The lower dental formula is 3i/1c/13pc (Fig. 5). The incisors are subconical with their tip located on the lingual side, and slightly procumbent. The second and third incisors are slightly smaller than the first. They exhibit wear on their labial surfaces. There is no diastema between the last incisor and the canine. The canine is stout, transversely narrow, and slightly curved distally. The tip of the left canine is broken and shows extensive wear on its mesiolabial surface that reaches the alveolar border. The right canine is complete, with large mesiolingual and small mesiolabial wear facets. The internal facet is more

likely the product of contact with the wall of the upper paracanine fossa, whereas the external facet was likely produced by the contact between upper and lower canines. Notably, the left canine has more extensive wear on the labial side than the right canine. Between the lower canine and the first postcanine there is a relatively large diastema.

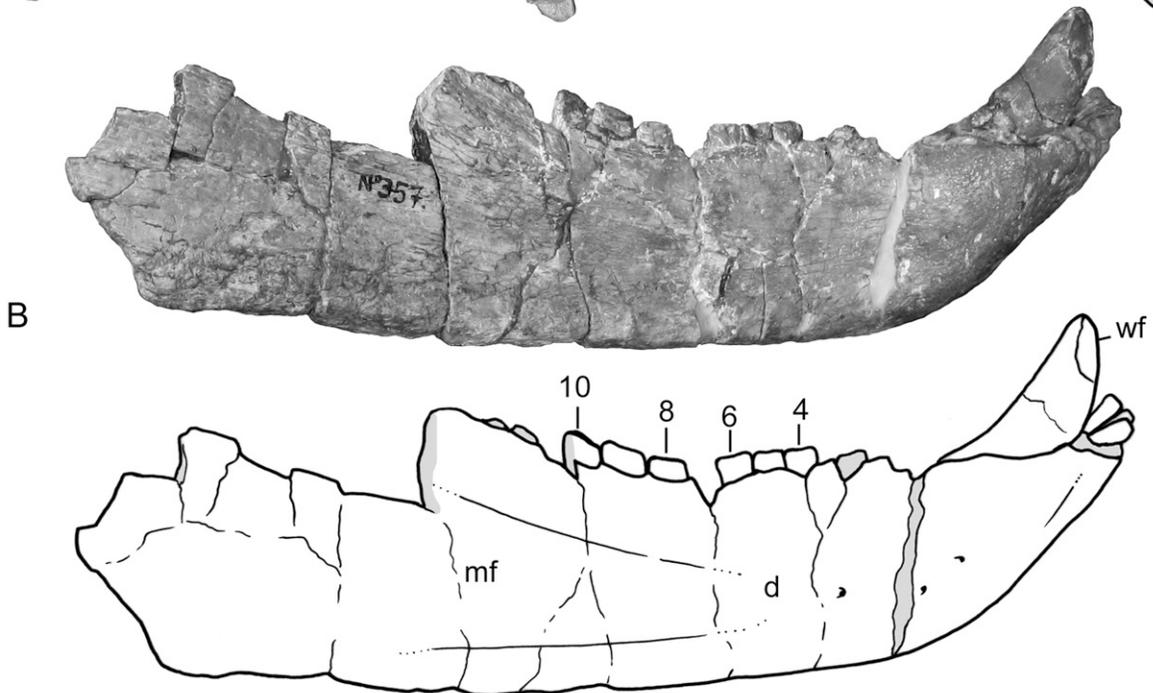
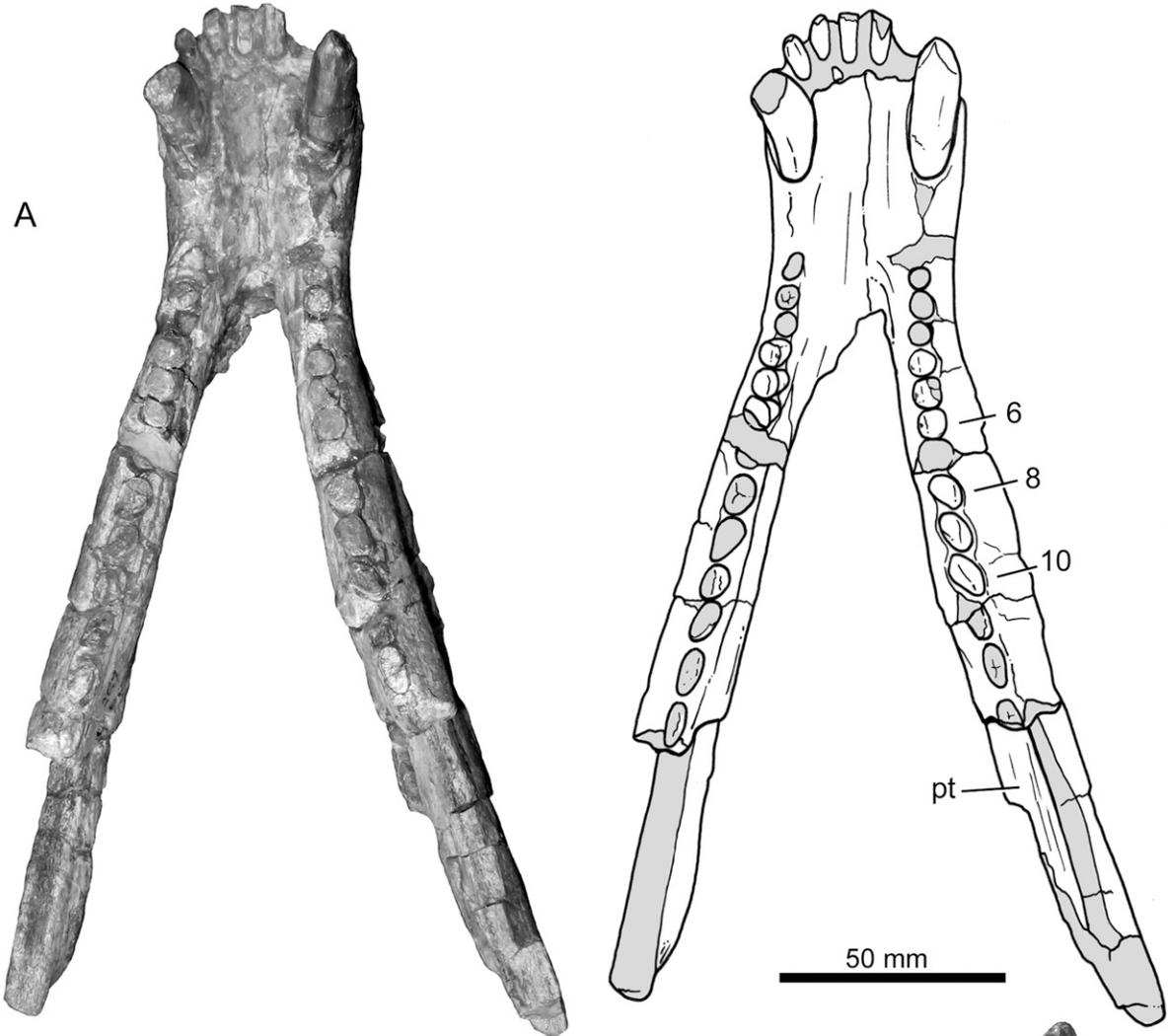
Postcanines 1 to 7 are circular in cross section, increasing their size slightly toward the back. Postcanines 9 to 10 are slightly oval in cross section, while postcanines 11 to 13 are transversely narrow. On the right side seven postcanines (1 to 3, 7, and 11 to 13) are broken. The remaining teeth are badly worn. Postcanine 4 has oblique surfaces of wear on its lingual and labial sides, whereas postcanines 5, 6 and 8 have the crowns worn to the base. Postcanine 9 has oblique wear facets on the lingual and labial sides and postcanine 10 only on its lingual side.

Due to the poor preservation of the crown morphology it is difficult to establish the place of differentiation between conical, gomphodont and sectorial teeth in the lower dental series. There is a gradual increase in size of the gomphodont teeth posteriorly. Postcanine 9 is the last gomphodont tooth (more likely the transitional one) and postcanines 10 to 13 are considered sectorial teeth. On the left lower tooth row the same pattern is observed (Fig. 5).

DISCUSSION AND CONCLUSION

Diademodontid taxonomy: the case of Titanogomphodon crassus

There are different taxonomic ideas resulting from the latest revisions of diademodontid cynodonts. We agree with the synonymy of the majority of the taxa previously recognized *Diademodon*



tetragonus, as expressed by Grine and colleagues (Grine, 1978; Grine and Hahn, 1978; Grine et al., 1978; Bradu and Grine, 1979). But we would like to address the issue of the taxonomic identity of *Titanogomphodon crassus* from the Omingonde Formation of Namibia. The largest basal skull size found in complete skulls among the extensive sample of hundreds of specimens of *Diademodon* recovered in the Karoo Basin is between 287 and 290 mm (BP/1/2522 and UCMP 42445, respectively; Bradu and Grine, 1979; Abdala, pers. obs.) In the preserved skull of *T. crassus* (GSN R323), from the occipital condyle to approximately the posterior portion of the snout, the measurement is 270 mm long. A reconstruction of the complete skull results in an estimated length of approximately 400 mm. Therefore, there exists a size gap of around 100 mm between the largest specimens of *D. tetragonus* and the holotype of *T. crassus*. The only specimen from the extensive sample of diademodontids from the Karoo that can partially fill this gap is BP/1/3757, represented by a snout of 165 mm in length (Brink, 1963b:99), still making it smaller than *T. crassus* with an estimated snout length of 190 mm. Besides the limited evidence of specimens of large size in the Karoo, there are some features of *T. crassus* that are certainly not present in known specimens of *D. tetragonus*. These include the presence of a well-developed boss on the postorbital bar (Brink, 1988), the basicranial girder which is extremely wide and short, and the subtemporal fossa which is substantially smaller than in *D. tetragonus* (Abdala, pers. obs.). All this evidence suggests that *T. crassus* should be considered a valid taxon within Diademodontidae.

Taxonomic identity of MHNSR–Pv 357

There are several features that indicate clearly that specimen MHNSR–Pv 357 is a diademodontid cynodont. Among these are: a) overall skull shape (e.g., narrow and elongated snout with a concave outline in dorsal view); b) morphology of the zygoma with the jugal forming most of the dorsoventral depth, with a well excavated external auditory meatus; and c) heterodonty of postcanines including circular outlined anterior teeth, ovoid gomphodont teeth in the middle, and sectorial teeth at the end of the series. The estimated skull length of MHNSR–Pv 357 is approximately 290 mm with a snout length of 142 mm (Table). These measurements fit well in the size range of the largest specimens of *Diademodon* recovered in the Karoo Basin. In addition to its size, there is no evidence in MHNSR–Pv 357 of the presence of a boss on the postorbital bar, and the inferred subtemporal fossa in the South American specimen seems to be larger than that observed in *Titanogomphodon* (Abdala, pers. obs.). Considering these proportional and morphological characters, we assign MHNSR–Pv 357 to *Diademodon tetragonus*.

Dental evidence from the South American specimen—including an anterior alveolus plugged with bone (right PC1), strongly worn gomphodont teeth, lack of wear in the first upper sectorial postcanines (PC11), and the presence of an additional erupting sectorial tooth at the back of the tooth row—fit the tooth replacement pattern interpreted for *Diademodon* (e.g., Hopson, 1971; Grine, 1977). Furthermore, the number of each tooth class in the upper and lower rows coincides with the pattern present in the recognized growth series of *Diademodon*. Unfortunately details of the postcanine crowns and of portions of the skull remain uncertain in the Argentinean specimen. Additional material of Argentinean and Namibian diademodontids is needed along with a cautious evaluation of several cranial features in diademodontids to improve our taxonomic understanding of this family. With these caveats in mind, MHNSR–Pv 357 is consid-

ered the first record of the gomphodont cynodont *Diademodon tetragonus* in South America.

Peculiarly, cynodonts present many shared genera between South American and African Triassic terrestrial faunas. *Diademodon tetragonus* is the fourth cynodont found to be common to these continents. The remaining three are *Cynognathus crateronotus* from the same locality of *D. tetragonus* (Bonaparte, 1969a; Abdala, 1996), the traversodontid *Luangwa*, recently documented in southern Brazil (Abdala and Teixeira, 2004), and the Ladinian-Carnian probainognathian *Chiniquodon*, now reported in a Middle Triassic Namibian fauna (Abdala, pers. ob.).

Biostratigraphic Implications

Two tetrapod-bearing levels were recognized in the Puesto Viejo Group and represent the Puestoviejan Local Age (Bonaparte, 1982). The lower unit, recently renamed the Quebrada de los Fósiles Formation (Stipanovic et al., 2007), and referred to as the Agua de Los Burros Local Fauna, has produced large and medium-sized dicynodonts and indeterminate archosaurs (Bonaparte, 1981, 1982), and was correlated to the *Lystrosaurus* AZ of South Africa (Bonaparte, 1981). The upper unit, the Río Seco de la Quebrada Formation (Stipanovic et al., 2007), traditionally known as the Puesto Viejo Local Fauna, has yielded the medium-sized kannemeyeriid dicynodonts *Kannemeyeria argentinensis* and *Vinceria* sp. (but see Renaut and Hancox, 2001 for a different interpretation of *K. argentinensis*) and the cynodonts *Pascualgnathus polanskii* and *Cynognathus crateronotus* (Bonaparte, 1966a, b, 1969a; Abdala, 1996). The Río Seco de la Quebrada Formation was correlated to the *Cynognathus* AZ of South Africa (Bonaparte, 1982) and suggested an Olenekian (e.g., Bonaparte, 1966b, 1973, 1982; Lucas, 1998) or Anisian age (Bonaparte, 1966c, 1967). The Puesto Viejo Local Fauna has a stronger resemblance to African assemblages such as the Burgersdorp Formation of the Karoo Basin and the Omingonde Formation of Namibia (Kitching, 1995; Smith and Swart, 2002). These similarities include the occurrence of *Cynognathus crateronotus* (Abdala, 1996) and *Diademodon tetragonus*, the two most common cynodonts from the *Cynognathus* AZ of South Africa (Kitching, 1995).

In the last decade, the *Cynognathus* AZ has been informally divided into three subzones based mainly on its temnospondyl amphibian taxa (Hancox et al., 1995; Shishkin et al., 1995) and also supported by other tetrapod components (Abdala et al., 2005). The oldest subzone A was dated as Upper Olenekian with *Cynognathus*, the trirachodontid *Langbergia*, and a recently described taxon presenting allotherian-like postcanines as cynodont representatives (Abdala et al., 2007b). The subzone B (or the classical *Cynognathus* AZ) is considered Lower Anisian, and besides *Cynognathus* and *Diademodon*, it also presents the trirachodontid *Trirachodon* and the sectorial toothed *Lumkuia* and *Bolotridon* (Kitching, 1995; Hopson and Kitching, 2001). The younger subzone C is interpreted as Upper Anisian (Hancox, 2000; Hancox and Rubidge, 2001; Damiani and Hancox, 2003; Abdala et al., 2005) and both *Cynognathus* and *Diademodon* are also present here, but the most common cynodont is the trirachodontid *Cricodon* (Abdala et al., 2005). A faunal comparison suggests a possible temporal correlation of the Río Seco de la Quebrada Formation (the upper unit of the Puesto Viejo Group) with subzones B and C of the *Cynognathus* AZ, where both *Cynognathus* and *Diademodon* are known. The record of traversodontids in the Puesto Viejo fauna represents an important difference between South American and South African faunas. The absence of this group in the subzones B and C of

the *Cynognathus* AZ is unexpected. Even when the fossil record of the Subzone C is scanty, that from the widespread Subzone B is indeed rich, representing one of the most diverse Anisian terrestrial faunas known so far. In addition, traversodontid cynodonts are also known in apparently contemporaneous faunas from East Africa and Namibia (Crompton, 1955; Brink, 1963; Kemp, 1980). Taking all these points into account it seems possible to consider the age of the upper fauna of the Puesto Viejo Group (i.e. Río Seco de la Quebrada Formation) as Anisian, with the record of the traversodontid cynodont in the fauna suggesting a Late Anisian age. This age correlation coincides, at least in part, with previous interpretations (e.g. Bonaparte, 1966c), yet has enabled a refinement of the biostratigraphic scheme of Gondwana.

Two noteworthy differences between gomphodont cynodonts from the Río Seco de la Quebrada Formation and the subzones B and C of the *Cynognathus* AZ of South Africa should be highlighted. First, the Río Seco de la Quebrada Formation contains traversodontids, whereas these are absent from the South African faunas. Therefore the occurrence of the basal traversodontid *Pascualgnathus* along with typical African cynodonts is a singular feature of the Argentinean record. Second, trirachodontid gomphodonts are hitherto unknown in South America whereas this family is well represented in the *Cynognathus* AZ of Africa and also recognized in other regions such as India (Bandyopadhyay and Sengupta, 1999, 2006), China (Sun, 1988), and possibly Russia (Tatarinov, 2002). These differences were initially less apparent because *Pascualgnathus* was originally considered a diademodontid closely related to *Trirachodon* (Bonaparte, 1966b, 1967). The ovoid-ellipsoid upper postcanines, with the transverse crest across the centre of the crown in *Pascualgnathus* are indeed reminiscent of trirachodontid teeth. Unfortunately the available specimens of *Pascualgnathus* do not have well preserved postcanine crowns, especially in the lower teeth, and further knowledge of their dentition is pending. The presence of overlapping processes in the ribs—which are also known in diademodontids and trirachodontids—can be added to the postcanine similarities. *Pascualgnathus* has thus been interpreted as a basal traversodontid (Hopson and Kitching, 1972; Barberena, 1974), a placement confirmed through cladistic analysis (Abdala and Ribeiro, 2003).

Another South American faunal association often interpreted as being contemporaneous with the Río Seco de la Quebrada Formation (e.g. Bonaparte, 1978, 1982) is the Río Mendoza Local Fauna (Cerro de las Cabras Formation) located about 58 km southwest of Mendoza city. There are some discrepancies about the exact stratigraphic provenance (Cerro de las Cabras versus Río Mendoza formations) of the fossils of this fauna (see Bonaparte, 2002 and Zavattieri and Arcucci, 2007 for a recent summary). In addition, there are disagreements concerning the age of these levels, with plant macrofossils indicating an Early Triassic to early Middle Triassic age (Morel et al., 2003) and palynology indicating a late Middle Triassic to lowest Late Triassic age (Zavattieri and Arcucci, 2007).

The Río Mendoza local fauna from Cerro Bayo of Potrerillos includes the dicynodont *Vinceria andina* and the cynodonts *Andescynodon mendozensis*, *Rusconiodon mignonei* and *Cromptodon mamiferoides* (Bonaparte, 1969b, 1972; Goñi and Goin, 1987, 1988; Goñi and Abdala, 1988) and is generally correlated to the upper unit of the Puesto Viejo Group (e.g., Bonaparte, 1982; sensu Stipanovic et al., 2007). The dicynodont *Vinceria* is the only common to these faunas (e.g., Bonaparte, 1982; Marsicano et al., 2001). In addition, both faunas contain traversodontid cynodonts, although the taxa represented in them are different. Recent cladistic analyses show different placements for *Andescynodon* and *Pascualgnathus*. In Abdala and Ribeiro (2003) they formed a monophyletic group in a basal polytomy of traversodontids. Increasing taxa and characters by Abdala et al. (2006)

produced hypotheses in which *Pascualgnathus* represented a more basal taxon than *Andescynodon* among traversodontids. In both phylogenies the traversodontids from these faunas are basal to those from the Ischigualasto-Villa Union Basin (i.e., *Massetognathus* from the Chañares Formation). Based on the phylogenetic relationships of the traversodontids in combination with the absence of the genera *Cynognathus* and *Diademodon* in Cerro de las Cabras Formation, the cynodont assemblage from the Cerro Bayo of Potrerillos may prove to be somewhat younger than the Río Seco de la Quebrada Formation (as suggested by Bonaparte, 1973:100; sensu Stipanovic et al., 2007), possibly dating at the latest Anisian, but indeed older than the Ladinian Chañares fauna (Romer, 1972; Bonaparte, 2000; Rogers et al., 2001). Both Middle Triassic faunal associations from Mendoza Province are still poorly studied when compared with other Triassic regions of South America. We are confident that future fieldwork in the Puesto Viejo Group and Cerro de las Cabras Formation will provide a better understanding of the age and composition of the South American Early-Middle Triassic span.

ACKNOWLEDGMENTS

We thank J. F. Bonaparte for providing useful information on the Puesto Viejo Group. For access to collections we thank G. Schneider, H. Mocke (GSN), B. Zipfel (BP), and P. Holroyd (UCMP). FA research was funded by PAST (Palaeontological Scientific Trust, Johannesburg) and the Oppenheimer Foundation, Johannesburg. We thank A. Forasiepi for comments on the ms and C. Kemp provided language and editorial assistance. J. Fröbisch, an anonymous reviewer, and the editor C. Sidor made valuable comments that greatly improved the paper.

LITERATURE CITED

- Abdala, F. 1996. Redescripción del cráneo y reconsideración de la validez de *Cynognathus minor* (Eucynodontia-Cynognathidae) del Triásico Inferior de Mendoza. *Ameghiniana* 33:115–126.
- Abdala, F. 1999. Elementos postcraneanos de *Cynognathus* (Synapsida-Cynodontia) del Triásico Inferior de la Provincia de Mendoza, Argentina. Consideraciones sobre la morfología del húmero en cinodontes. *Revista Española de Paleontología* 14:13–24.
- Abdala, F. 2000. Catalogue of non-mammalian cynodonts in the Vertebrate Paleontology Collection of the Instituto Miguel Lillo, Universidad Nacional de Tucumán, with comments on species. *Ameghiniana* 37:463–475.
- Abdala, F., and A. M. Ribeiro. 2003. A new traversodontid cynodont from the Santa Maria Formation (Ladinian–Carnian) of southern Brazil, with a phylogenetic analysis of Gondwanan traversodontids. *Zoological Journal of the Linnean Society* 139:529–545.
- Abdala, F., and A. M. Sa-Teixeira. 2004. A traversodontid cynodont of African affinity in the South American Triassic. *Palaeontologia Africana* 40:11–22.
- Abdala, F., P. J. Hancox, and J. Neveling. 2005. Cynodonts from the uppermost Burgersdorp Formation, South Africa, and their bearing on the biostratigraphy and correlation of the Triassic *Cynognathus* Assemblage Zone. *Journal of Vertebrate Paleontology* 25:192–199.
- Abdala, F., J. Neveling, and J. Welman. 2006. A new trirachodontid cynodont from the lower levels of the Burgersdorp Formation (Lower Triassic) of the Beaufort Group, South Africa and the cladistic relationships of Gondwanan gomphodonts. *Zoological Journal of the Linnean Society* 147:383–413.
- Abdala, F., R. Damiani, A. Yates, and J. Neveling. 2007a. A non-mammaliaform cynodont from the Upper Triassic of South Africa: a therapsid Lazarus taxon? *Palaeontologia Africana* 42:17–23.
- Abdala, F., H. Mocke, and P. J. Hancox. 2007b. Lower Triassic postcanine teeth with allotherian-like crowns. *South African Journal of Science* 103:245–247.
- Bandyopadhyay, S., and D. P. Sengupta. 1999. Middle Triassic vertebrates of India. *Journal of African Earth Sciences* 29:233–241.
- Bandyopadhyay, S., and D. P. Sengupta. 2006. Vertebral faunal turnover during the Triassic–Jurassic transition: and Indian scenario; pp. 77–85 in J. D. Harris, S. G. Lucas, J. A. Spielman, M. G. Lockley,

- A. R. C. Milner, and J. I. Kirkland (eds.), The Triassic-Jurassic terrestrial transition. New Mexico Museum of Natural History and Science, Bulletin 37.
- Barberena, M. C. 1974. Contribuição ao conhecimento dos cynodontes gonfodontes (Cynodontia-Tritylodontoidea) do Brasil. Ministério de Educação e Cultura, Universidade Federal do Rio Grande do Sul, 194 pp.
- Bonaparte, J. F. 1966a. Sobre nuevos terápsidos triásicos hallados en el centro de la Provincia de Mendoza, (Therapsida, Dicyodontia y Cynodontia). *Acta Geológica Lilloana* 8:95–100.
- Bonaparte, J. F. 1966b. Una nueva "fauna" Triásica de Argentina. (Therapsida: Cynodontia - Dicyodontia). Consideraciones filogenéticas y paleobiogeográficas. *Ameghiniana* 4:243–296.
- Bonaparte, J. F. 1966c. Cronología de algunas formaciones Triásicas Argentinas basada en restos de tetrápodos. *Revista de la Asociación Geológica Argentina* 21:20–38.
- Bonaparte, J. F. 1967. New vertebrate evidence for a southern transatlantic connection during the Lower or Middle Triassic. *Palaeontology* 10:554–563.
- Bonaparte, J. F. 1969a. *Cynognathus minor* n. sp. (Therapsida-Cynodontia). Nueva evidencia de vinculación faunística Afro-Sudamericana a principios del Triásico. *Gondwana Stratigraphy, I.U.G.S., Coloquio Mar del Plata 1967*:273–281.
- Bonaparte, J. F. 1969b. Dos nuevas "faunas" de reptiles triásicos de Argentina. *Gondwana Stratigraphy, I.U.G.S., Coloquio Mar del Plata 1967*:283–302.
- Bonaparte, J. F. 1971. Los tetrápodos del sector superior de la Formación Los Colorados, La Rioja, Argentina (Triásico Superior). *Opera Lilloana* 22:1–183.
- Bonaparte, J. F. 1972. *Cromptodon mamiferooides*, Galesauridae de la Formación Río Mendoza, Mendoza, Argentina (Therapsida-Cynodontia). *Ameghiniana* 9:343–353.
- Bonaparte, J. F. 1973. Edades/Reptil para el Triásico de Argentina y Brasil. *Actas V Congreso Geológico Argentino* 3:93–129.
- Bonaparte, J. F. 1978. El Mesozoico de América del Sur y sus tetrápodos. *Opera Lilloana* 26:1–596.
- Bonaparte, J. F. 1981. Notas sobre una nueva fauna del Triásico Inferior del Sur de Mendoza, Argentina, correspondiente a la Zona de *Lystrosaurus* (Dicyodontia-Proterosuchia). Segundo Congreso Latinoamericano de Paleontología, *Annales* 1:227–288.
- Bonaparte, J. F. 1982. Faunal replacement in the Triassic of South America. *Journal of Vertebrate Paleontology* 2:362–371.
- Bonaparte, J. F. 2000. Comentarios críticos sobre el Triásico Inferior de Puesto Viejo y Potrerillos. *Boletín de la Academia Nacional de Ciencias, Córdoba*, 64:147–152.
- Bonaparte, J. F. 2002. Río Mendoza Fauna Local; pp. 250–251 in P. N. Stipanovic and C. A. Marsicano (eds.), *Léxico Estratigráfico de la Argentina. Volumen VIII. Triásico*. Asociación Geológica Argentina, Serie B (Didáctica y Complementaria) 26.
- Borrello, A. V. 1962. Fanglomerado Río Mendoza (Triásico, Provincia de Mendoza). Comisión Investigaciones Científicas de la Provincia de Buenos Aires, *Notas* 1:3–9.
- Botha, J., and A. Chinsamy. 2000. Growth patterns deduced from the bone histology of the cynodonts *Diademodon* and *Cynognathus*. *Journal of Vertebrate Paleontology* 20:705–711.
- Bradu, D., and F. E. Grine. 1979. Multivariate analysis of *Diademodon* crania from South Africa and Zambia. *South African Journal of Science* 75:441–448.
- Brink, A. S. 1955a. A study on the skeleton of *Diademodon*. *Palaeontologia Africana* 3:3–39.
- Brink, A. S. 1955b. On the Cynognathidae. *Palaeontologia Africana* 3:47–55.
- Brink, A. S. 1956. Speculations on some advanced mammalian characteristics in the higher mammal-like reptiles. *Palaeontologia Africana* 4:77–96.
- Brink, A. S. 1963a. Two cynodonts from the Ntawere Formation in the Luangwa valley of Northern Rhodesia. *Palaeontologia Africana* 8:79–96.
- Brink, A. S. 1963b. Notes on some *Diademodon* specimens in the collection of the Bernard Price Institute. *Palaeontologia Africana* 8:97–111.
- Brink, A. S. 1979. Genera and species of the Diademodontinae. *Bulletin of the Geological Survey of South Africa* 65:1–50.
- Brink, A. S. 1988. Illustrated bibliographical catalogue of the Synapsida. Part II. Department of Mineral and Energy Affairs, Geological Survey, South Africa, 26 pp.
- Broili, F., and J. Schröder. 1934. Zur osteologie des kopfes von *Cynognathus*. *Sitzungsberichte der Bayerischen Akademie der Wissenschaften* 1934:95–128.
- Broili, F., and J. Schröder. 1935. Beobachtungen and Wirbeltieren der Karooformation. IX Über den Schädel von *Gomphognathus* Seeley. *Sitzungsberichte der Bayer, Akademie der Wissenschaften* 1935:115–182.
- Broom, R. 1905. On the use of the term Anomodontia. *Records of the Albany Museum* 1:266–269.
- Broom, R. 1911. On the structure of the skull in cynodont reptiles. *Proceedings of the Zoological Society of London* 1911:893–925.
- Broom, R. 1919. On the genus *Gomphognathus* and its allies. *Records of the Albany Museum* 3:223–232.
- Crompton, A. W. 1955. On some Triassic cynodont from Tanganyika. *Proceeding of the Zoological Society of London* 125:617–669.
- Crompton, A. W. 1972. Postcanine occlusion in cynodonts and tritylodonts. *Bulletin of the British Museum (Natural History), Geology* 21:29–71.
- Damiani, R., and P. J. Hancox. 2003. New mastodontosaurid temnospondyls from the Cynognathus Assemblage Zone (Upper Beaufort Group; Karoo Basin) of South Africa. *Journal of Vertebrate Paleontology* 23:54–66.
- Fourie, S. 1963. Tooth replacement in the gomphodont cynodont, *Diademodon*. *South African Journal of Science* 59:211–213.
- González Díaz, E. 1964. Rasgos geológicos y evolución geomorfológico de la Hoja 27-D (San Rafael) y zona occidental vecina (Provincia de Mendoza). *Revista de la Asociación Geológica Argentina* 19:151–188.
- González Díaz, E. P. 1966. El hallazgo del Infra?-Mesotriásico continental en el Sur del área pedemontana mendocina. *Acta Geológica Lilloana* 8:101–134.
- González Díaz, E. P. 1972. Descripción geológica de la Hoja 27d, San Rafael, Provincia de Mendoza. *Boletín del Servicio Minero Nacional* 132:1–127.
- Goñi, R., and F. J. Goin. 1987. El origen de los postcaninos gonfodontes de *Andescynodon mendozensis* Bonaparte (Cynodontia, Traversodontidae). *Ameghiniana* 24:235–239.
- Goñi, R., and F. J. Goin. 1988. Morfología dentaria y biomecánica masticatoria de los cinodontes (Reptilia, Therapsida) del Triásico Argentino: I. *Andescynodon mendozensis* Bonaparte (Traversodontidae). *Ameghiniana* 25:139–148.
- Goñi, R., and F. Abdala. 1988. Consideraciones sobre la morfología craneodentaria de *Rusconiodon mignonei* Bonaparte (Cynodontia: Traversodontidae): diagnosis, afinidades y variaciones ontogenéticas. *Ameghiniana* 25:327–336.
- Grine, F. E. 1977. Postcanine tooth function and jaw movement in the gomphodont cynodont *Diademodon* (Reptilia; Therapsida). *Palaeontologia Africana* 20:123–135.
- Grine, F. E. 1978. Notes on a specimen of *Diademodon* previously referred to as *Cyclogomphodon*. *Palaeontologia Africana* 21:167–174.
- Grine, F. E. 1981. *Cragievarus kitchingi* Brink, 1965: a subjective junior synonym of *Diademodon tetragonus* Seeley, 1894 (Reptilia, Therapsida). *Annals of the South African Museum* 84:151–168.
- Grine, F. E., and B. D. Hahn. 1978. Allometric growth in the Diademodontinae (Reptilia; Therapsida): a preliminary report. *Palaeontologia Africana* 21:161–166.
- Grine, F. E., B. D. Hahn, and C. E. Gow. 1978. Aspect of relative growth and variability in *Diademodon* (Reptilia; Therapsida). *South African Journal of Science* 74:50–58.
- Grine, F. E., D. Mitchell, C. E. Gow, J. W. Kitching, and B. R. Turner. 1979. Evidence for salt glands in the Triassic reptile *Diademodon* (Therapsida; Cynodontia). *Palaeontologia Africana* 22:35–39.
- Hammer, W. R. 1995. New therapsids from the upper Fremouw Formation (Triassic) of Antarctica. *Journal of Vertebrate Paleontology* 15:105–112.
- Hancox, P. J. 2000. The Continental Triassic of South Africa. *Zentralblatt für Geologie und Paläontologie, Teil I, Heft11-12*, 1998:1285–1324.
- Hancox, P. J., and B. S. Rubidge. 2001. Breakthroughs in the biodiversity, biogeography, biostratigraphy and basin analysis of the Beaufort Group. *Journal of African Earth Sciences* 33:563–577.
- Hancox, P. J., M. A. Shishkin, B. S. Rubidge, and J. W. Kitching. 1995. A threefold subdivision of the *Cynognathus* Assemblage Zone (Beaufort Group, South Africa) and its palaeogeographic implications. *South African Journal of Science* 91:143–144.

- Hopson, J. A. 1971. Postcanine replacement in the gomphodont cynodont *Diademodon*; pp. 1–21 in D. M. Kermack, and K. A. Kermack (eds.), Early mammals. Zoological Journal of the Linnean Society 50 (Suppl. 1).
- Hopson, J. A., and H. Barghusen. 1986. An analysis of therapsid relationships; pp. 83–106 in N. Hotton, P. D. MacLean, J. J. Roth, and E. C. Roth (eds.), The ecology and biology of mammal-like reptiles. Smithsonian Institution Press, Washington DC.
- Hopson, J. A., and J. W. Kitching. 1972. A revised classification of cynodonts (Reptilia, Therapsida). *Palaeontologia Africana* 14:71–85.
- Hopson, J. A., and J. W. Kitching. 2001. A probainognathian cynodont from South Africa and the phylogeny of nonmammalian cynodonts. *Bulletin of the Museum of Comparative Zoology* 156:5–35.
- Kemp, T. S. 1980. Aspect of the structure and functional anatomy of the Middle Triassic cynodont *Luangwa*. *Journal of Zoology* 191: 193–239.
- Kemp, T. S. 1982. Mammal-like reptiles and the origin of mammals. Academic Press, London, 363 pp.
- Keyser, A. W. 1973a. A new Triassic vertebrate fauna from South West Africa. *Palaeontologia Africana* 16:1–15.
- Keyser, A. W. 1973b. New Triassic vertebrate fauna from South West Africa. *South African Journal of Science* 69:113–115.
- Kitching, J. W. 1977. The distribution of the Karoo vertebrate fauna. *Bernard Price Institute for Palaeontological Research, Memoir* 1:1–131.
- Kitching, J. W. 1995. Biostratigraphy of the *Cynognathus* Assemblage Zone; pp. 40–45 in B. Rubidge (ed.), Biostratigraphy of the Beaufort Group (Karoo Supergroup). Biostratigraphic Series 1. Pretoria, South African Committee for Stratigraphy.
- Lucas, S. G. 1998. Global Triassic tetrapod biostratigraphy and biochronology. *Palaeogeography, Palaeoclimatology, Palaeoecology* 143:347–384.
- Marsicano, C., O. Gallego, and A. Arcucci. 2001. Faunas del Triásico: relaciones patrones de distribución y sucesión temporal; pp. 131–141 in A. E. Artabe, E. M. Morel, and A. B. Zamuner (eds.), El Sistema Triásico en la Argentina. Fundación Museo de La Plata “Francisco Pascasio Moreno”, La Plata.
- Morel, E. M., A. E. Artabe, and L. A. Spalletti. 2003. Triassic floras from Argentina: biostratigraphy, floristic events and comparison with other areas from Gondwana and Laurasia. *Alcheringia* 27:231–243.
- Osborn, J. W. 1974. On tooth succession in *Diademodon*. *Evolution* 28:141–157.
- Owen, R. 1859. On some reptilian fossils from South Africa. *Quarterly Journal of the Geological Society of London* 16:49–63.
- Owen, R. 1861. *Palaeontology, or a Systematic Summary of Extinct Animals and their Geological Relations*, Second Edition. Edinburgh, Adam and Black, xvi+163 pp.
- Renaut, A. J., and P. J. Hancox. 2001. Cranial description and taxonomic re-evaluation of *Kannemeyeria argentinensis* (Therapsida: Dicotydomia). *Palaeontologia Africana* 37:81–91.
- Rogers, R. R., A. B. Arcucci, F. Abdala, P. C. Sereno, C. A. Forster, and C. L. May. 2001. Palaeoenvironment and taphonomy of the Chañares Formation tetrapod assemblage (Middle Triassic), north-western Argentina: spectacular preservation in volcanogenic concretions. *Palaios* 16:461–481.
- Romer, A. S. 1972. The Chañares (Argentina) Triassic reptile fauna. XVII. The Chañares gomphodonts. *Breviora* 396:1–9.
- Seeley, H. G. 1894. Research on the structure, organization, and classification of the Fossil Reptilia. Part IX, Section 3. On *Diademodon*. *Philosophical Transactions of the Royal Society of London* 185:1029–1041.
- Seeley, H. G. 1895. Research on the structure, organization, and classification of the Fossil Reptilia. Part IX, Section 4. On the Gomphodontia. *Philosophical Transactions of the Royal Society of London* 185:1–57.
- Shishkin, M. A., B. S. Rubidge, and P. J. Hancox. 1995. Vertebrate biozonation of the Upper Beaufort Series of South Africa – A new look on correlation of the Triassic biotic events in Euramerica and southern Gondwana; pp. 39–41 in A. Sun, and Y. Wang (eds.), Sixth symposium on Mesozoic terrestrial ecosystems and biota, Short papers. Beijing: China Ocean Press.
- Smith, R. M. H., and R. Swart. 2002. Changing fluvial environments and vertebrate taphonomy in response to climatic drying in a Mid-Triassic rift valley fill: the Omingonde Formation (Karoo Supergroup) of central Namibia. *Palaios* 17:249–267.
- Stipanovic, P. N., E. González Díaz, and A. M. Zavattieri. 2007. Grupo Puesto Viejo *nom. transl.* por Formación Puesto Viejo González Díaz, 1964, 1967: nuevas interpretaciones paleontológicas, estratigráficas y cronológicas. *Ameghiniana* 44:759–761.
- Sun, A.-L. 1988. Additional study on *Sinognathus gracilis* (Cynodontia; Reptilia). *Vertebrata Palasiatica* 26:173–180.
- Sun, A.-L., J. Li, X. Ye, Z. Dong, and L. Hou. 1992. The Chinese fossil reptiles and their kins. Science Press, Beijing, 260 pp.
- Tatarinov, L. P. 2002. Gomphodont cynodonts (Reptilia, Theriodontia) from the Middle Triassic of Orenburg Region. *Paleontological Journal* 36:176–179.
- Watson, D. M. S. 1911. The skull of *Diademodon*, with notes on those of some other cynodonts. *The Annals and Magazine of Natural History* (sr. 8), 8:293–330.
- Watson, D. M. S. 1913. Further notes on the skull, brain, and organs of special sense of *Diademodon*. *The Annals and Magazine of Natural History* (sr. 8), 12:217–228.
- Zavattieri, A. M., and A. B. Arcucci. 2007. Edad y posición estratigráfica de los tetrápodos del cerro Bayo de Potrerillos (Triásico), Mendoza, Argentina. *Ameghiniana* 44:133–142.

Submitted January 5, 2008; accepted October 29, 2008.