

The first record of dinocephalians in South America: Late Permian (Rio do Rasto Formation) of the Paraná Basin, Brazil

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With 7 figures and 1 table

LANGER, M. C. (2000): The first record of dinocephalians in South America: Late Permian (Rio do Rasto Formation) of the Paraná Basin, Brazil. – N. Jb. Geol. Paläont. Abh., **215**: 69–95; Stuttgart.

Abstract: Dinocephalian therapsids are reported for the first time in South America. The remains, mostly isolated teeth, were collected in the Rio do Rasto Formation (Late Permian of the Paraná Basin), cropping out at the Posto Queimado locality, South Brazil. Two dinocephalian groups were recognised, the subfamily Brithopodinae and the family Titanosuchidae. The chronological distribution of Dinocephalia ranges from the Ufimian to the Early Tatarian, characterising the Posto Queimado fauna as the oldest known for the Rio do Rasto Formation.

Zusammenfassung: Zum ersten Mal werden Dinocephalen in Südamerika nachgewiesen. Das Material, drei isolierte Zähne und ein Kieferfragment, stammt aus der Rio do Rasto Formation (Oberes Perm des Paraná-Beckens) von Posto Queimado in Südbrasilien. Die Zähne werden Vertretern der Familie Titanosuchidae sowie der Unterfamilie Brithopodinae zugeordnet. Die Dinocephalen-Reste datieren die Fauna von Posto Queimado als Ufimium bis frühes Tatarium, und identifizieren sie als die älteste von drei sukzessiven Faunenvergesellschaftungen in der Rio do Rasto Formation.

Introduction

The Late Permian Rio do Rasto Formation of South Brazil is well known for its tetrapods. The dicynodont *Endothiodon*, and various rhinesuchoid temnospondyls, have been recorded from outcrops in the Serra do Cadeado area, Paraná State (BARBERENA 1998, BARBERENA & ARAÚJO 1975,

BARBERENA & DIAS 1998). In addition, the pareiasaur *Provelosaurus* is known only from sediments assigned to this stratigraphic unit in the Rio Grande do Sul State (ARAÚJO 1985). A Late Tatarian age is usually accepted for the Rio do Rasto Formation, based mostly on the correlation of its tetrapod fauna with the classic “*Daptocephalus*” and “*Cistecephalus*-zones” of the Karroo Basin, South Africa (BARBERENA et al. 1985 a, b).

The fragmentary fossil remains described here provide valuable biogeographic and biochronologic information on the Late Permian of the Paraná Basin. They were collected in the Rio do Rasto beds of the Posto Queimado locality (Rio Grande do Sul State) and can be assigned to the Dinocephalia. These therapsids were, until now, unknown in South America, and this record increases the palaeogeographic distribution of the group. Moreover, dinocephalians are only known in Ufimian to Early Tatarian deposits, an older age than was previously accepted for the Rio do Rasto Formation.

Posto Queimado locality

The Posto Queimado outcrops are located on a private piece of land approximately 20 km to the NW of São Gabriel municipality, Rio Grande do Sul State, Brazil (30° 01' S; 54° 09' W). The rocks are exposed in several ravines about 300 m long, covering an area of approximately one square kilometre.

The strata that outcrop at the Posto Queimado locality are assigned to the Morro Pelado Member of the Rio do Rasto Formation (LAVINA 1991). This is a well known stratigraphic unit of the Paraná Basin, that occurs in the states of Rio Grande do Sul, Santa Catarina, Paraná and São Paulo (Fig. 1). The Morro Pelado sediments were deposited in shallow lakes with intercalated aeolian dunes (BARBERENA et al. 1980), and represent the latest expression of the gigantic water body that covered the Paraná Basin for most of the Late Permian.

Aeolian sandstones, however, are unknown at the Posto Queimado locality, where only two distinct sedimentary facies are present. Red laminated mudstones suggest a low-energy depositional environment, probably related to highly oxidising ephemeral lakes, while conglomerates represent high-energy flows that spread through these lakes. Indeed, according to LAVINA (1991), the strata cropping out at the Posto Queimado locality include the last purely lacustrine deposit of the Rio do Rasto Formation in the region. Just above these strata, the record of aeolian dunes starts (Fig. 2), which represents a major desertification phase.

Few studies have been carried out on the fauna of the Posto Queimado locality. LANGER et al. (1998) and LANGER (1998) commented upon dinocephalian remains, while RICHTER & LANGER (1998) noticed the ichthyofau-



Fig. 1. Outcropping areas (stippled) of the Late Permian rocks of the Paraná Basin, in the states of Rio Grande do Sul, Santa Catarina, Paraná and São Paulo (modified from ZALAN et al. 1990). The tetrapod bearing localities (white squares) of the Rio do Rasto Formation are: **A**: Bagé-Aceguá Road; **B**: Posto Queimado; **C**: Serra do Cadeado. a-b = transept depicted in Figure 2.

na of this locality. The fish remains include actinopterygians (Palaeonisciformes), a gnathorhizid dipnoan, and a possible hybodontiform shark. Some tooth-bearing jaw fragments also indicate the presence of an unidentified temnospondyl amphibian.

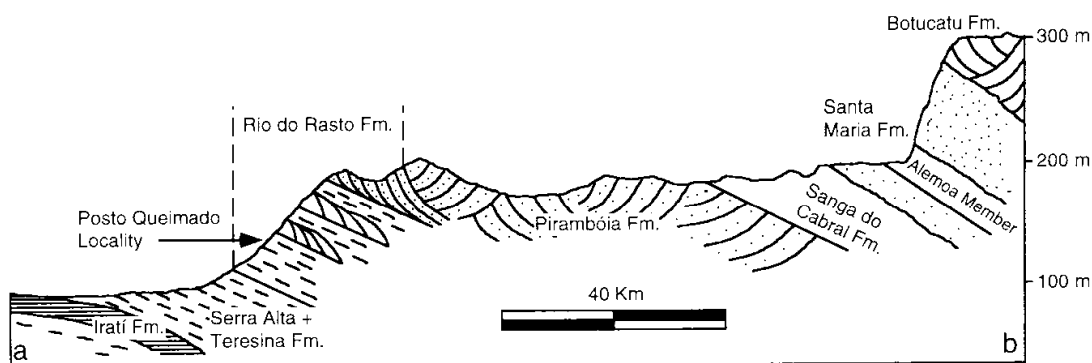


Fig. 2. Transept through the Gondwanic sequence of the Paraná Basin in the Rio Grande do Sul State (see Fig. 1): From the Permian shales of the Irati Formation to the Jurassic aeolian sandstones of the Botucatu Formation (modified from LAVINA 1991).

Institutional abbreviations

MCP: Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil; **UFRGS:** Coleção de Palaeovertebrados do Departamento de Palaeontologia e Estratigrafia, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil; **MCN:** Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil.

Systematic Palaeontology

Three isolated teeth (MCP 3838-PV, UFRGS PV0314P, MCN PV2351) and a tooth-bearing bone fragment (UFRGS PV0249T) are here referred to the *Dinocephalia* SEELEY (1894 sensu BOONSTRA 1962). All specimens were collected in the Rio do Rasto deposits of the Posto Queimado locality, the isolated teeth from the conglomerate, and the single bone from the fine-grained deposits.

Dinocephalians are a well-known group of therapsids that flourished in the Late Permian, during a short period of about 5 Myr. Dinocephalian fossil remains have been known since the middle of the eighteenth century, with the description of Russian and South African forms by KUTORGA and OWEN, respectively (KING 1988). However, only with the work of BOONSTRA (1962, 1963) on the dentition of these animals, were dinocephalians definitively defined as a natural group.

Indeed, the monophyly of Dinocephalia has recently been established by a series of cladistic works (HOPSON & BARGHUSEN 1986, KING 1988, RUBIDGE & VAN DEN HEEVER 1997). Several proposed dinocephalian synapomorphies concern the morphology of the teeth: the presence of intermeshing incisors (HOPSON & BARGHUSEN 1986, KING 1988, RUBIDGE & VAN DEN HEEVER 1997), the reduction in size of postcanine teeth (KING 1988), the presence of heels on the incisors (HOPSON & BARGHUSEN 1986), and the upturning of the alveolar margin (RUBIDGE & VAN DEN HEEVER 1997).

The presence of heeled teeth is no longer accepted as a dinocephalian synapomorphy. KING (1988) and RUBIDGE & VAN DEN HEEVER (1997) have clearly shown the absence of heels on the incisors of estemmenosuchid dinocephalians, and KING (1988) regarded the presence of this dental morphology as a synapomorphy of a less inclusive group within dinocephalians, the Anteosaurioidea. It is accepted, however, that the intermeshing of the lower and upper jaw teeth is a unique characteristic of dinocephalians. These teeth are easily identifiable, even when found isolated, by the wear facets produced by this occlusal pattern.

Among the teeth collected at the Posto Queimado locality, MCP 3838-PV and UFRGS PV0314P show wear facets for the intermeshing of the teeth. Moreover, UFRGS PV0314P possesses another supposed dinocephalian synapomorphy, showing signs of an upturning alveolar margin on its lingual face. MCN PV2351 and UFRGS PV0249T, on the other hand, do not have wear facets for the intermeshing of the teeth, but MCN PV2351 has an incipient heel-like protuberance in its lingual face, a feature that can also be assumed to be characteristic of most dinocephalians. The tooth-bearing fragment UFRGS PV0249T does not show any dinocephalian synapomorphy, and its affinity with this group is here proposed only based on its close similarity with some dinocephalian postcanines (see discussion below).

In the following sections, the Brazilian specimens assigned to Dinocephalia are listed according to their most probable taxonomic assignment. They are briefly described and their taxonomic affinities are discussed.

MCP 3838-PV

(Fig. 3)

Titanosuchidae BOONSTRA, 1972 (sensu KING 1988)

Description: MCP 3838-PV is the labial half of an incisiform tooth crown. Its basal portion is a simple cylindrical structure, as reconstructed based on the preserved labial part (10 mm in diameter). It is 8 mm deep, showing a slight increase in width towards the apex. Internally, as exposed at the fractured area, the tooth has a bulbous pulp cavity (Fig. 3D).

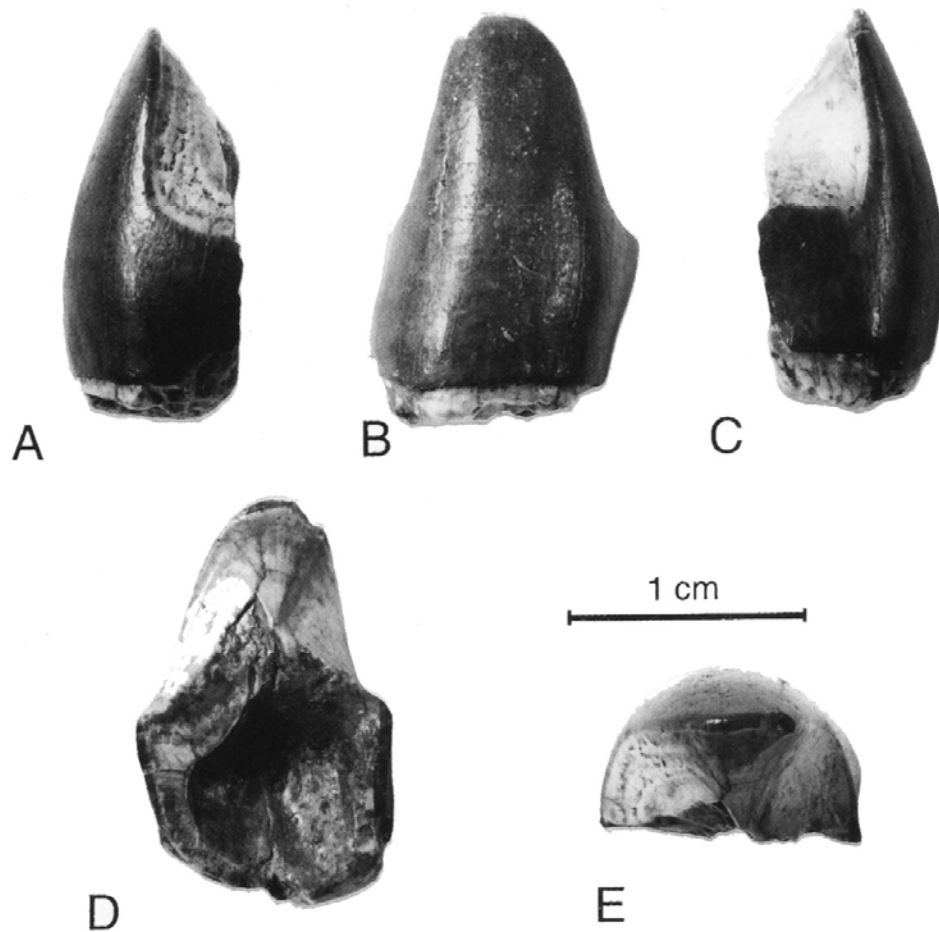


Fig. 3. MCP 3838-PV, Titanosuchidae incisiform. **A:** medial view, **B:** labial view, **C:** lateral view, **D:** lingual view, **E:** occlusal view.

The apical portion of the tooth, 9 mm deep, is mostly composed of an elongated talon that is restricted to its labialmost part (Fig. 3 A, C, E). The talon has a basal area that is almost the same width as the rest of the tooth and it tapers apically to a rounded point. It is slightly curved towards one side, also showing labio-lingual compression (Figs. 3 B, D).

The lingual face of the talon has two clear wear facets on its sides, being more apically developed in its middle part (Figs. 3 A, C). A small portion of the heel is seen, both in lingual and labial views (Figs. 3 B, D), just on the basal end of each wear facet. As in some dinocephalians, one wear facet is

less basally developed (Fig. 3B), indicating that the occlusal surface of the heel was slightly diagonal.

The lingualmost part of the tooth is missing. Projections based on the preserved portion, however, indicate that its linguo-labial expression should be equal to, or greater than that of the labial part. This suggests that the heel is at least as developed as the talon, but no sign of a well developed crushing surface is seen on it.

Discussion: The presence of clear facets for the intermeshing of the teeth indicates the dinocephalian affinity of MCP 3838-PV. Within Dinocephalia, however, not only the incisors have intermeshing occlusion (although this is true for most of these therapsids), but this is a condition also present in most other teeth of the Tapinocephalinae.

The clear talon-and-heel morphology of MCP 3838-PV precludes its assignment to the estemmenosuchids (TCHUDINOV 1983, KING 1988). These structures, on the other hand, are known in the incisors of all other dinocephalians, including the Brithopodinae (ORLOV 1958) and Anteosaurinae (BOONSTRA 1962, 1963, contra ROMER 1961). The heels of the incisors of these dinocephalians, however, are much less developed than inferred for the tooth here described, a condition that seems to be shared with the styraccephalids (BOONSTRA 1963, RUBIDGE & VAN DEN HEEVER 1997). Moreover, the talons of the anteosaurid incisors are much longer, and they do not show linguo-labial compression.

The controversial Russian dinocephalian *Deuterosaurus* is possibly an Anteosaurinae (BOONSTRA 1965, KING 1988). Some of its incisors, as figured by EFREMOV (1954, figs. 19-20), bear well marked lingual heels. These teeth, however, seem to belong to a different animal, probably a primitive Tapinocephalinae (BOONSTRA 1965). In any case, also according to BOONSTRA (1965) and KURKIN (1997), the heels of the real *Deuterosaurus* incisors are more developed than in any other Anteosaurinae (as can be seen in EFREMOV, 1954; figs. 16-17), which makes it closer to the morphology of MCP 3838-PV.

The titanosuchids are, however, the dinocephalians that typically have incisors with protuberant heels, as inferred for MCP 3838-PV, a morphology that is usually regarded as a synapomorphy of the group (HOPSON & BARGHUSEN 1986, KING 1988, RUBIDGE & VAN DEN HEEVER 1997). Within titanosuchids, the Titanosuchinae incisors show wear facets that make up two cutting surfaces on the labial side of the talon, and no well developed crushing heel (BOONSTRA 1962). This morphology is similar to that of MCP 3838-PV, which, however, does not show the long pointed and laterally compressed talons of the Titanosuchinae incisors (BOONSTRA 1962, fig. 2). Some Titanosuchinae incisors, on the other hand, seem to be more similar to

MCP 3838-PV, and do not present a well developed talon (BOONSTRA 1962, fig. 12, 18).

The Tapinocephalinae is the only group of dinocephalians in which non-incisor teeth have intermeshing wear facets as well as a well developed talon-and-heel morphology (RUBIDGE 1991). The more anterior incisors, however, bear laterally compressed crowns (EFREMOV 1954, fig. 19, BOONSTRA 1962, p. 99), a feature that is absent in 3838-PV. Moreover, in most of these teeth, the crushing surface of the heel is much more expanded than the cutting one, forming a deep oval hollow (BOONSTRA 1962).

Accompanying the great development of the crushing heel, the lingual side of the talon in most Tapinocephalinae incisors shows a single vertical surface (GREGORY 1926, pls. XVII-XX, EFREMOV 1940, fig. 19, 1954, figs. 19, 20, BOONSTRA 1962, fig. 34). This area in MCP 3838-PV, on the other hand, shows the two cutting facets. Some Russian Tapinocephalinae (EFREMOV 1940, fig. 11, 1954, fig. 21), however, seem to show incisiform teeth that are less derived than those of the South African forms (GREGORY 1926, BOONSTRA 1962). The hollowed crushing surfaces of the heel, as well as the lateral compression of the crown, is not seen, and they are more like MCP 3838-PV.

In conclusion, MCP 3838-PV can with certainty be regarded as a titanosuchid incisiform tooth. It is, however, distinct from typical long-taloned Titanosuchinae incisors, as well as from the anteriormost Tapinocephalinae crushing-heeled ones. Moreover, based on the comparison of the curved talon of MCP 3838-PV with those of some dinocephalian incisiforms, it is possible to define the lateral and medial sides of the tooth. In these teeth (EFREMOV 1940, 1954) the pointed talon is laterally curved, providing the means to identify MCP 3838-PV as a left inferior or a right superior incisiform tooth. This assignment is also corroborated by the less basal development of its supposed lateral wear facet.

UFRGS PV0249T

(Fig. 4)

Anteosauridae BOONSTRA, 1954 (sensu HOPSON & BARGHUSEN 1986)

Brithopodinae EFREMOV, 1954 (sensu King 1988)

Description: UFRGS PV0249T is a massive bone fragment (Figs. 4 A, B) in which four antero-posteriorly aligned teeth are deeply implanted. It has a roughly cylindrical shape, and is anteriorly and posteriorly broken. Its lateral and medial edges are intact, showing a maximum width of 32 mm. The face opposite the teeth, on the other hand, is also broken, and a longitudinal

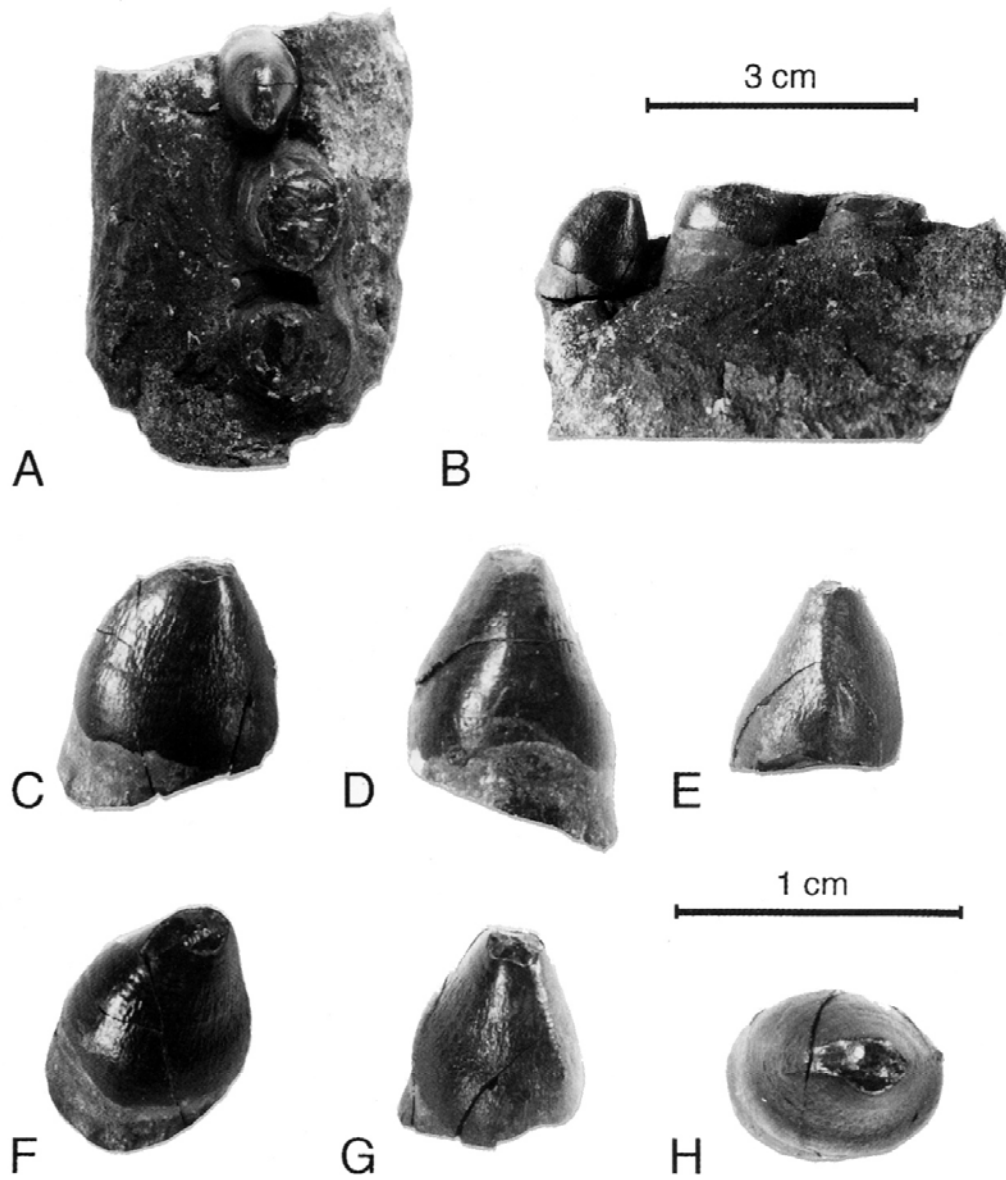


Fig. 4. UFRGS PV0249T, Brithopodinae tooth-bearing bone fragment (A-B) and its anteriormost tooth (C-H). **A, H:** occlusal view, **B, C:** lingual view, **D:** anterior view, **E:** posterior view, **F:** antero-lingual view, **G:** postero-lingual view.

groove is seen in this area. The groove is tentatively identified as the Meckelian canal, suggesting that UFRGS PV0249T is a dentary fragment.

The anteriormost tooth of UFRGS PV0249T is the most complete one. It has a well preserved crown (Figs. 4C-H) and root, showing thecodont implantation. The anterior broken face of PV0249T exposes the root in longitudinal section, which is drop-shaped and 29 mm deep. The crown (8 mm deep, 7 mm broad and 9 mm long) is bluntly conical, posteriorly curved, and slightly laterally compressed, being clearly delimited by the enamel covering. The bulbous appearance of the crown is the result of constrictions seen on its base and apical two thirds, in comparison to its more voluminous basal third (Figs. 4C, E). The apex of the tooth shows a characteristic wear facet that is antero-posteriorly elongated and wider posteriorly (Fig. 4H). The anterior and posterior margins of the tooth bear crenulae, and the posterior one is longer (Figs. 4C, E-G). Each crenulated border is composed of a series of aligned small bulbs of enamel. The 1 mm long anterior crenula is composed of three denticles. The posterior crenula is 5.5 mm long, with four enamel bulbs in each millimetre. The more apical bulbs are less defined, and were probably worn down during the animal's life.

The crowns of the other three teeth are only partially preserved, and the root of the most posterior one is also incomplete. For the second and third tooth, the basal area of the crown is present, but the apical area is broken. The posterior breakage of UFRGS PV0249T exposes the root of the third tooth in transverse section, showing its posterior curvature and a clear pulp channel.

Discussion: The deep cylindrical shape of UFRGS PV0249T precludes its assignment to a palatal bone, and its teeth are certainly from the marginal series. Moreover, the teeth are aligned along the longitudinal axis of the bone, instead of being placed laterally to one another. This arrangement is not seen in teeth of the premaxilla or the anterior part of the dentary, and UFRGS PV0249T is more probably a maxillary or posterior dentary fragment. It is not possible to determine with assurance, however, whether the specimen is an upper or lower jaw fragment, since the nature of fossilisation of the material does not reveal any non-dental anatomical detail other than the possible Meckelian canal.

The antero-posterior orientation of UFRGS PV0249T can be determined based on the development of crenulae and the posterior curvature of the more complete tooth (compared with carnivorous synapsids and archosauriforms). The medial and lateral sides, in their turn, can be determined by the curvature of the bone, which is slightly medially concave. Therefore, it is possible to assign the fragment either to a left maxilla, or to a right dentary, the last option being more probable.

Among the medium to large carnivores of the Late Permian, the full thecodont implantation, the presence of a clear boundary between the crown and the root, and the general bulbous morphology of the anteriormost tooth with a more voluminous basal area, clearly indicate the therapsid affinity of UFRGS PV0249T. An assignment to temnospondyls or archosauriforms can be easily excluded (CHASE 1963, SENNIKOV 1988, WELMAN 1998).

The anteriormost tooth of UFRGS PV0249T is distinct in shape from the sabre-like canines of most basal therapsids. This condition, together with the arrangement of the teeth, strongly suggests that the teeth compose a postcanine series. Among therapsids, postcanines with bulbous crowns, like the anteriormost tooth of UFRGS PV0249T, are common. The presence of slight lateral compression and clear crenulation on both keels of the tooth, however, precludes its assignment to a biarmosuchid or eotitanosuchian postcanine (SIGOGNEAU & TCHUDINOV 1972). Moreover, its large size and blunt shape are not exactly what is expected in a postcanine of ictidorhinid (SIGOGNEAU 1970), gorgonopsian (COLBERT 1948, MANTEN 1958, HOPSON & BARGHUSEN 1986) or therocephalian (BRINK 1958, KEMP 1972, MENDREZ 1974), which have reduced, undifferentiated, and usually slender postcanines. Therefore, the assignment of UFRGS PV0249T to the Dinocephalia is here suggested.

The anteriormost tooth of UFRGS PV0249T is, however, clearly not a dinocephalian incisor, since it does not have the characteristic wear facets for the intermeshing of the teeth. Moreover, it also does not fit either of the two basic morphologies of such teeth: the sharply pointed and the heeled (HOPSON & BARGHUSEN 1986, KING 1988, RUBIDGE & VAN DEN HEEVER 1997). UFRGS PV0249T is also clearly not a dinocephalian canine, since these are usually long and sharply pointed, except for the advanced Tapinocephalinae. Accordingly, the postcanine affinity of the UFRGS PV0249T teeth is corroborated.

Within the three categories of dinocephalian postcanines listed by RUBIDGE & VAN DEN HEEVER (1997), the anteriormost tooth of UFRGS PV0249T is clearly a bulbous type, a plesiomorphic condition shared by the Anteosauridae and Styracocephalidae, according to these authors. HOPSON & BARGHUSEN (1986), on the other hand, state that bulbous postcanines are autapomorphic for their Anteosauridae, including *Syodon*, *Titanophoneus*, *Doliosauriscus* and *Anteosaurus*.

The more derived dinocephalian postcanines are clearly distinct from that here described. These teeth are leaf-like in Titanosuchinae and Estemmenosuchidae (BOONSTRA 1962, TCHUDINOV 1983), while Tapinocephalinae shows typical heeled ones (EFREMOV 1940, BOONSTRA 1962). BOONSTRA (1963, contra RUBIDGE & VAN DEN HEEVER 1997) described the styraco-

cephalid postcanines as heeled, but the bad preservation of this structure in *Styracocephalus* makes further comparison impossible.

According to the postcanine classification of RUBIDGE & VAN DEN HEEVER (1997), UFRGS PV0249T should be assigned to the Anteosauridae. Anteosaurinae postcanines, however, are usually described as Titanosuchinae-like, bluntly spatulate elements (BOONSTRA 1954, 1962, 1963, King 1988). *Deuterosaurus* has well preserved postcanines for comparison and KURKIN (1997) defined these teeth as Brithopodinae-like, with a posteriorly curved apex and a smooth convex medial face. However, EFREMOV (1954, fig. 22) figured a *Deuterosaurus* postcanine that is quite similar to the leaf-like ones of Titanosuchinae, and BOONSTRA (1965) also noted the similarity of the spatulate Anteosaurinae postcanines and those of *Deuterosaurus*. Therefore, the assignment of UFRGS PV0249T to the Anteosaurinae is not likely.

UFRGS PV0249T is extremely similar to the postcanines of Russian Brithopodinae (ORLOV 1958, TCHUDINOV 1968, IVACHENKO 1995) and its assignment to this subfamily is here proposed. Those teeth are bluntly conical, posteriorly curved and slightly laterally compressed. ROMER (1961) emphasised the presence of crenulation on the keel of the Brithopodinae postcanines, and the wear facet of UFRGS PV0249T is closely similar to that seen in some of those teeth (ORLOV 1958, fig. 35c). Brithopodinae dinocephalians are also known in South Africa and North America (OLSON 1962, RUBIDGE 1994). The more important morphological features of the tooth crowns, however, are not well preserved in the teeth of those forms, which makes comparison with the present specimen difficult.

UFRGS PV0314 P

(Fig. 5)

Anteosauroida BOONSTRA, 1962 (sensu KING 1988)

Description: UFRGS PV0314P is an incomplete tooth, with only the crown and part of the root preserved. The enamel covering defines the crown area, and is more basally developed on the labial face of the tooth (Figs. 5 A, C). In its basal portion, the tooth is slightly laterally compressed, with a transverse section of 7/9 mm. Further apically, where the enamel covers its whole perimeter, the crown widens (9/9 mm in circumference) making a clear, but not well developed, heel (Figs. 5 B, D).

The heel of UFRGS PV0314P is not lingually protuberant, and the lingual face of the tooth is almost straight (Figs. 5 A, C). The occlusal face of the heel is marked by two wear facets, which indicates intermeshing with two adjacent teeth of the opposite jaw. One of these wear facets is more basally

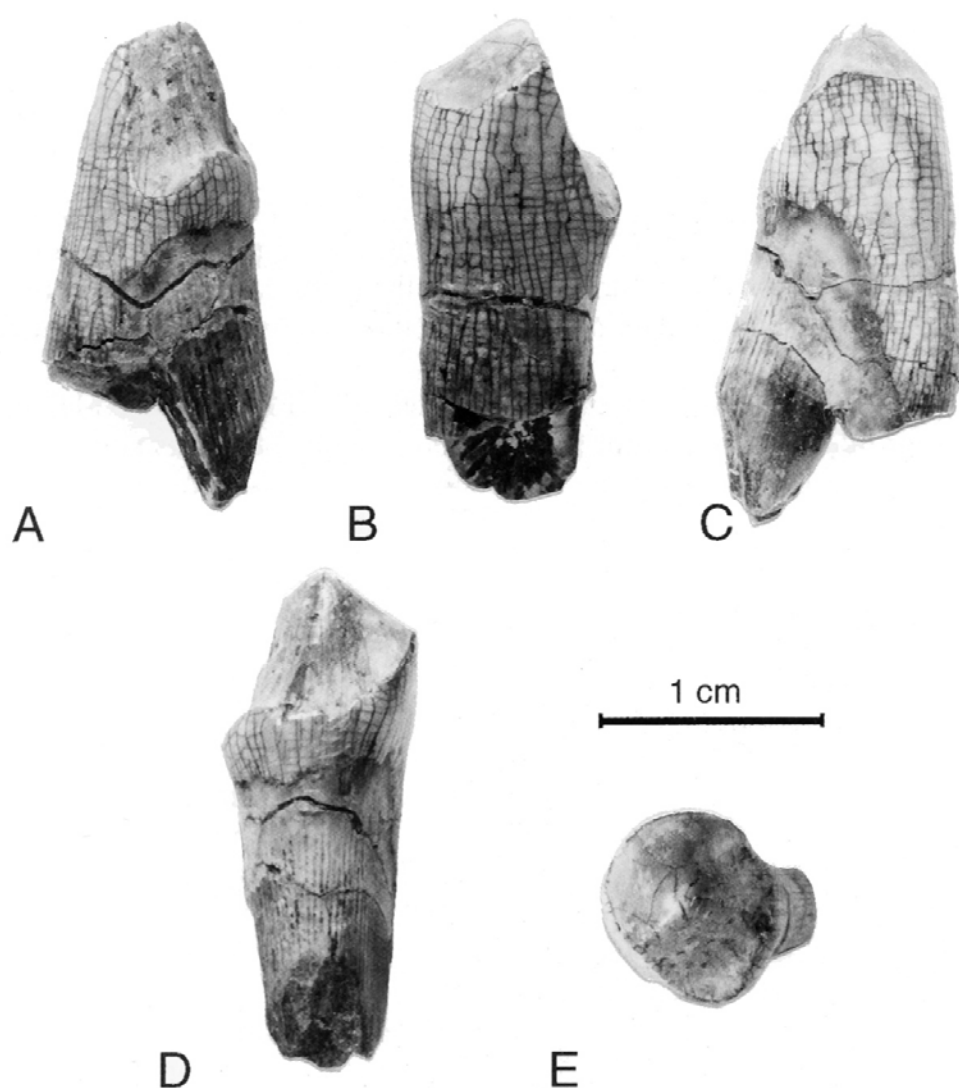


Fig. 5. UFRGS PV0314P, Anteosauroid tooth. **A:** medial view, **B:** labial view, **C:** lateral view, **D:** lingual view, **E:** occlusal view.

developed than the other, resulting in a diagonally oriented heel (Fig. 5D). According to BOONSTRA's (1962, fig. 1) study of dinocephalian incisors, the portion of these teeth that has the less developed wear facet, and a consecutive more apically developed heel, corresponds to the medial one. Thus, it is suggested that the tooth here described is an upper left or a lower right incisiform.

From the basal portion of the heel to the apex, UFRGS PV0314P is 10 mm deep. It has a short and blunt talon (6 mm long) that is lingually delimited by the two wear facets. Moreover, a labial wear facet is also seen on the apical portion of this structure (Fig. 5A-C).

Discussion: The assignment of UFRGS PV0314P to a dinocephalian incisor, or an anterior Tapinocephalinae tooth, is suggested by the presence of clear wear facets for the intermeshing of the teeth. Moreover, the presence of a lingual heel suggests an affinity with the Anteosaurioidea (sensu KING 1988).

It is difficult to determine the affinities of UFRGS PV0314P below Anteosaurioidea. Its heel is not lingually protuberant, and it is similar in this respect to the incisors of most anteosaurid dinocephalians (ORLOV 1958, BOONSTRA 1963, King 1988), an exception being *Deuterosaurus* (BOONSTRA 1965). The heel of UFRGS PV0314P, as well as those of the Brithopodinae incisors (ORLOV 1958, fig. 35a), is outlined only by the lingual wear facets that restricts the talon to a more labial position. On the other hand, as already discussed, titanosuchid dinocephalians have apomorphically enlarged heels on the incisors (HOPSON & BARGHUSEN 1986, KING 1988, RUBIDGE & VAN DEN HEEVER 1997). Indeed, in South African Titanosuchinae (BOONSTRA 1962, fig. 2), as well as in some Russian Tapinocephalinae (EFREMOV 1940, 1954; figs. 19-20), the heels are much more lingually protuberant than that of UFRGS PV0314P. Moreover, in most Tapinocephalinae, the enlarged crushing surfaces make these teeth even more dissimilar to that here described (GREGORY 1926, pls. XVII-XX; EFREMOV 1954, fig. 19-20; BOONSTRA 1962, figs. 34, 35).

The talon of UFRGS PV0314P is on the other hand, much shorter than the elongated and sharply pointed ones of the Anteosauridae and most Titanosuchinae incisors (ORLOV 1958, BOONSTRA 1962, fig. 2, 1963, TCHUDINOV 1968, IVACHNENKO 1995). In this respect, it seems to be morphologically closer to some other Titanosuchinae incisors (BOONSTRA 1962, fig. 18) and Tapinocephalinae teeth (EFREMOV 1940, BOONSTRA 1962), which have shorter and blunter talons. Moreover, the heel of the Tapinocephalinae teeth can be ontogenetically less developed, and thus they are not always very protuberant. BOONSTRA (1962) attested that on the posterior part of the dental series of these animals, the heels are significantly less developed, while the talon remains short, a morphology closer to that of UFRGS PV0314P. These less developed teeth, on the other hand, usually do not have well-defined wear facets as the tooth here described.

The much more basal development of the enamel on the labial side of UFRGS PV0314P, also seems to be of taxonomic significance. HOPSON & BARGHUSEN (1986), as well as RUBIDGE & VAN DEN HEEVER (1997),

defined the exaggerated upturning of the alveolar margin as a characteristic of the anteosaurids. In fact, as seen in the lower incisors of *Syodon* and *Titanophoneus* (ORLOV 1958, figs. 29, 31), the lingual borders of the alveoli are much more dorsally developed than the labial ones. Accordingly, these teeth show an enamel distribution closely similar to that of UFRGS PV0314P. Upturning alveolar margins are also known in other dinocephalians, as *Ulemosaurus* and other Russian forms (EFREMOV 1940, figs. 9, 11; 1954, fig. 19, 20), but, as pointed out by RUBIDGE & VAN DEN HEEVER (1997), this condition seems to be more marked in anteosaurids.

Another conspicuous feature of UFRGS PV0314P is the presence of the apical wear facet on the labial face. A similar structure was not described for anteosaurids, but it is seen in one of the incisiforms of *Ulemosaurus* figured by EFREMOV (1940, fig. 9).

In UFRGS PV0314P the lingual wear facets do not have equal basal extensions, making up a heel composed of two platforms, a horizontal on the lateral side and an apically inclined on the medial side (Fig. 5 d). BOONSTRA (1962) used this feature to differentiate between Titanosuchinae and Tapinocephalinae incisors, stating that the medial portion of the heel is much higher than the lateral in the Tapinocephalinae. Comparing the incisors of *Jonkeria* (BOONSTRA 1962) and *Ulemosaurus* (EFREMOV 1940), however, it is possible to state that this difference is not so marked, and that both groups are very similar to the specimen here described on this feature, as well as to *Syodon* and other Brithopodinae (ORLOV 1958, fig. 35a).

In conclusion, although the anteosaurid affinity of UFRGS PV0314P seems to be more probable, its unambiguous assignment to an anteosaurid or titanosuchid incisiform is not possible. In assuming an anteosaurid affinity, a strong wear on the talon must be also accepted, since this structure is much shorter in UFRGS PV0314P than in those dinocephalians. On the other hand, if a titanosuchid affinity is assumed, it is necessary to accept PV0314P as a tooth with an ontogenetically or phylogenetically less protuberant lingual heel.

MCN PV2351

(Fig. 6)

Dinocephalia SEELEY, 1894

Description: MCN PV2351 is the smallest tooth here described. It is 9 mm deep, with a maximum width of 6 mm, and only half of the crown is preserved. Its basal part has a bulbous form, getting wider from the root boundary to its middle portion, where it has an inferred circular cross section. The apical half of the crown is labio-lingually compressed, resulting

in a spatulate shape. This compression was not equal in both sides of the tooth, and an incipient “heel” is seen on the supposed lingual side (Fig. 6 B-C). The spatulate apex bears a curved single wear facet, that runs along all its antero-posterior length (Fig. 6 D), and there is no sign of crenulations.

Discussion: The presence of an incipient heel-like structure on the lingual side of MCN PV2351 is the only morphological feature indicating a dinocephalian affinity. Moreover, the absence of intermeshing wear facets, the blunt morphology, and the small size precludes its assignment to a canine or incisor of those therapsids.

Various groups of dinocephalians have non-incisor teeth that are somehow heeled, although only the posterior teeth of Tapinocephalinae have these structures really well developed. MCN PV2351, however, does not seem to correspond to a typical heeled posterior teeth of Tapinocephalinae, and it resembles more the type of postcanine usually named spatulate, or leaf-shaped (BOONSTRA 1963, RUBIDGE & VAN DEN HEEVER 1997).

The spatulate type of dinocephalian postcanines is characterised by a crown that is bulbous at the base and shows a linguo-labial constriction on the apex. This constriction defines an incipient protuberance on the lingual side of the tooth that is supposed to be homologous to the heel of the heeled dinocephalian teeth. This type of postcanine is well known in Titanosuchinae (JANENSCH 1959, BOONSTRA 1962), but also seems to be present in the Estemmenosuchidae (TCHUDINOV 1983, RUBIDGE & VAN DEN HEEVER 1997) and Anteosaurinae (EFREMOV 1954, fig. 22, BOONSTRA 1962, KING 1988). The morphology of those teeth is closely similar to that of MCN-PV2351, and even a curved crown apex, and consequently a curved wear facet as seen in MCN PV2351, was described for *Jonkeria* (JANENSCH 1959, fig. 8). Some of these teeth, however, are more strongly laterally compressed than MCN PV2351 (BOONSTRA 1962, TCHUDINOV 1983) and also bear crenulations, which are usually placed basally to the wear facets (EFREMOV 1954, fig. 22, JANENSCH 1959, fig. 8).

MCN PV2351 is also, to some extent, similar to Tapinocephalinae teeth that do not have well developed heels and wear facets. In fact, in some of these teeth the heel seems to be (ontogenetically or phylogenetically) less developed, showing a different morphology. BOONSTRA (1962) states that the more posterior teeth of Tapinocephalinae have a Titanosuchinae-like spatulate shape, as seen in *Ulemosaurus* (EFREMOV 1940, fig. 10) and *Struthiocephalus* (BOONSTRA 1962, fig. 35). The penultimate tooth of *Struthiocephalus*, figured by BOONSTRA (1962, fig. 35), closely resembles that here described, showing a well marked bulbous lingual side (the incipient heel) and uncrenulated edges. In its turn, the primitive Tapinocephalinae *Tapino-*

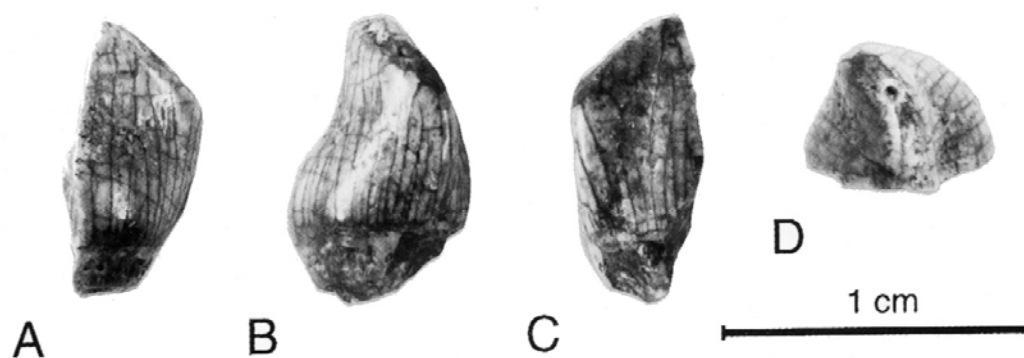


Fig. 6. MCN PV2351, Dinocephalia tooth. **A:** labial view, **B:** anterior/posterior view, **C:** lingual view, **D:** occlusal view.

caninus has bulbous postcanines with small heel on the lingual side (RUBIDGE 1991).

Although HOPSON & BARGHUSEN (1986) and RUBIDGE & VAN DEN HEEVER (1997) suggest that all anteosaurids have typical bulbous postcanines, this seems to be true only for the Brithopodinae (BOONSTRA 1962, KING 1988), and possibly also the Styracocephalidae (RUBIDGE & VAN DEN HEEVER 1997). The Brithopodinae dinocephalians show bluntly conical, slightly laterally compressed, crenulated, and posteriorly curved postcanines (ORLOV 1958, ROMER 1961), that are clearly different from MCN PV2351.

In conclusion, the tooth here described can be assigned either to an Anteosaurinae or Titanosuchinae postcanine, since the overall shape of these teeth is quite similar to that of PV2351. Moreover, in spite of being usually crenulated, postcanines of these two subfamilies frequently have these structures worn down, what can be the case PV2351. Nonetheless, the assignment of PV2351 to a Tapinocephalinae tooth with a not well developed talon-and-heel morphology should also not be discarded.

Biostratigraphic Considerations

Previously to this study, two tetrapod-based faunal associations have been recognised in the Rio do Rasto Formation: the Local Faunas of Aceguá and Serra do Cadeado (BARBERENA et al. 1985b). The fossil fauna of the Posto Queimado locality is a third one, that is ecologically and chronologically distinct from the precedents.

Table 1. Taxonomic content of the Late Permian tetrapod-based faunas of Rio do Rasto Formation (Paraná Basin), South Brazil.

Posto Queimado locality fauna

- Chondrichthyes
 - Cf. Hybodontiformes* - RICHTER & LANGER (1998)
- Actinopterygii indet - RICHTER & LANGER (1998)
- Dipnoi
 - Cf. Gnathorhizidae* - RICHTER & LANGER (1998)
- “Temnospondyl” indet. - LANGER (1998)
- Dinocephalia
 - Anteosauroida - LANGER et al. (1998)
 - Brithopodinae - LANGER (1998)
 - Titanosuchidae - LANGER (1989)

Serra do Cadeado Local Fauna (BARBERENA et al. 1985b)

- “Temnospondyls”
 - Rhinesuchoidea
 - Australerpeton cosgriffi* - BARBERENA (1998)
 - Rhinesuchus*-like form - BARBERENA & DIAS (1998)
- Dicynodontia
 - Endothiodon* sp. - BARBERENA & ARAÚJO (1975)

Aceguá Local Fauna (BARBERENA et al. 1985b)

- “Temnospondyls”
 - Cf. Archegosauridae* (E. V. DIAS 1998; pers. com.)
- “Pareiasaurs”
 - Provelosaurus americanus* - ARAÚJO (1985), LEE (1997)

The Serra do Cadeado Local Fauna (Table 1) has been recorded in the Morro Pelado Member and the upper part of the Serrinha Member of the Rio do Rasto Formation, in the Serra do Cadeado area, Paraná State (BARBERENA et al. 1980, 1985a). Two rhinesuchoid temnospondyls and the dicynodont *Endothiodon* have been recognised in this fauna (BARBERENA 1998, BARBERENA & ARAÚJO 1975, BARBERENA & DIAS 1998), which was dated as Tatarian (BARBERENA et al. 1985a, b), based on correlation with the classic “*Cistecephalus*-zone” of the Karroo Basin (KITCHING 1977).

The Aceguá Local Fauna (Table 1) includes the pareiasaur *Provelosaurus americanus* (ARAÚJO 1985) and a long-snouted temnospondyl (possibly an archegosaurid). This fauna has been recorded in the Bagé-Aceguá Road

locality, where crop out rocks assigned to the Morro Pelado Member of the Rio do Rasto Formation (LAVINA 1991). BARBERENA et al. (1985 a, b) related the Aceguá Local Fauna to the classic “*Daptocephalus*-zone” of the Karroo Basin (KITCHING 1977), dating it as Tatarian.

LANGER (1998), LANGER et al. (1998) and RICHTER & LANGER (1998) presented preliminary accounts on the vertebrate fauna of the Posto Queimado locality. The fossil record of this locality is, however, still poor, and includes, apart from the dinocephalians, only fragmentary amphibian and fish remains (Table 1).

The age of the Posto Queimado locality fauna

Among the tetrapod and fish taxons with a well defined occurrence in the Posto Queimado locality, the dinocephalians provide the more detailed basis for biostratigraphic assignments (LANGER 1998). Other groups as the gnathorhizid dipnoans, for example, that range from the Upper Carboniferous to the Lower Triassic (SCHULTZE 1993), are not useful in dating stages of the Late Permian.

Dinocephalians are well known from deposits of the Karroo Basin, in South Africa, and the Russian Platform, in Eastern Europe (RUBIDGE et al. 1995, SENNIKOV 1996). Primitive forms have also been registered in the San Angelo Formation, Texas (OLSON 1962). The San Angelo dinocephalians are the oldest known representatives of the group, and the best known taxon, *Eosyodon*, is usually assigned to the subfamily Brithopodinae (KEMP 1982, KING 1988). Based on OLSON (1962) and KLEIN & BEAUCHAMP (1994), this stratigraphic unit can be tentatively dated as Ufimian.

The Russian and South African dinocephalians are far better known, providing a more reliable basis for biostratigraphic comparisons. In the Russian Platform, these therapsids are known from two different faunal associations (OLSON 1962, ANDERSON & CRUICKSHANK 1978, KING 1988, SENNIKOV 1996). Most Estemmenosuchidae (e.g. *Estemmenosuchus*) and more primitive Brithopodinae such as *Archaeosyodon* occur in the Ocher fauna (Zone I). The dinocephalian fauna of Isheyevov (Zone II) is much more diverse, including the primitive Tapinocephalinae *Ulemosaurus*, most Brithopodinae (*Doliosauriscus*, *Syodon*, *Titanophoneus*), the possible Anteosaurinae *Deuterosaurus*, as well as the Estemmenosuchidae *Molybdopygus*. ANDERSON & CRUICKSHANK (1978) dated Zones I and II as Kazanian (Wordian), whereas SENNIKOV (1996) dated the Ocher and Isheyevov communities as Late Kazanian and Early Tatarian, respectively.

The South African dinocephalians are also distributed in two different faunal associations in the Beaufort Group, Karroo Supergroup. The *Eodicynodon* Assemblage Zone (RUBIDGE 1990, 1995) includes the primitive

Tapinocephalinae *Tapinocaninus* as well as the Brithopodinae *Australosynodon* (RUBIDGE 1991, 1994). The *Tapinocephalus* Assemblage zone (SMITH & KAYSER 1995a) has a much more diverse dinocephalian fauna, including most Titanosuchinae (*Jonkeria* and *Titanosuchus*), all the more derived Tapinocephalinae (*Moschops*, *Tapinocephalus*, *Struthiocephalus* and others), the Anteosaurinae *Anteosaurus*, as well as *Styracocephalus*.

The *Eodicynodon* Assemblage Zone is the lowermost biozone of the Beaufort Group (RUBIDGE 1990, 1995). On the basis of the correlation with the Russian Ocher fauna, RUBIDGE (1995) dated this biozone as Kazanian. In its turn, the *Tapinocephalus* Assemblage Zone represents the lower part of the classic “*Tapinocephalus*-zone” of the Karroo Basin (KITCHING 1977, RUBIDGE et al. 1995), which was dated as Early Capitanian (Early Tatarian) by ANDERSON & CRUICKSHANK (1978). SMITH & KAYSER (1995a) agreed with this assignment, also dating the *Tapinocephalus* Assemblage Zone as Early Tatarian.

In conclusion, based on the presence of dinocephalian remains, the Posto Queimado fauna is biostratigraphically related to the Zone I and II (Ocher and Isheyevo communities) of the Russian Platform and to the *Eodicynodon* and *Tapinocephalus* Assemblage Zones of the Karroo Supergroup, providing an age assignment of Late Kazanian to Early Tatarian (Fig. 7).

Comparison to other tetrapod faunas of the Rio do Rasto Formation

The most relevant component of the Aceguá Local Fauna, the pareiasaur *Provelosaurus americanus*, was recognised, in the phylogenetic revision of LEE (1997), as the sister taxon of the South African “dwarf-pareiasaurs” (*Anthodon*, *Nanopareia* and *Pumiliopareia*). *Anthodon* is known from the *Cistecephalus* and *Dicynodon* Assemblage Zones of the Karroo Supergroup (SMITH & KEYSER 1995b, KITCHING 1995), while the other two genera have a more restricted stratigraphic distribution, occurring only in the *Cistecephalus* Assemblage Zone (LEE 1997).

Fig. 7. Chronological distribution of some vertebrate groups registered in the Rio do Rasto Formation, based on the stratigraphic record of Europe and South Africa (OLSON 1962, SCHULTZE 1993, MILNER 1993, BENTON 1993, RUBIDGE et al. 1995, SENNIKOV 1996) and the stratigraphic position of the Rio do Rasto Local Faunas in relation to the biostratigraphic zones of the Karroo Supergroup and Russian Platform.

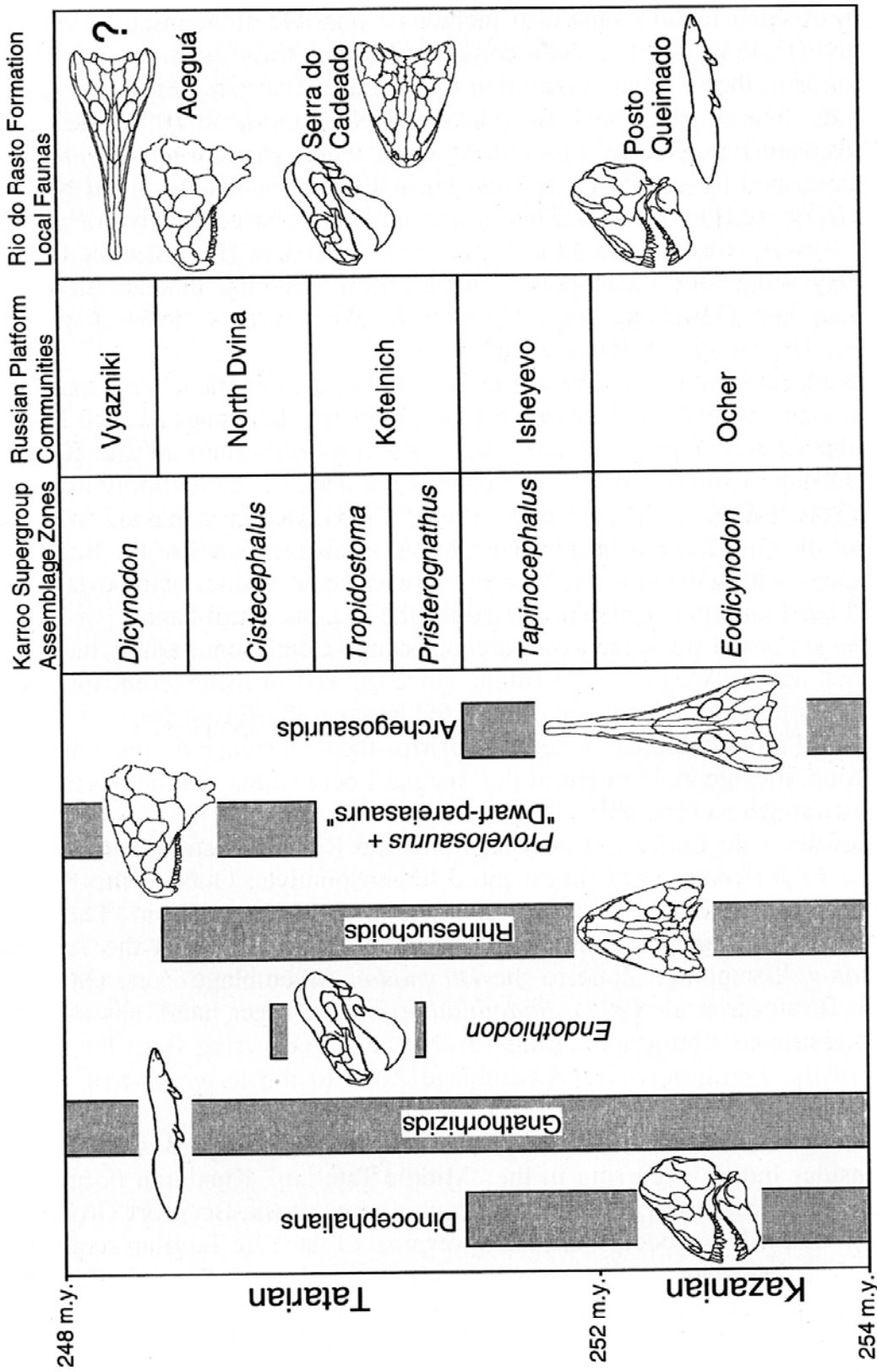


Fig. 7 (Legend see p. 88)

The Aceguá Local Fauna also includes a possible archegosaurid temnospondyl (E. V. DIAS 1998, pers. com.). In Europe, these temnospondyls are known from the Asselian/Sakmarian to the Early Tatarian, but do not reach the Late Tatarian (OLSON 1962, MILNER 1993, SENNIKOV 1996). Archegosaurids were also recorded in South America, where *Prionosuchus plummeri* was described for the Pedra de Fogo Formation (Parnaíba Basin) of North-Eastern Brazil (PRICE 1948). This stratigraphic unit, based mostly in *Prionosuchus* itself, is usually dated as Late Permian (COX & HUTCHINSON 1991), but palynologic and palaeobotanic data, on the contrary, indicate an Early Permian age (MULLER 1962, MESNER & WOOLDRIDGE 1964, CALDAS, MUSSA, LIMA FILHO & ROSSLER 1989).

Based on the phylogenetic affinity between *Provelosaurus* and the “dwarf-pariasaurs”, a close age relation between the Aceguá Local Fauna and the *Cistecephalus* and *Dicynodon* Assemblage Zones of the Karroo Supergroup is suggested. These biozones are usually dated simply as Tatarian (SMITH & KEYSER 1995b, KITCHING 1995). However, having in mind that all the post-*Tapinocephalus* Permian Assemblage Zones of the Beaufort Group are within the Late Tatarian, these two (the latest ones) can be dated as Late Late Tatarian, age also proposed for the Aceguá Local Fauna.

The supposed presence of an archegosaurid clearly contradicts the Late Tatarian age of Aceguá Local Fauna, since the last of these temnospondyls were recorded in the Early Tatarian of the Russian Platform (Zone II). However, until more complete material confirms the occurrence of this amphibian group, the age assignment of the Aceguá Local Fauna will be based only on *Provelosaurus* (Fig. 7).

The Serra do Cadeado Local Fauna of the Rio do Rasto Formation includes *Endothiodon* and rhinesuchoid temnospondyls. Outside the Paraná Basin, rhinesuchoids were only recorded in the Karroo Basin. They are distributed through the Tatarian of the Beaufort Group, from the *Tapinocephalus* Assemblage Zone to the *Dicynodon* Assemblage Zone (MILNER 1993, RUBIDGE et al. 1995). *Endothiodon*, on the other hand, has a much more restricted stratigraphic range in that basin, occurring from the upper part of the *Pristerognathus* Assemblage Zone to the lower part of *Cistecephalus* Assemblage Zone (RUBIDGE et al. 1995).

Endothiodon is also known in the Pranhita-Godavari Basin (Central Peninsular India), occurring in the “Middle Tatarian” Kundaran Formation (RAY 1998). Moreover, the biostratigraphic units of the Beaufort Group, in which *Endothiodon* occurs, are the lowermost of the Late Tatarian sequence. Therefore, based mostly in the record of *Endothiodon*, the Serra do Cadeado Local Fauna is dated as Early Late Tatarian.

In conclusion, as summarised in Figure 7, the fauna of the Posto Queimado locality is dated as Late Kazanian to Early Tatarian, supporting its

assignment as the oldest known from the Rio do Rasto Formation. The Serra do Cadeado Local Fauna is slightly younger, of Early Late Tatarian age, while the Aceguá Local Fauna, the latest in the Rio do Rasto Formation, is dated as Late Late Tatarian.

Acknowledgements

My sincere thanks to Drs. MARTHA RICHTER and CESAR SCHULTZ, Porto Alegre, for their advise and encouragement during this project. Thanks also to Drs. BRUCE RUBIDGE, Johannesburg, and JURI VAN DEN HEEVER, Stellenbosch for fruitful discussions about dinocephalians. I am indebted to Profs. CESAR SCHULTZ (UFRGS), JORGE FERIGOLO (Pró-Guaíba Project and MCN) and MARTHA RICHTER (MCP), who organised and funded the field work by means of their institutions, and also allowed me to study the specimens under their responsibility. Mr. ANTONIO MODESTO kindly allowed the prospective work to be done on his property, my sincere thanks for this. Thanks also to the people who helped me in the field: Dr. FERNANDO ABDALA, EDUARDO BORSATO, Dr. MICHAEL HOLZ, Dr. ERNESTO LAVINA, Dr. CLAUDIA MALABARBA, ANA MARIA RIBEIRO, and CLAITON SCHERER. Drs. AXEL HUNGERBÜHLER and MICHAEL BENTON, Bristol, made useful critical comments on first drafts of the paper. Informative discussion on the Brazilian Permian was carried on with E. V. DIAS and R. IANNUZZI. My work on this project was funded by a Recém-Mestre scholarship from the Brazilian agency FAPERGS.

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Manuscript received December 15, 1998.

Revised version accepted by the Tübingen editors February 10, 1999.

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