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FIRST RECORD OF NON-MAMMALIAN CYNODONTS (THERAPSIDA) IN THE SANGA DO CABRAL FORMATION (EARLY TRIASSIC) OF SOUTHERN BRAZIL

by

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ABSTRACT

New material from the Sanga do Cabral Formation in southern Brazil is described, including one distal and three proximal portions of femora, and a distal portion of a humerus. Comparative studies indicate affinities of the proximal femora and the distal humerus with non-mammalian cynodonts, whereas the distal femur cannot be attributed with certainty to this group. These postcranial elements are the first record of non-mammalian cynodonts for the Sanga do Cabral Formation and demonstrate the presence of small- to medium-sized representatives of this group in the Early Triassic fauna of Brazil.

KEYWORDS: Triassic, non-mammalian cynodonts, Sanga do Cabral Formation, Brazil.

INTRODUCTION

Permian and Triassic outcrops of the Paraná Basin in southern Brazil have produced abundant remains of continental tetrapods (Barberena *et al.* 1985; Schultz 1995; Abdala *et al.* 2001). The earliest Triassic deposits of the basin correspond to the Sanga do Cabral Formation, known from several localities in the Rio Grande do Sul state (Figure 1). Strata varying from tabular to lenticular, with a thickness of 0,5 to 1,5 m, characterize this unit. Calcium carbonate concretions of varying size, as well as small mudstone intraclasts, are frequently dispersed in the sandstones or form conglomerates (Andreis *et. al.* 1980; Barberena *et. al.* 1981). Isolated and mostly fragmentary fossil remains of small size are found within the intraformational conglomerates, rendering taxonomic identification difficult.

The fossil assemblage of the Sanga do Cabral Formation has long been considered Early Triassic in age (Lavina 1983; Barberena *et. al.* 1985; Langer & Lavina 2000), with the tetrapod fauna dominated by procolophonids. In addition, amphibian remains, tentatively assigned to Lydekkerinidae and Rhytidosteidae (Barberena *et al.* 1981; Lavina & Barberena 1985; Dias-da-Silva & Schultz 1999) are also present. More recently, protorosaur vertebrae

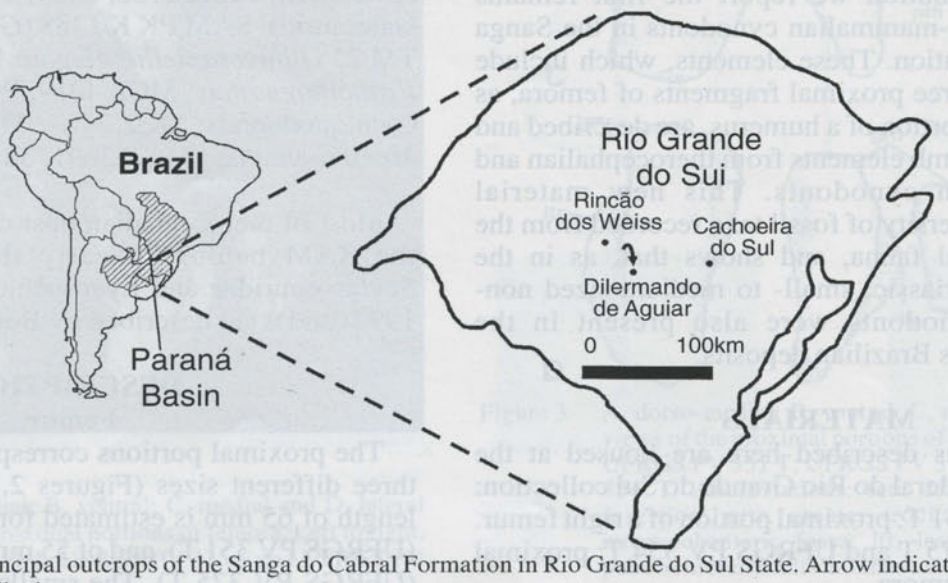

Figure 1. Map of the principal outcrops of the Sanga do Cabral Formation in Rio Grande do Sul State. Arrow indicates provenance of the material described.

(Langer & Schultz 1997; Dias-da-Silva 1998; Langer & Lavina 2000) and two dicynodont stapes (Schwanke & Kellner 1999) have been reported.

The correlation of the Sanga do Cabral Formation with the *Lystrosaurus* Assemblage Zone of the Karoo basin in South Africa is based on the presence of *Procolophon* and rhytidosteid and lydekkerinid amphibians (Barberena *et al.* 1985). The *Lystrosaurus* Assemblage Zone, which includes the Palingkloof Member of the Balfour Formation, the Katberg Formation and the lower third of the Burgersdorp Formation, is overwhelmingly dominated by the dicynodont *Lystrosaurus* (95% of the fauna). Also frequently found are remains of the amphibian *Lydekkerina*, the procolophonid *Procolophon*, the proterosuchian *Proterosuchus*, the therocephalian *Moschorhinus*, and the cynodont *Thrinaxodon* (Groenewald & Kitching 1995). Recent studies (Neveling *et al.* 1999) indicate the existence of an "Impoverished Zone" situated between the *Lystrosaurus* Assemblage Zone and the *Cynognathus* Assemblage Zone. This zone records *Procolophon* and *Thrinaxodon* in the last portion of the Katberg Formation. It also yields the non-mammalian cynodont *Trirachodon*, the capitosaurid amphibian *Kestrosaurus* (the most abundant taxon in the "Impoverished Zone"), and the procolophonid *Thelegnathus* in the lower portion of the Burgersdorp Formation. The amphibian *Trematosuchus* is recorded in both formations and, importantly, there are no records of *Lystrosaurus* for the "Impoverished Zone" (Neveling *et al.* 1999).

When comparing the Sanga do Cabral fauna with the *Lystrosaurus* Assemblage Zone or with the "Impoverished Zone", the scarcity of non-mammalian therapsids in the south Brazilian fauna is surprising. The only therapsid specimens recovered from the Sanga do Cabral Formation are two stapes of dicynodonts, considered to be *Lystrosaurus* with different degrees of taxonomic confidence (Schwanke & Kellner 1999; Langer & Lavina 2000).

In this contribution we report the first remains attributed to non-mammalian cynodonts in the Sanga do Cabral Formation. These elements, which include one distal and three proximal fragments of femora, as well as a distal portion of a humerus, are described and compared with limb elements from therocephalian and non-mammalian cynodonts. This new material increases the diversity of fossil taxa recorded from the Sanga do Cabral fauna, and shows that, as in the African Early Triassic, small- to medium-sized non-mammalian cynodonts were also present in the contemporaneous Brazilian deposits.

MATERIALS

The specimens described here are housed at the Universidade Federal do Rio Grande do Sul collection:

UFRGS PV 351 T: proximal portion of a right femur.

UFRGS PV 375 T and UFRGS PV 354 T: proximal portions of left femora.

UFRGS PV 353 T: distal portion of a left femur.

UFRGS PV 332 T: distal portion of a right humerus.

Except for UFRGS PV 375 T, the locality of which is unknown, all the other specimens were collected from a series of outcrops known as Catuçaba (Barberena *et al.* 1985) because they were situated in the area covered by the geologic map of that name. However, the locality of Catuçaba is distant from these outcrops and, therefore, we prefer to avoid use of that name for them in Figure 1. The outcrops are located approximately 15 km south of the city of Dilermando de Aguiar, beside an unfinished railroad between Dilermando de Aguiar and São Gabriel, which was under construction in the1980s (Barberena *et al.* 1981).

These specimens were compared to postcranial material from the following collections: BP: Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg; MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, Massachussets; PVL: Paleontologia de Vertebrados Lillo collection, Universidad Nacional de Tucumán, Argentina; QR: National Museum, Bloemfontein; SAM: South African Museum (Iziko Museums), Cape Town; and TM: Transvaal Museum (Northern Flagship Institution), Pretoria.

Comparative material included the following specimens:

Femora

Therocephalian: SAM PK K 306, 353, 1387, 7809, 12185 (*Zinnosaurus paucidens* holotype).
Thrinaxodon: BP/1/1730, 2820, 3911, 5208; QR 1864; SAM PK K 8004; TM 132,172.
Probainognathus: PVL 4677.
Chiniquodontids: MCZ 3781.
Massetognathus: MCZ 3691; PVL 4613.

Humeri

Therocephalian: BP/1/3849 (*Moschorhinus*); QR 3375 (*Theriognathus*); SAM PK K 1387, 7809, 12185 (*Zinnosaurus paucidens* holotype).
Thrinaxodon: BP/1/1720, 2531, 2820, 4534, 5208, 5372; SAM PK K 1126, 8004; TM 4192.
Galesaurids: SAM PK K 1388 (*Galesaurus planiceps*); TM 25 (*Platycraniellus elegans* holotype).
Probainognathus: MCZ 4019; PVL 4677, 4725.
Chiniquodontids: MCZ 3781, 4163.
Massetognathus: MCZ 3691, 3813, 4017; PVL 4613.

Most of therocephalian post-cranial materials from the SAM belong to early therocephalians (i.e. Scylacosauridae and Lycosuchidae: van den Heever, 1994) and were described by Boonstra (1964).

DESCRIPTION

Femur

The proximal portions correspond to individuals of three different sizes (Figures 2, 3; Table 1). A total length of 65 mm is estimated for the largest specimen (UFRGS PV 351 T), and of 55 mm for the middle-sized (UFRGS PV 375 T). The smallest fragment (UFRGS

PV 354 T) would correspond to a femur of approximately 30 mm in length. The distal fragment (UFRGS PV 353 T) would correspond to a bone with a length intermediate between 55 and 65 mm.

All of the proximal fragments have the portion corresponding to the head somewhat directed dorsally in relation to the shaft (Figures 2C, D; 3C, D). The head itself is absent, apparently through a lack of ossification, although preservational bias cannot be discounted; the greater trochanters are not preserved completely, and appear to have been continuous with the head (Figures 2A; 3A). The lesser trochanter, incompletely preserved in all of the specimens, forms a ventro-medial crest. A shallow intertrochanteric fossa is present between both trochanters (Figures 2B; 3B). This fossa is especially well defined in UFRGS PV 375 T.

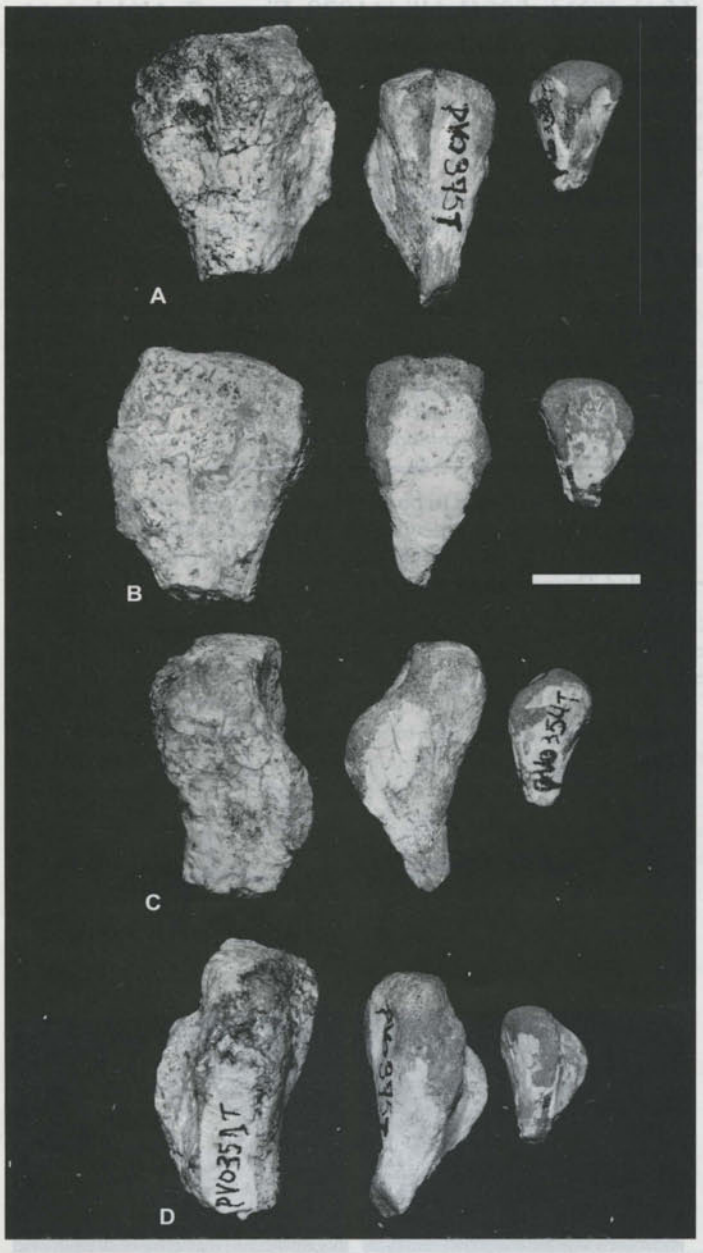

Figure 2. A, dorso-medial; B, ventral; C, medial and D, lateral views of the proximal portions of femora. Left to right, UFRGS PV 351 T; UFRGS PV 375 T and UFRGS PV 354 T. Scale 1 cm.

The proximal portion of the right femur (UFRGS PV 351 T) exhibits a distinct dorsal furrow between the head and the greater trochanter (Figures 2A; 3A). A shallower furrow is also present between the diaphysis and the lesser trochanter, probably for the insertion of the muscle puboischiofemoralis internus (Figures 2C; 3C; Jenkins 1971).

The distal fragment (UFRGS PV 353 T) shows well-preserved condyles, with a longitudinally restricted and shallow flexor fossa between them (Figure 4). The lateral condyle is ventrolaterally oriented and more developed than the medial. A narrow patellar groove is present dorsally, ending at the level of the flexor fossa.

Humerus

The distal end of the humerus (UFRGS PV 332 T) is approximately 25 mm wide (Figure 5, Table 1). The

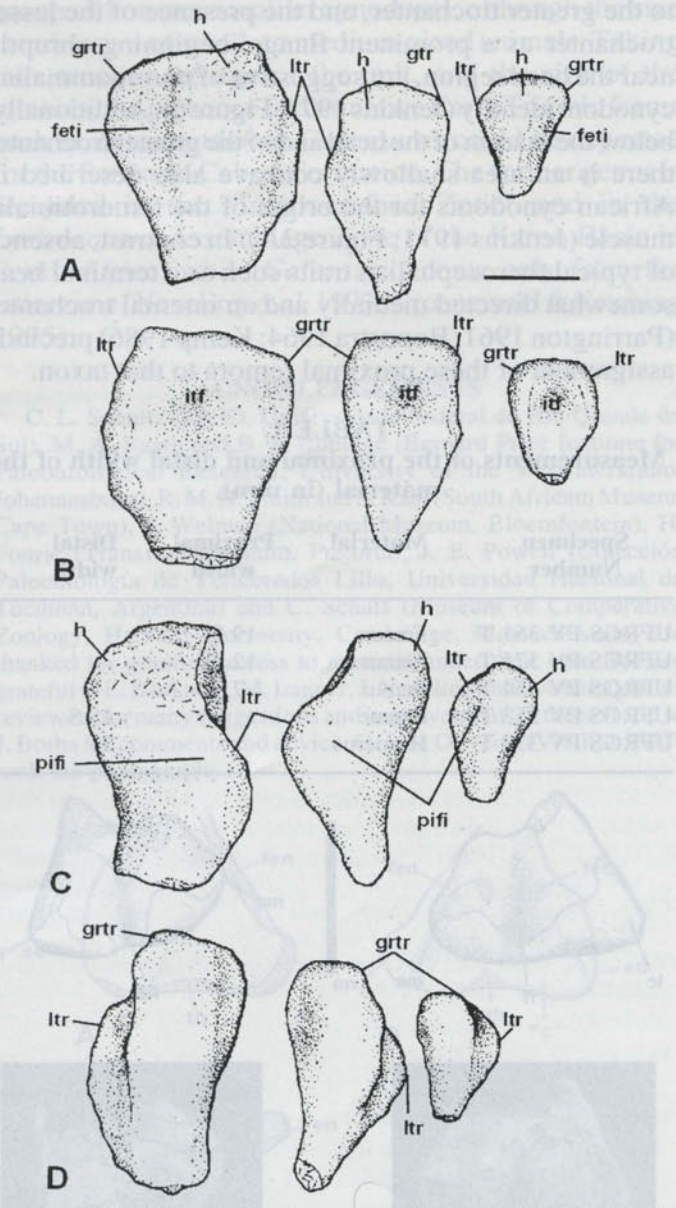

Figure 3. A, dorso-medial; B, ventral; C, medial and D, lateral views of the proximal portions of femora. Left to right, UFRGS PV 351 T; UFRGS PV 375 T and UFRGS PV 354 T. Abbreviations: feti: femorotibialis muscle insertion; grtr, greater trochanter; h, head; itf, intertrochanteric fossa; ltr, lesser trochanter; pifi, puboischiofemoralis internus muscle insertion. Scale 1 cm.

entepicondyle is slightly more projected laterally than the ectepicondyle. The ovoid entepicondylar foramen is incomplete without trace of the osseous bar that delimits it ventro-medially. There is no vestige of the ectepicondylar foramen because both the ectepicondyle and its lateral border are incompletely preserved. The distal border of the trochlea is not ossified, and the capitulum appears as a partially ossified ventral projection.

DISCUSSION

The material described here presents several features indicating its therapsid identity, with many of them suggesting a more specific assignment to non-mammalian cynodonts. In the proximal fragments of the femora, the head region somewhat reflected dorsally, the continuity of the head region with that corresponding to the greater trochanter, and the presence of the lesser trochanter as a prominent flange, beginning abruptly near the head region, are suggestive of non-mammalian cynodont identity (Jenkins 1971; Figure 6). Additionally, below the margin of the head and of the greater trochanter there is an area shallowly concave also described in African cynodonts for the origin of the femorotibialis muscle (Jenkins 1971; Figure 2A). In contrast, absence of typical therocephalian traits such as a terminal head somewhat directed medially and an internal trochanter (Parrington 1961; Boonstra 1964; Kemp 1986) preclude assignment of these proximal femora to that taxon.

TABLE 1.
Measurements of the proximal and distal width of the material (in mm).

Specimen Number	Material	Proximal width	Distal width
UFRGS PV 351 T	Femur	19.8	
UFRGS PV 375 T	Femur	12.4	
UFRGS PV 354 T	Femur	7.9	
UFRGS PV 353 T	Femur		15.5
UFRGS PV 332 T	Humerus		25

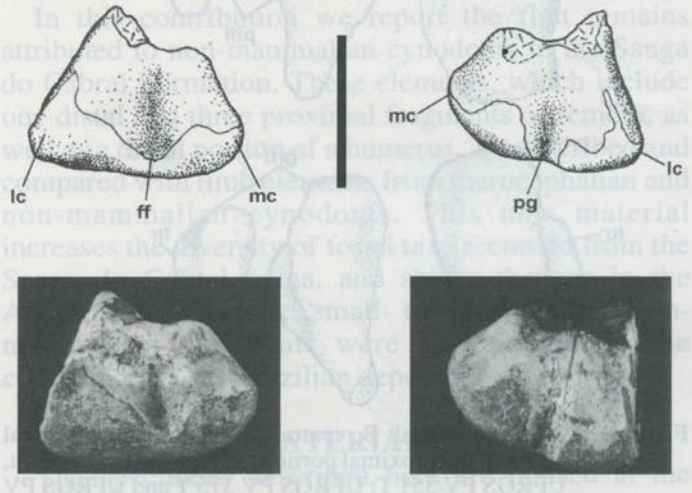

Figure 4. Ventral and dorsal view of the distal portion of femur (UFRGS PV 353 T). Abbreviations: ff, flexor fossa; lc, lateral condyle; mc, medial condyle; pg, patellar groove. Scale 1 cm.

The difference in size between the medial and lateral condyles of the distal femur, also suggest non-mammalian cynodont affinity. The lateral condyle is wider than the medial in different non-mammalian cynodonts, such as *Exaeretodon* (Bonaparte, 1963: Figure 11B), *Massetognathus* (Jenkins 1970: Figure 7), *?Cynognathus* (*?Diademodon*) (Jenkins 1971: Figure 48), and *Luangwa* (Kemp, 1980b: Figure 14). The shallow flexor fossa of the specimen precludes its assignment to procynosuchid cynodonts, which are characterized by a deep fossa (Kemp 1980a). A therocephalian identity for this element cannot, however, be ruled out conclusively.

Regarding the sizes estimated for the complete femora, the largest proximal fragment matches femoral sizes of *Procynosuchus* (Kemp, 1980a: Figure 14), chiniquodontid cynodonts (MCZ 3801) and *Massetognathus* (Jenkins 1970: Figure 7; Abdala, pers. obs.). The middle-sized element agrees with the galesaurid described by Parrington (1934; see Table 2),

TABLE 2.
Total lengths and proximal and distal widths of femora of Early Triassic non-mammalian cynodonts from South Africa (in mm).

Reference	Taxon	Total length	Proximal width	Distal width
Jenkins (1971)	*Thrinaxodon*	33	12	10.5
Parrington (1934)	Galesauridae*	50	13	12
Haughton (1924)	*Glochinodontoides***	53	22.5	17.5

*Originally considered to be *Galesaurus* sp. by Parrington (1934); Jenkins (1971) regards specimen UMC R.2722, on which the femur description is based, as Galesauridae (at that time the family included *Thrinaxodon*).
***Glochinodontoides* is a synonym of *Galesaurus* (Hopson & Kitching 1972).

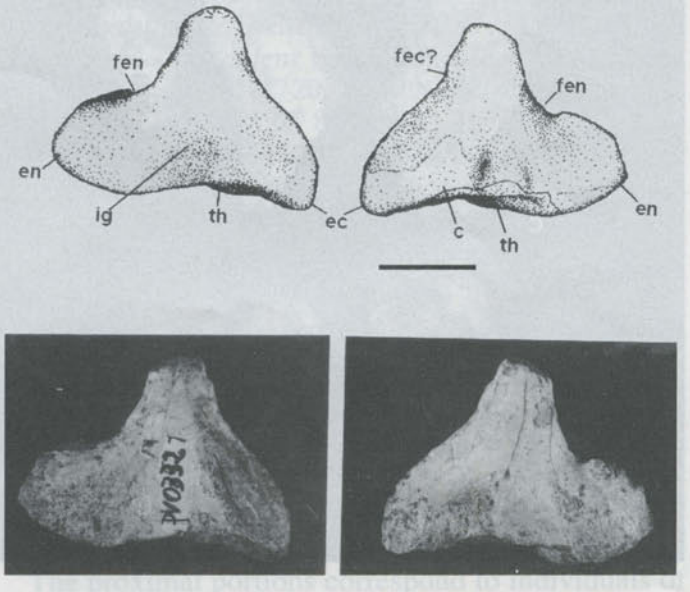

Figure 5. Dorsal and ventral views of the distal portion of humerus (UFRGS PV 332 T). Abbreviations: c, capitulum; ec, ectepicondyle; en, entepicondyle; fec?, ectepicondylar foramen; fen, entepicondylar foramen; ig, intercondylar groove; th, trochlea. Scale 1 cm.

while the small-sized fragment matches those of *Thrinaxodon* (Jenkins 1971; Figure 6, Table 2) and *Probainognathus* (Abdala 1996). The size estimated for the complete bone matching the fragment of the distal end of the femur fits more closely with those of traversodontid cynodonts such as *Pascualgnathus* (Bonaparte 1966: Figures 13A,B) and *Massetognathus* (Jenkins 1970: Figure 7). Femora with this size would be possible to find in galesaurids, considering the largest skull size in the group of 11.4 cm (QR 860).

The distal portion of the humerus is more confidently identified as pertaining to non-mammalian cynodont, considering the absence of an extended flexor fossa, commonly present in therocephalians (= 'fossa for olecranon' of Boonstra, 1964). The distinct lateral projection of the entepicondyle found in this specimen is also observed in galesaurids (Parrington, 1934), chiniquodontid cynodonts (Abdala 1999; MCZ 4163) and, to a lesser extent, in *Thrinaxodon* (Figure 7A; Jenkins, 1971). On the contrary, this projection is markedly less developed in *Probainognathus* (MCZ 4019; PVL 4677) and many traversodontids, such as *Massetognathus* (MCZ 4017), *Exaeretodon* (Bonaparte 1963) and *Luangwa* (Kemp 1980b), although not *Pacualgnathus* (Bonaparte, 1966: Figure 10A). Moreover, the specimen described here approaches more closely to *Thrinaxodon* (Figure 7B) and *Galesaurus* (Jenkins 1971) in the lack of ossification in the trochlea and the partial ossification of the capitulum, but in contrast to the condition in these genera (see Figure 7C), the ectepicondylar thickness is greater than the entepicondylar. The distal width of the humerus matches that of galesaurids (Table 3) and the traversodontid *Pascualgnathus* (Bonaparte 1966: Figures 10A, B).

The postcranial elements described here are the first record of non-mammalian cynodonts for the Sanga do Cabral Formation. Morphological criteria alone are insufficient to confidently assign them to a specific group of non-mammalian cynodonts, although the size is indicative of small- to medium-sized animals. Taking into account the age of the unit, and the size of the remains, the presence of distinctive Early Triassic forms such as *Thrinaxodon* or *Galesaurus* could be expected for the Sanga do Cabral Formation. The former genus is recorded in the "Impoverished Zone" and in the *Lystrosaurus* Assemblage Zone of the Karoo Basin in South Africa, while *Galesaurus* come only from the latter zone (Neveling *et al.* 1999; Groenewald & Kitching 1995).

TABLE 3.
Total lengths and distal widths of humeri of Early Triassic non-mammalian cynodonts from South Africa (in mm).

Material	Taxon	Total length	Distal width
BP/1/2820	*Thrinaxodon*	31.2	17.5
BP/1/2820b	*Thrinaxodon*	30.4	16.9
BP/1/5208	*Thrinaxodon*	33.2	18.4
Jenkins (1971)	*Thrinaxodon*	36	18.5
Parrington (1934)	Galesauridae*	46	26
Haughton (1924)	*Glochinodontoides***	52	26.5

*Originally considered to be *Galesaurus* sp. by Parrington (1934); Jenkins (1971) regards specimen UMC R.2722 on which the humerus description is based, as Galesauridae (at that time, the family included *Thrinaxodon*).
***Glochinodontoides* is a synonym of *Galesaurus* (Hopson & Kitching 1972).

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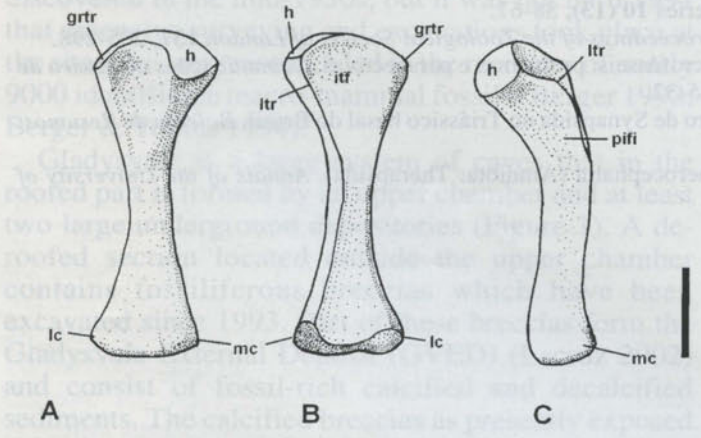

Figure 6. A, dorsal; B, ventral and C, medial views of the femur of *Thrinaxodon*. Abbreviations: grtr, greater trochanter; h, head; itf, intertrochanteric fossa; lc, lateral condyle; ltr, lesser trochanter; mc, medial condyle; pifi, puboischiofemoralis internus muscle insertion (modified from Jenkins, 1971). Scale 1 cm.

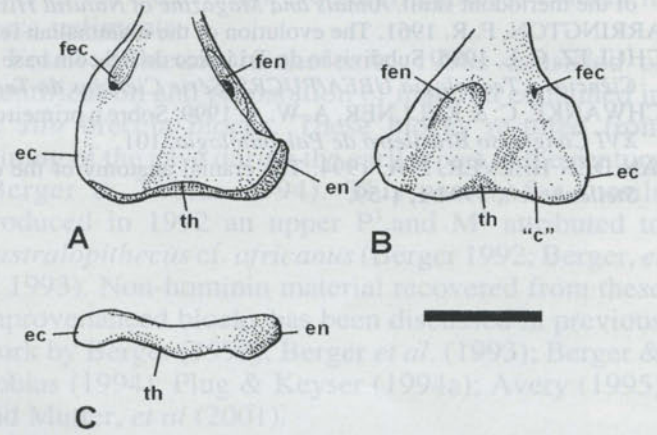

Figure 7. A, dorsal; B, ventral and C, distal views of the distal portion of the right humerus of *Thrinaxodon*. Abbreviations: " c", capitulum; ec, ectepicondyle; en, entepicondyle; fec, ectepicondylar foramen; fen, entepicondylar foramen; th, trochlea (modified from Jenkins, 1971). Scale 1 cm.

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