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REASSESSMENT OF THE POSTCRANIAL ANATOMY OF *PROZOSTRODON BRASILIENSIS* AND IMPLICATIONS FOR POSTURAL EVOLUTION OF NON-MAMMALIAFORM CYNODONTS

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ABSTRACT—Postcranial anatomical studies on non-mammaliaform cynodonts are essential for understanding postural and locomotor advances in mammalian evolution and provide information about the transition from the sprawling posture of basal synapsids to a more erect posture. Nevertheless, the number of functional analyses of this group remains small because little postcranial material has been discovered and the articular surfaces of bones are rarely preserved. Here, we present a detailed description of the postcranial skeleton of *Prozostrodon brasiliensis* (Probainognathia, Prozostrodontia), a non-mammaliaform cynodont from the Upper Triassic of Brazil (*Hyperodapedon* Assemblage Zone, Candelária Sequence), closely related to Mammaliaformes. The study adds new information on postcranial morphology, and functional implications are investigated. *Prozostrodon brasiliensis* had a semisprawling forelimb and a more therian-like erect hind limb. These results confirm that the evolution of an erect posture and a new muscular orientation of the hind limb occurred within Cynodontia before the appearance of the clade Mammaliaformes.

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INTRODUCTION

Non-mammaliaform cynodonts are considered a crucial therapsid group because their remains document the anatomical steps that led to the mammalian pattern. First recorded from the early part of the late Permian of South Africa (Botha et al., 2007; Kammerer, 2016), cynodonts survived the end-Permian crisis and underwent a broad radiation during the Triassic with the clade Eucynodontia (Abdala, 2007; Ruta et al., 2013). Recent cladistic analyses support a major dichotomy of Eucynodontia into mainly, although not exclusively, herbivorous/omnivorous cynognathians (with its basal-most form being a carnivorous taxon) and the mainly faunivorous probainognathians (Hopson and Kitching, 2001; Ruta et al., 2013; Martinelli et al., 2017b), in which crown group Mammalia is included (Rowe, 1988; Kielan-Jaworowska et al., 2004). Non-mammaliaform probainognathians include several morphologically disparate clades, such as Ecteniiniidae, Chiniquodontidae, Probainognathidae, Tritheledontidae, Tritylodontidae, and Brasilodontidae, in addition to several species unassigned to family, such as *Prozostrodon brasiliensis*, *Botucaratherium belarminoi*, and *Alemoatherium huebneri* (Fig. 1). *Prozostrodon brasiliensis*, from the Upper Triassic of Brazil, is considered a derived probainognathian and a key taxon in the origin of the clade Prozostrodontia (sensu Liu and

Olsen, 2010), being its basal-most member (Ruta et al., 2013; Soares et al., 2014; Martinelli et al., 2016, 2017b).

In spite of the key phylogenetic position of *P. brasiliensis*, several aspects of its anatomy remain unclear. The holotype was originally described as *Thrinaxodon brasiliensis* by Barberena et al. (1987) based on the apparent similarity of its ‘triconodont’ postcanine teeth (Fig. 2) to those of the African epicynodont *Thrinaxodon liorhinus* Seeley, 1894. Subsequently, the specimen was restudied and placed in the new genus *Prozostrodon* by Bonaparte and Barberena (2001). These authors summarized most, but not all, of the available elements of the only known specimen at that time. After those contributions, several cranial and dental features of *P. brasiliensis* were addressed by other authors (e.g., Martinelli et al., 2005, 2016, 2017a, 2017b; Liu and Olsen, 2010; Soares et al., 2014). More recently, Pacheco et al. (2017) reported the second known specimen of this taxon, based on an isolated lower jaw.

Here, we present a detailed postcranial description of this basal prozostrodontian, reassessing the already known postcranial elements and describing new material of the holotype specimen. Moreover, functional implications of the postcranium are also investigated to improve our knowledge of postural and locomotor advances in pre-mammalian evolution.

Institutional Abbreviations—CAPP/UFMS, Centro de Apoio à Pesquisa Paleontológica, Universidade Federal de Santa Maria, São João do Polêsine, Brazil; MNHN, Museum National d’Histoire Naturelle, Paris, France; MVP, Museu de

*Corresponding author.

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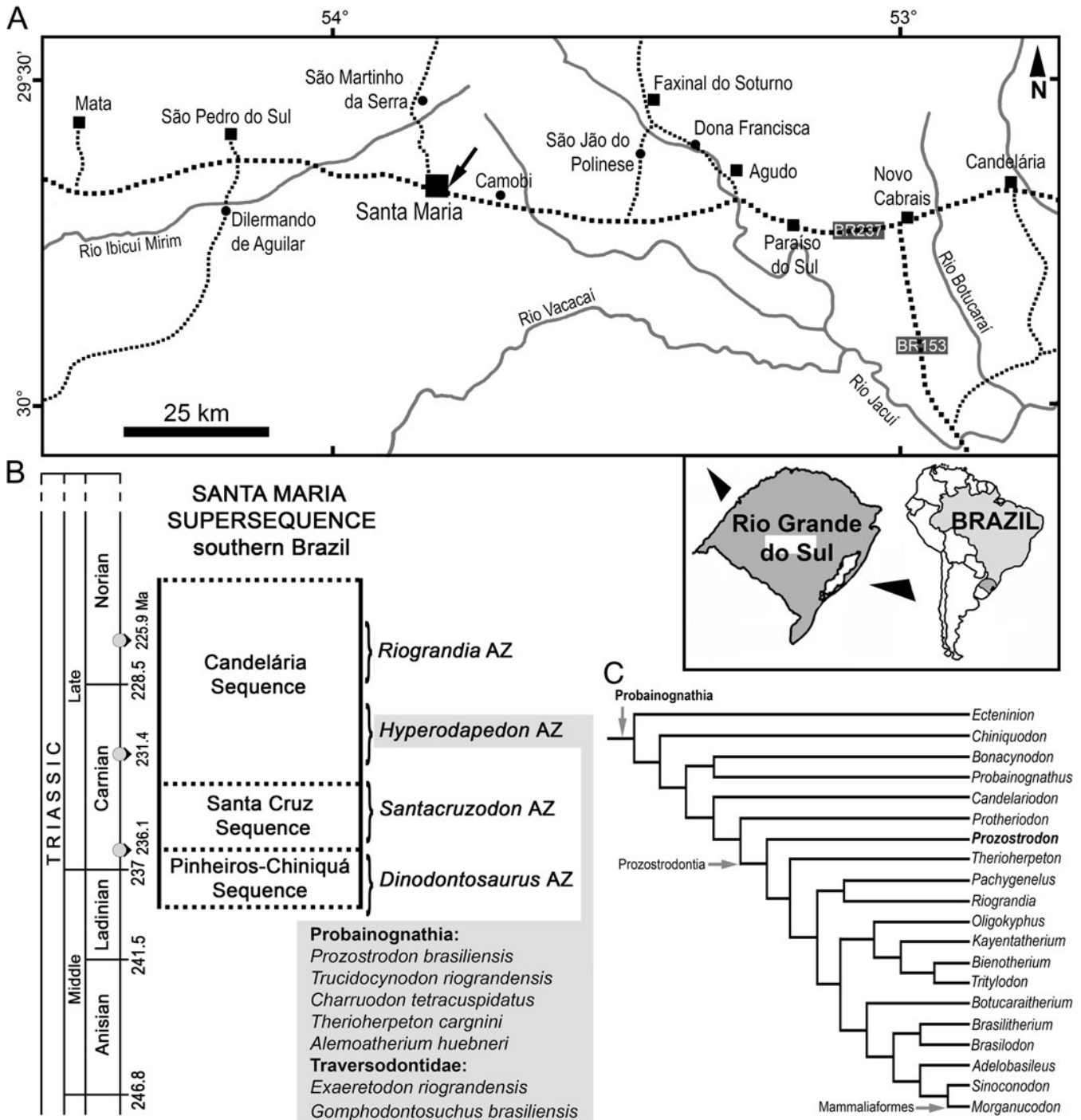


FIGURE 1. **A**, location map of Santa Maria city, state of Rio Grande do Sul, Brazil, where the holotype specimen of *P. brasiliensis* was found. **B**, chrono- and biostratigraphy of the Triassic Santa Maria Supersequence from southern Brazil with vertebrate assemblage zones (AZ), detailing the non-mammaliaform cynodont fossil content of *Hyperodapedon* Assemblage Zone. The ages of the column follow Ogg et al. (2016). The radiometric dates of 236.1, 231.4, and 225.9 Ma correspond to the first half of the Chañares Formation (Marsicano et al., 2016), the base of the Ischigualasto Formation, and the base of Los Colorados Formation (Martinez et al., 2013), respectively. **C**, phylogenetic relationships of *P. brasiliensis* (based on Liu and Olsen, 2010; Martinelli et al., 2017b).

Patronato Alves Ramos, Santa Maria, Brazil; **NHMUK**, Natural History Museum, London, U.K.; **OUMNH**, Oxford University Museum of Natural History, Oxford, U.K.; **UFRGS**, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil; **UMZC**, University Museum of Zoology, University of Cambridge, Cambridge, U.K.

MATERIALS AND METHODS

The postcranial description of *P. brasiliensis* is based on a single specimen, the holotype UFRGS-PV-0248-T, housed at the Departamento de Paleontologia e Estratigrafia, Instituto de Geociências, Universidade Federal do Rio Grande do Sul

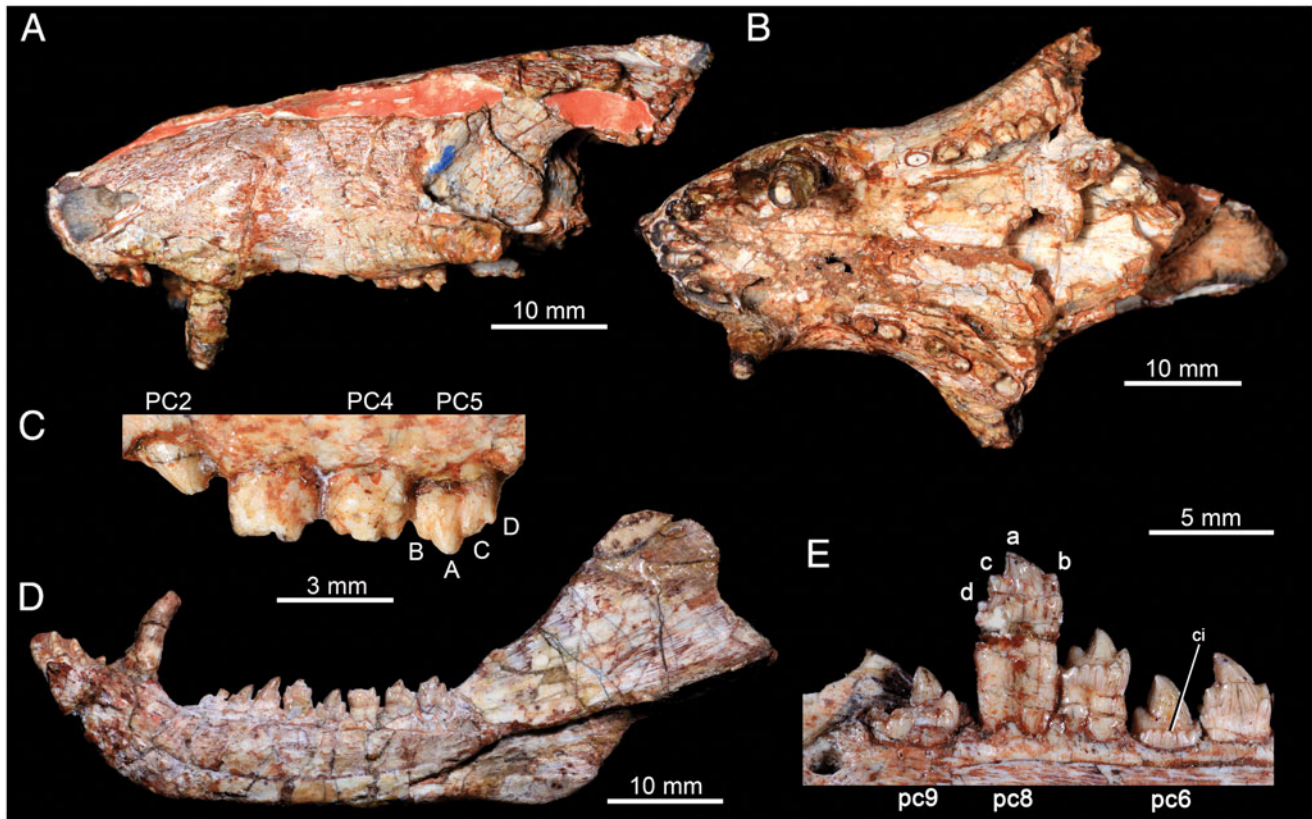


FIGURE 2. *Prozostrodon brasiliensis*, UFRGS-PV-0248-T, holotype. **A–B**, skull in **A**, left lateral and **B**, ventral views. **C**, left second to sixth left upper postcanines in labial view. **D**, right lower jaw in lingual view. **E**, detail of left lower fifth to ninth postcanines in lingual view. **Abbreviations:** **A/a, B/b, C/c, D/d**, upper/lower cusps; **ci**, cingulum; **PC/pc**, upper and lower postcanine teeth.

(UFRGS), Porto Alegre, Brazil. The specimen includes the skull, jaws, and an incomplete and disarticulated axial and appendicular skeleton. Most postcranial elements are well preserved, in spite of lack of the epiphyses of the long bones.

The postcranial elements of *P. brasiliensis* were directly compared with other non-mammaliaform cynodonts: *Aleodon cromptoni* (UFRGS-PV-0146-T); *Trucidocynodon riograndensis* (UFRGS-PV-1051-T); *Irajatherium hernandezii* (UFRGS-PV-599-T, UFRGS-PV-1068-T); *Brasilodon quadrangularis* (UFRGS-PV-1043-T); *Therioherpeton cagnini* (MVP-05.22.04); *Cricodon metabolus* (UMZC T905); *Cynognathus crateronotus* (NHMUK-R2571); *Cynognathus* sp. (NHMUK-R3772a); *Diademodon* sp. (NHMUK-R2803, R3581, UMZC T433, T436, T447, T448, T449, T455, T456, T489–502, T503, T971, T1017); *Galesaurus planiceps* (UMZC T823); *Galesaurus* sp. (UMZC T820–821); *Luangwa drysdalli* (OUMNH-TSK121); *Oligokyphus* sp. (NHMUK-R7386-7491); *Scalenodon angustifrons* (UMZC T925, T972); *Scalenodon* sp. (NHMUK-R36802, R9391, UMZC T974); and *Thrinaxodon liorhinus* (NHMUK-R15957, UMZC T1101). For comparative purposes, we also considered extant monotremes, marsupials, and placentals, such as *Ornithorhynchus anatinus* (MNHN 1906-484), *Tachyglossus aculeatus* (MNHN 1903-537, 1903-538), *Caluromys philander* (MNHN 1999-1061), *Didelphis marsupialis* (MNHN 1978-538), *Marmosa demerarae* (MNHN 1998-1832), and *Canis lupus familiaris* (UFRGS-PV-14-Z).

Comparisons with other non-mammaliaform cynodonts (e.g., *Procynosuchus*, *Menadon*) and early mammaliaforms (e.g., *Eozostrodon*, *Megazostrodon*) were also made on the basis of detailed descriptions in the literature (e.g., Jenkins and

Parrington, 1976; Kemp, 1980a; Gambaryan and Averianov, 2001; Kammerer et al., 2008).

Further preparation of the holotype was done, using needles and a pneumatic hammer (PaleoTools Micro-Jack 2.0, 5.0). The postcranial measurements were taken directly on the specimen with digital calipers to the nearest 0.1 mm. Angle measurements were made with the software Inkscape, based on photographs.

Some structures (fossae, crests) present on the appendicular skeleton of *P. brasiliensis* permit determination of the approximate position or development of muscles. The origin and insertion of the main muscles were estimated using homology models, including non-mammaliaform therapsids (Romer, 1922; Jenkins, 1971a; Kemp, 1980b), and studies dealing with osteology and myology of living amphibians (Mivart, 1869; Davison, 1895; Walthall and Ashley-Ross, 2006), squamates (Holmes, 1977; Jenkins and Goslow, 1983; Zaaf et al., 1999), crocodylians (Romer, 1956; Meers, 2003; Otero et al., 2010; Lima et al., 2016), monotremes (Howell, 1937a; Walter, 1988; Gambaryan et al., 2002, 2015), metatherians (Howell, 1937b; Jenkins and Weijs, 1979; Stein, 1981; Argot, 2002), and eutherians (McEvoy, 1982; Thorington et al., 1997; Fisher et al., 2007, 2008, 2009, 2010).

‘Mammalian’ rather than ‘reptilian’ terminology is used to designate bone structures and muscles, but the ‘reptilian’ homologue of each structure and muscle is given the first time the structure/muscle is mentioned. Muscle nomenclature and homology between mammals and reptiles are mainly based on the work of Ellsworth (1974), Diogo et al. (2009), and Abdala and Diogo (2010).

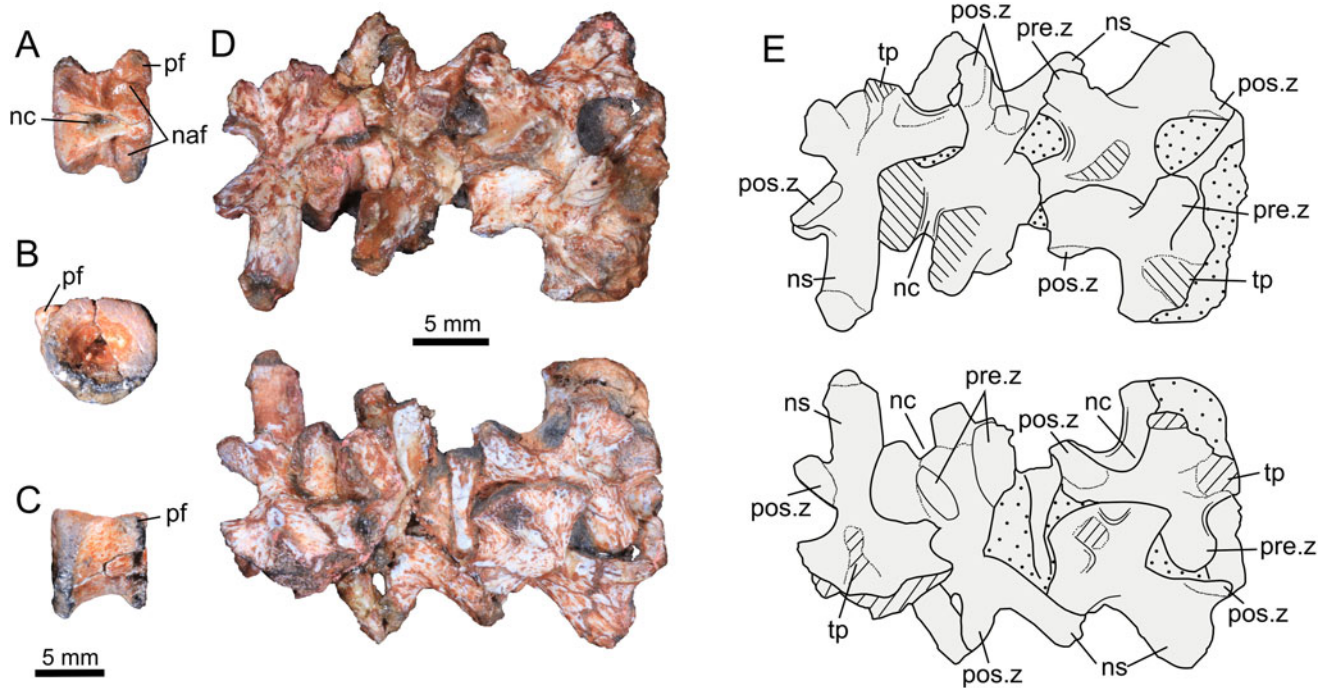


FIGURE 3. *Prozostrodon brasiliensis*, UFRGS-PV-0248-T, holotype, axial skeleton. **A–C**, dorsal centrum in **A**, dorsal, **B**, posterior, and **C**, lateral views. **D**, photographs and **E**, schematic drawings of the four preserved neural arches, from both sides. **Abbreviations:** naf, facet for neural arch; nc, neural canal; ns, neural spine; pf, parapophyseal facet; pos.z, postzygapophysis; pre.z, prezygapophysis; tp, transverse process (eroded).

SYSTEMATIC PALEONTOLOGY

CYNODONTIA Owen, 1861

PROBAINOGNATHIA Hopson, 1990

PROZOSTRODONTIA Liu and Olsen, 2010

PROZOSTRODON Bonaparte and Barberena, 2001

PROZOSTRODON BRASILIENSIS Barberena,
Bonaparte, and Teixeira, 1987

Holotype—UFRGS-PV-0248-T, anterior portion of skull with dentition but without zygomatic arches, complete right and partial left dentary with dentition (Fig. 2), 17 vertebral centra, four dorsal neural arches, three sacral vertebrae, fragments of ribs, right clavicle, interclavicle, partial right and left humeri, right ilium, both ischia, both femora, both tibiae, partial left fibula, and partial left foot (Figs. 3–6).

Referred Material—CAPPA/UFSM 0123, right lower jaw with partial dentition (Pacheco et al., 2017).

Emended Diagnosis—Probainognathian cynodont with the following association of features (autapomorphies marked with an asterisk*): four upper incisors, increasing in size posteriorly; four lower incisors, slightly spatulate, decreasing in size posteriorly, with the apical third of the crown posteriorly inclined; lower canine with finely serrated distal margin; middle and posterior upper postcanine teeth with low crown, without distinctive cingula, with four mesiodistally aligned cusps (A–D), with cusps $A > C \geq B \gg D^*$; posterior-most upper postcanine with distolabial accessory cusp; anterior lower postcanine teeth with conspicuous cusp a and small cusps b, c, and usually d*; posterior lower postcanine teeth of ‘triconodont’ type, with cusps $a > c > b > d$, with continuous lingual cingulum bearing up to nine small discrete cusps*; length of the lower tooth row more than half the length of the dentary; lacrimal with large dorsal exposure; pronounced posterodorsal process of the

premaxilla between the septomaxilla and maxilla; frontal, palatine, and orbitosphenoid contact in the orbital wall; secondary bony palate extended posteriorly beyond the last upper postcanine tooth; ribs without expanded processes; ‘Y’-shaped interclavicle; weakly twisted humerus with a perpendicularly projected deltopectoral crest, reaching the midshaft; expanded distal end representing about 58% of the humeral length; presence of an ectepicondylar foramen; iliac blade with a reduced postacetabular portion and a well-developed anterodorsally projected preacetabular region; bulbous femoral head confluent with the greater trochanter and the shaft; short and medially projected lesser trochanter; and oval intertrochanteric fossa without marked trochanteric ridge (modified from Bonaparte and Barberena, 2001; Pacheco et al., 2017; pers. observ. of UFRGS-PV-0248-T).

Locality and Horizon—The holotype UFRGS-PV-0248-T was found about 200 m northwest of Cerriquito Hill, in a road cut of Highway BR-287, Santa Maria, Rio Grande do Sul, Brazil (Fig. 1). The presence of the rhychosaur *Hyperodapedon* allowed its inclusion within the *Hyperodapedon* Assemblage Zone of the Candelária Sequence (Horn et al., 2014), Santa Maria Supersequence (Zerfass et al., 2003). The *Hyperodapedon* Assemblage Zone is biostratigraphically correlated to the lower section of the Ischigualasto Formation of western Argentina (e.g., Langer et al., 2007), and is late Carnian in age (e.g., Martínez et al., 2011, 2013).

DESCRIPTION AND COMPARISON

Axial Skeleton

The presacral vertebrae and ribs of *P. brasiliensis* were briefly described and figured by Bonaparte and Barberena (2001). Here, additional material of the holotype specimen,

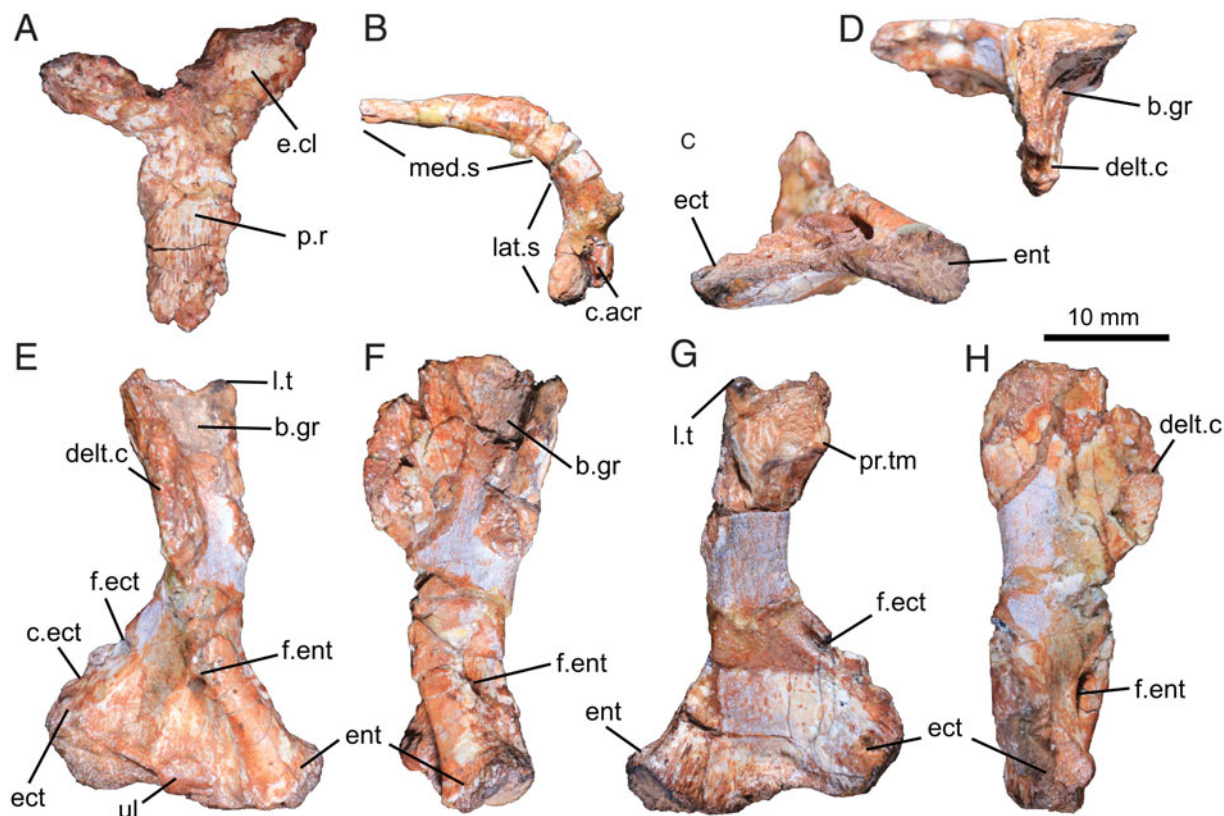


FIGURE 4. *Prozostrodon brasiliensis*, UFRGS-PV-0248-T, holotype, pectoral girdle and forelimb. **A**, interclavicle in dorsal view. **B**, right clavicle in dorsal view. **C–H**, right humerus in **C**, distal, **D**, proximal, **E**, anterior, **F**, medial, **G**, posterior, and **H**, lateral views. **Abbreviations:** **b.gr**, bicipital groove; **c.acr**, concavity for reception of the acromial process; **c.ect**, ectepicondylar crest; **delt.c**, deltopectoral crest; **e.cl**, extension for articulation with medial end of the clavicle; **ect**, ectepicondyle; **ent**, entepicondyle; **f.ect**, ectepicondylar foramen; **f.ent**, entepicondylar foramen; **lat.s**, lateral segment; **l.t**, lesser tuberosity; **med.s**, medial segment; **p.r**, posterior ramus; **pr.tm**, process for insertion of the *M. teres minor*; **ul**, ulnar condyle.

such as sacral vertebrae and the possibly first caudal vertebra, is described.

Vertebrae—Neither atlas nor axis is preserved. In addition to 17 isolated centra of presacral vertebrae, four isolated neural arches are also preserved without their respective centra. Additionally, four sacral and the first caudal vertebrae are articulated but isolated from the rest of the vertebral column.

All the centra are approximately circular in cross-section and are deeply amphicoelous as in most non-mammaliaform cynodonts (e.g., Jenkins, 1970; Abdala, 1999; Liu and Powell, 2009; Oliveira et al., 2009, 2010; Reichel et al., 2009). However, the centra of some tritylodontids, such as *Tritylodon* and *Bienotheroides*, are anteriorly and posteriorly flat (platycoelous), as in the early mammaliaform *Eozostrodon* (Jenkins and Parrington, 1976; Gaetano et al., 2017). There is no evidence of intercentra in *P. brasiliensis*. Most cynodonts have been described as lacking intercentra, but cervical intercentra are retained in *Galesaurus* (Parrington, 1934), *Thrinaxodon* (Jenkins, 1971a), *Cynognathus* (Jenkins, 1971a), *Diademodon* (Gaetano et al., 2018), and *Menadon* (Kammerer et al., 2008).

In cynodonts, the boundary between the cervical and dorsal vertebral series is marked by an abrupt change in zygapophyseal orientation, which is inclined 35°–55° from the sagittal plane in cervical vertebrae to become nearly vertical in anterior thoracic vertebrae (Jenkins, 1971a). This structure is not preserved in the vertebral elements of *P. brasiliensis*, so this distinction cannot be made. However, two centra may be considered to be cervical because they are anteroposteriorly short, dorsoventrally low, and transversely wide (length/width ratios

of 0.58 and 0.59), and oval in anterior view. This morphology is seen in the cervical vertebrae of *Therioherpeton*, *Bienotheroides*, and *Tritylodon* (Sun et al., 1985; Maisch et al., 2004; Gaetano et al., 2017). Two facets for the neural arches are located dorsally, but the arches are not preserved. The neural canal is large and represents approximately 50% of the width of the centrum. Two parapophyseal facets lie ventrolaterally on the anterior edge of the centrum. The cervical centra of *P. brasiliensis* lack parapophyseal facets at their posterior edge, implying that the cervical ribs did not articulate intervertebrally. This condition is also observed in tritylodontids (Gaetano et al., 2017). By contrast, cervical centra of basal cynodonts (e.g., *Galesaurus*, *Thrinaxodon*, *Cynognathus*) have dorsally positioned parapophyseal facets both anteriorly and posteriorly (Jenkins, 1971a; Butler, 2009).

The remaining centra are longer anteroposteriorly, with a higher length-to-width ratio (from 0.74 to 1.04) and a circular shape in anterior view (Fig. 3A–C). We refer to them as dorsal vertebrae given the incompleteness of the material and the uncertainty concerning the thoracic-lumbar transition in the taxon. Their neural arch is narrower than that in cervical vertebrae and never exceeds 40% of the width of the centrum. The parapophyseal facets of the dorsal vertebrae are displaced dorsally compared with the cervical vertebrae, lying dorsolaterally on the anterior edge of the centrum.

On four preserved neural arches, no accessory zygapophyseal articulations (anapophyses) are present (Fig. 3D, E). Anapophyses occur in all basal epicynodonts (e.g., *Galesaurus*, *Thrinaxodon*) and several cynognathians (e.g., *Cynognathus*,

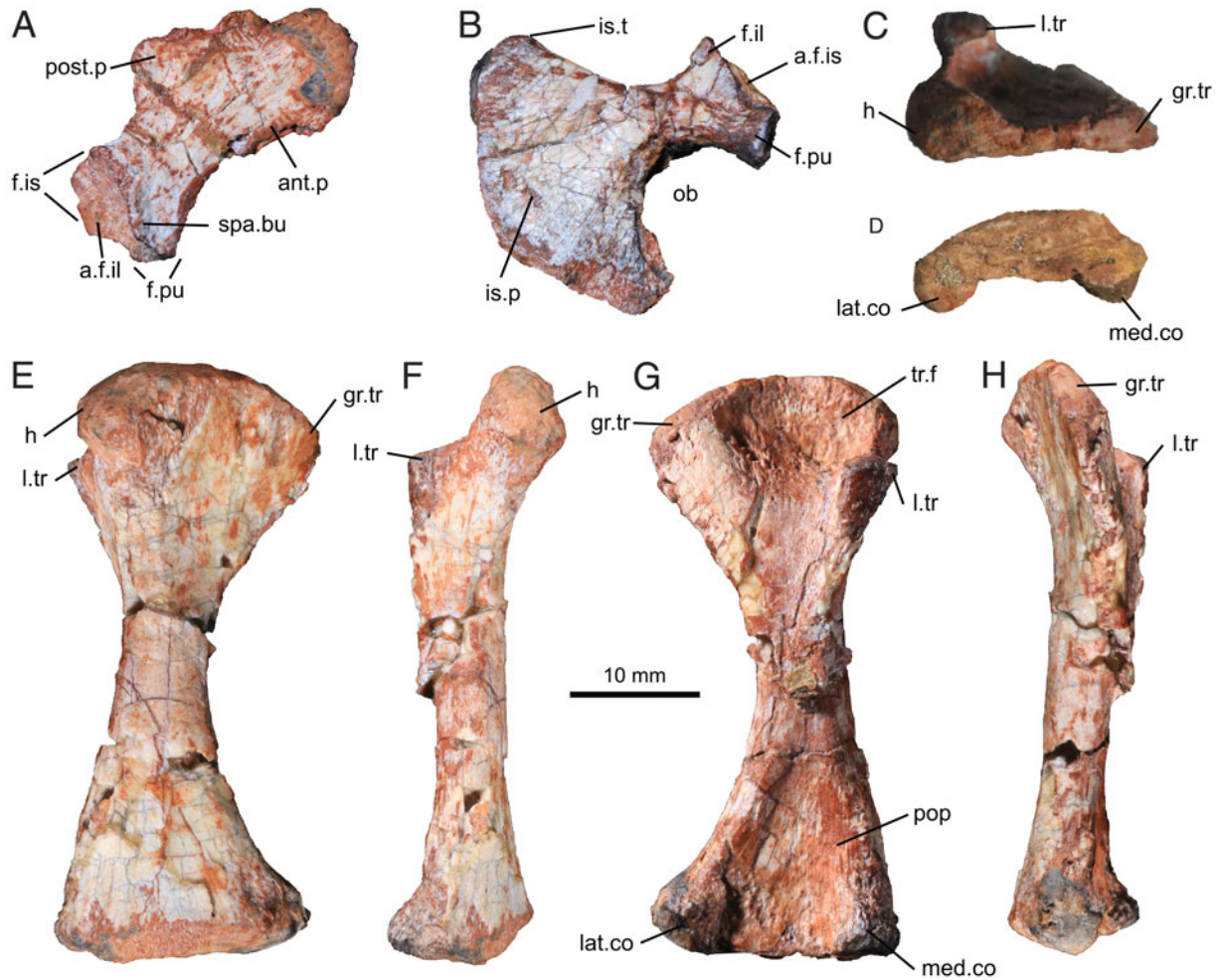


FIGURE 5. *Prozostrodon brasiliensis*, UFRGS-PV-0248-T, holotype, pelvic girdle, and hind limb (stylopod). **A**, right ilium in lateral view; **B**, right ischium in ventral view; **C**, left femur in proximal view; **D**, left femur in distal view; **E**, left femur in anterior view; **F**, right femur in medial view; **G**, left femur in posterior view; **H**, left femur in lateral view. **Abbreviations:** **a.f.il**, acetabular facet of the ilium; **a.f.is**, acetabular facet of the ischium; **ant.p**, anterior process of the ilium; **f.il**, facet for articulation with the ilium; **f.is**, facet for articulation with the ischium; **f.pu**, facet for articulation with the pubis; **gr.tr**, greater trochanter; **h**, femoral head; **is.p**, ischial plate; **is.t**, ischium tuberosity; **lat.co**, surface for the lateral condyle; **l.tr**, lesser trochanter; **med.co**, surface for the medial condyle; **ob**, obturator foramen; **pop**, popliteal fossa; **post.p**, postacetabular portion of the ilium; **spa.bu**, supraacetabular buttress of the ilium; **tr.f**, trochanteric fossa.

Diademodon, *Cricodon*, *Andescynodon*, *Luangwa*, *Protuberum*; Liu and Powell, 2009; Reichel et al., 2009). They are not observed in the axial skeleton of *Procynosuchus* (Kemp, 1980a), several traversodontids (e.g., *Menadon*, *Massetognathus*, *Exaeretodon*; Jenkins, 1970; Oliveira et al., 2007; Kammerer et al., 2008), and probainognathians (Bonaparte and Barberena, 2001; Sues and Jenkins, 2006; Oliveira et al., 2009).

Two different morphologies are found in the neural arches. Three neural arches have a long neural spine inclined posteriorly about 30°–35°, with parallel anterior and posterior borders. Their prezygapophyses are not visible, but the postzygapophyses are inclined about 45° from the parasagittal plane and narrowly spaced, about 1.9 mm apart. In non-mammaliaform cynodonts, this inclination is usually found in cervical vertebrae or posterior thoracic or lumbar vertebrae (Jenkins, 1971a; Abdala, 1999). The neural canals have a width of about 4 mm. Transverse processes are eroded.

One arch has a different morphology, with a more inclined neural spine (40°–45°) that appears shorter, although the top of the spine is eroded. The prezygapophyses are spaced 4.6 mm apart, with nearly vertical orientation. The postzygapophyses are spaced

2.0 mm apart and are nearly horizontal (ca. 70°). This neural arch is interpreted to be that of the first lumbar vertebra, because zygapophyses of the lumbar series appear to be nearly horizontal in most cynodonts (Bonaparte, 1963; Jenkins, 1970; Kemp, 1980a).

The four preserved sacral vertebrae are articulated with their respective ribs, except for the first and the last one, which are articulated with only one rib. They are associated with the two ischia and a possible first caudal vertebra. Because the connection with the lumbar series is not preserved, *P. brasiliensis* possibly had more sacral vertebrae. Indeed, it has been suggested that *Andescynodon* and *Aleodon* had four sacral vertebrae (Liu and Powell, 2009; Oliveira et al., 2009), whereas *Thrinaxodon* had five (Jenkins, 1971a), *Massetognathus* had six (Jenkins, 1970), and *Exaeretodon* had seven (Bonaparte, 1963).

The prezygapophyses and postzygapophyses of sacral vertebrae are located at the same level and are firmly connected to each other. The prezygapophyses are widely spaced (4.5 mm), as are the facets of the postzygapophyses, which are spaced 3.5 mm apart. Although the articular surfaces of the pre- and postzygapophyses in the articulated vertebrae are difficult to observe, the zygapophyses seem to be nearly vertical and are

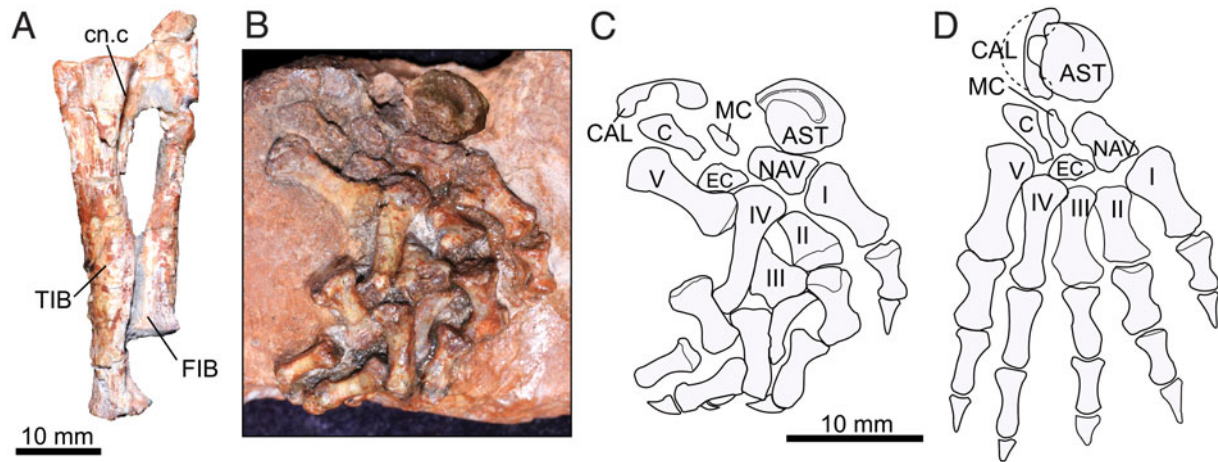


FIGURE 6. *Prozostrodon brasiliensis*, UFRGS-PV-0248-T, holotype, hind limb (zeugopod and autopod). **A**, left tibia and fibula in anterior view; **B**, right foot as preserved; **C**, schematic drawing of the right foot; **D**, reconstruction of the right foot in dorsal view. **Abbreviations:** AST, astragalus; C, cuneiform; CAL, calcaneum; **cn.c**, cnemial crest of the tibia; EC, ectocuneiform; FIB, fibula; MC, mesocuneiform; NAV, navicular; TIB, tibia; I–V, metatarsals I–V.

inclined only about 10° from the parasagittal plane. The neural spines are eroded. The transverse processes are very short and stout. The centra of the sacral vertebrae cannot be described more precisely because they are overlapped by the two ischia.

A last vertebra is connected posteriorly to the fourth sacral vertebra. Because there is no rib associated with this vertebra, it is difficult to refer it to the sacral or caudal series. Its morphology is similar to that of the sacral vertebrae, except for the wider space between the prezygapophyses (5.0 mm) and their more inclined orientation (about 30° from the parasagittal plane). These differences suggest that this vertebra is the first caudal vertebra. The poor preservation of this element does not permit the description of the postzygapophyses or the posterior part of the centrum.

Ribs—Nine presacral ribs are present, but they are isolated, incomplete, and damaged. Neither proximal nor distal ends are preserved, and in view of their poor preservation no remarkable features can be described. They are long and slightly curved. None of the ribs show expanded costal plates, structures that are found in basal epicynodonts (e.g., *Galesaurus*, *Thrinaxodon*; Jenkins, 1971a) and most cynognathians (e.g., *Cynognathus*, *Diademodon*, *Luangwa*, *Andescynodon*, *Menadon*, *Protuberum*, *Pascualgnathus*, *Scalenodon*; Jenkins, 1971a; Kammerer et al., 2008; Liu and Powell, 2009; Oliveira et al., 2009; Reichel et al., 2009). Costal plates were probably common in all basal epicynodonts and were secondarily lost in derived traversodontids (e.g., *Exaeretodon*; Oliveira et al., 2007) to all the probainognathians (e.g., Hopson and Kitching, 2001). Short and stout sacral ribs are associated with the sacral vertebrae. Their distal end bears broad facets, connected to each other, forming a unique articular surface for the ilium.

Pectoral Girdle and Forelimb

The pectoral girdle preserves a right clavicle and an interclavicle. One little fragment of scapula is also preserved, but no remarkable features can be described in view of its poor preservation. The forelimb includes both humeri. All these elements were briefly described by Bonaparte and Barberena (2001).

Clavicle—Only the right clavicle is preserved. It is fragmented but almost complete, lacking only the lateral extremity. The clavicle is robust and curved (Fig. 4B), as in most non-

mammaliaform cynodonts. The medial long axis constitutes two-thirds of the clavicle. It is a slender shaft that extends proximally into a spatulate plate for the articulation with the interclavicle. The lateral third of the clavicle is a fairly robust rod that is projected posterodorsally.

The main difference from other non-mammaliaform cynodonts is the angle between the long axes of the lateral third and the medial two-thirds of the clavicle: the axes are almost perpendicular in *P. brasiliensis* (about 95°). The lateral third is projected more laterally in other non-mammaliaform cynodonts, with an angle between the long axes of about 130°–150° in *Procynosuchus* (Kemp, 1980a), *Galesaurus*, *Thrinaxodon* (Jenkins, 1971a), *Cynognathus* (Jenkins, 1971a), *Diademodon*, *Massetognathus* (Jenkins, 1970), *Andescynodon* (Liu and Powell, 2009), *Boreogomphodon* (Liu et al., 2017), *Exaeretodon* (Bonaparte, 1963), *Probainognathus* (Romer and Lewis, 1973), *Chiniquodon* (Romer and Lewis, 1973), *Pachygenelus* (Gow, 2001), and *Oligokyphus*, and in the mammaliaform *Eozostrodon* (Jenkins and Parrington, 1976). The angular clavicle of *P. brasiliensis* is a condition also observed in the ecteniniid *Trucidocynodon* and the tritylodontid *Kayentatherium* (Sues and Jenkins, 2006).

The medial end has several striations on the dorsal surface, which extend parallel to the longitudinal axis of the bone. These striations indicate the attachments of connective or ligamentous tissues, connecting the clavicle to the interclavicle. A flange is present on the ventral aspect of the lateral third. Distally, this flange should form the concavity for the acromion process of the scapula, although this feature is not seen because of the damaged lateral extremity.

Interclavicle—The interclavicle is retained in *P. brasiliensis*, as in other non-mammaliaform cynodonts. The right extension and the ventral surface of the interclavicle are damaged, and the posterior edge of the bone is missing. The interclavicle is a flat bone, bowed ventrally from front to back. It has a ‘Y’ shape, composed of a posterior ramus and two well-developed clavicular processes for the attachment of the clavicles (Fig. 4A). The two processes are flat, anterolaterally projected, and form an angle of about 105°.

This morphology contrasts with the plesiomorphic pattern found in basal epicynodonts (e.g., *Thrinaxodon*, *Galesaurus*; Jenkins, 1971a; Butler, 2009) and some gomphodonts (e.g., *Diademodon*, *Boreogomphodon*, *Massetognathus*; Jenkins,

TABLE 1. Degree of torsion of the humeral shaft in cynodonts. The angle was measured between the transversal axes of the proximal end and the distal end, based on pictures of the humerus in proximal aspect.

Taxon	Torsion of the humeral shaft	Source
<i>Galesaurus</i>	20–40°	UMZC-T820/T823
<i>Thrinaxodon</i>	40–50°	Jenkins, 1971
<i>Cynognathus</i>	20°	NHMUK-R3772a
<i>Diademodon</i>	20°	UMZC-T492
<i>Cricodon</i>	40°	Crompton, 1954
<i>Scalenodon</i>	5°	UMZC-T925
<i>Luangwa</i>	5°	OUMNH-TSK121
<i>Exaeretodon</i>	30°	Bonaparte, 1963
<i>Santacruzodon</i>	65°	Bertoni, 2014
<i>Prozostrodon</i>	5°	UFRGS-PV0248T
<i>Bienotheroides</i>	20–45°	Maisch et al., 2004; Sun et al., 1985
<i>Tritylodon</i>	30–40°	Gaetano et al., 2017
<i>Kayentatherium</i>	40°	Sues and Jenkins, 2006
<i>Brasilitherium</i>	15°	UFRGS-PV1043T
<i>Eozostrodon</i>	50°	Jenkins and Parrington, 1976
<i>Tachyglossus</i>	60°	MNHN-1903-537
<i>Ornithorhynchus</i>	75°	MNHN-1906-484
<i>Didelphis</i>	< 5°	MNHN-1878-538
<i>Canis</i>	< 5°	UFRGS-PV14Z

1970; Liu et al., 2017). These taxa lack the lateral extension, and the two clavicles articulate directly on shallow concavities located on the ventral surface of the proximal end of the plate. *Probainognathus* (Romer and Lewis, 1973), *Chiniquodon* (Romer and Lewis, 1973), *Exaeretodon* (Bonaparte, 1963), and *Trucidocynodon* have an intermediate morphology, with short lateral extensions. The lateral extensions are present in tritylodontids (Sun et al., 1985; Sues and Jenkins, 2006), early mammaliaforms, and monotremes (Jenkins and Parrington, 1976; Luo, 2015). However, in *Bienotheroides*, *Sinoconodon*, *Eozostrodon*, *Tachyglossus*, and *Ornithorhynchus*, extensions are longer and narrower than in *P. brasiliensis* and the interclavicle has a ‘T’ shape, with the two extensions projected laterally and forming an angle of about 180° (Luo, 2015). *Kayentatherium* is the only taxon with anterolaterally projected extensions, giving a ‘Y’ shape to the interclavicle, similar to that of *P. brasiliensis*.

The posterior ramus of the interclavicle is an elongate plate in *P. brasiliensis*. This is the most common condition in non-mammaliaform cynodonts (e.g., *Thrinaxodon*, *Galesaurus*, *Diademodon*, *Massetognathus*, *Chiniquodon*; Jenkins, 1970, 1971a; Romer and Lewis, 1973; Butler, 2009; Gaetano et al., 2018) and is seen in the mammaliaform *Eozostrodon* (Jenkins and Parrington, 1976). In *Exaeretodon* (Bonaparte, 1963), *Trucidocynodon* (Oliveira et al., 2010), and *Kayentatherium* (Sues and Jenkins, 2006), the posterior ramus is wide transversally and short anteroposteriorly. Striations are present on the dorsal surface of the posterior ramus for muscle attachment.

Humerus—The right humerus lacks almost completely the humeral head, the most medial region of the proximal end, and the proximal and distal epiphyses. The left humerus is only represented by the proximal midshaft, with part of the caput humeri. In both bones, the greater and lesser tuberosities are eroded. The bone is described with the shaft held vertically, in a mammalian orientation.

The shaft of the humerus is stout (Fig. 4C–H). It is almost straight, as in *Trucidocynodon*, *Chiniquodon* (Romer and Lewis, 1973), *Oligokyphus*, *Brasilodon*, *Eozostrodon* (Jenkins and Parrington, 1976), and living mammals such as *Ornithorhynchus*, *Tachyglossus*, and *Didelphis*. The shaft is

curved dorsally in most non-mammaliaform cynodonts (Jenkins, 1970; Kemp, 1980a; Sues and Jenkins, 2006; Liu and Powell, 2009; Oliveira et al., 2011; Bertoni, 2014; Fedak et al., 2015). The shaft differs from that in most non-mammaliaform cynodonts and monotremes by its weak torsion, because in proximal view the transverse axis of the proximal end lies almost in the same plane as the distal end (Table 1). This feature is not an effect of distortion because the right humerus is three-dimensionally preserved. It can also be observed in *Luangwa*, *Scalenodon*, and *Brasilodon*, as well as in generalized therians (Gambaryan and Kielan-Jaworowska, 1997). The humerus of other non-mammaliaform cynodonts has a more twisted shaft.

Although incomplete, the head of the left humerus appears flat as in most non-mammaliaform cynodonts. It was probably extended by a cartilaginous cap. *Brasilodon* and *Eozostrodon* (Jenkins and Parrington, 1976) differ from other non-mammaliaform cynodonts in having a subspherical humeral head. The head faces posterolaterally as in other non-mammaliaform cynodonts (Jenkins, 1970, 1971a; Romer and Lewis, 1973; Liu and Powell, 2009; Sues and Hopson, 2010; Bonaparte et al., 2012; Bertoni, 2014; Fedak et al., 2015). On the posterior surface, a conspicuous ridge runs distally from the humeral head to become confluent with the ectepicondylar crest at the distal end of the bone. On this posterior ridge, near the humeral head, a prominent osseous process faces laterally. This process indicates the area of insertion of the M. teres minor.

The deltopectoral crest is a rectangular flange extending for approximately half the length of the humerus, a common feature in non-mammaliaform cynodonts (Table 2). The flange is projected perpendicularly to the transverse axis formed by the head and the lesser tubercle (Fig. 4D). This projection is perpendicular also in *Platycraniellus*, *Massetognathus*, *Andescynodon*, *Pascualgnathus*, *Trucidocynodon*, *Irajatherium*, *Oligokyphus*, and the monotreme *Tachyglossus*. *Procynosuchus*, *Galesaurus*, *Thrinaxodon*, *Cynognathus*, *Exaeretodon*, *Probainognathus*, and *Chiniquodon* have the projection angle exceeding 120°, with the crest projected anterolaterally (Table 2). The crest is thicker along the connection with the shaft. As in most non-mammaliaform cynodonts, the crest is greatly expanded anteriorly in *P. brasiliensis* compared with generalized mammals. The teres crest is eroded. It originates distal to the lesser tuberosity and extends as far distally as the deltopectoral crest. The two crests and the shaft enclose a concave area, the bicipital or intertubercular groove, on the anterior surface of the humerus. The groove is broad and shallow. It is well marked proximally but becomes indistinct by the midlength of the shaft.

Distally, the deltopectoral crest connects with a robust ridge that runs mediolaterally to the bridge of the entepicondylar foramen. The entepicondyle protrudes medially and represents one-third of the distal end. It reaches distally to the level of the ulnar condyle. The ectepicondylar crest is well developed and extends proximal to the entepicondyle, along the distal half of the humeral diaphysis. In distal view, the entepicondyle is thicker anteroposteriorly than the ectepicondyle, resulting in an asymmetrical distal end of the humerus. This difference in thickness is observed in small non-mammaliaform cynodonts such as *Thrinaxodon* (Jenkins, 1971a) and *Kayentatherium* (Sues and Jenkins, 2006). In contrast, the ectepicondyle is thicker in larger cynodonts to transfer the weight onto the radius, whereas the weight is not such a critical factor in smaller forms (Jenkins, 1971a).

The entepicondylar foramen is oval and large. It is enclosed by a stout flange of bone and prolonged by a groove that continues to the distal end. This groove separates the prominent entepicondyle and the distal articular facet. As in most non-mammaliaform cynodonts, there is an ectepicondylar foramen near the ectepicondylar crest, opening distally. It is smaller

TABLE 2. Length ratio and angle of the deltopectoral crest in cynodonts. Length ratio = Length of deltopectoral crest / Humeral length × 100). The angle was measured between the deltopectoral crest and the axis ‘Lesser Tuberosity – Medial margin of the humeral head,’ based on pictures of the humerus in proximal aspect.

Taxon	Angle of the deltopectoral crest	Length ratio of the deltopectoral crest	Source
<i>Procynosuchus</i>	145°	52%	Abdala, 1999
<i>Galesaurus</i>	132°–135°	50%	UMZC-T820/T823
<i>Thrinaxodon</i>	135°	50%	Jenkins, 1971
<i>Platycraniellus</i>	90°	–	Abdala, 2007
<i>Cynognathus</i>	125°	60%	NHMUK-R3772a
<i>Diademodon</i>	105°–120°	58%	UMZC-T492/T433
<i>Cricodon</i>	–	50%	Crompton, 1954
<i>Scalenodon</i>	100°	50%	UMZC-T925
<i>Massetognathus</i>	90°	52%	Abdala, 1999
<i>Luangwa</i>	102°	53%	OUMNH-TSK121
<i>Andescynodon</i>	90°	54–61%	Abdala, 1999
<i>Boreogomphodon</i>	105°	50%	Liu et al., 2017
<i>Exaeretodon</i>	150°	52–60%	Abdala, 1999
<i>Pascualgnathus</i>	90°	58%	Bonaparte, 1966
<i>Trucidocynodon</i>	90°	50%	UFRGS-PV1051T
<i>Chiniquodon</i>	125°	54–57%	Abdala, 1999
<i>Probainognathus</i>	135°	45–50%	Abdala, 1999
<i>Prozostrodon</i>	95°	45%	UFRGS-PV0248T
<i>Irajatherium</i>	90°	53%	UFRGS-PV599T
<i>Riograndia</i>	100°	50%	UFRGS-PV833T
<i>Tritylodon</i>	100°	50%	Gaetano et al., 2017
<i>Oligokyphus</i>	95°	52%	NHMUK-R7402
<i>Kayentatherium</i>	–	53%	Sues and Jenkins, 2006
<i>Brasilitherium</i>	100°	48%	UFRGS-PV1043T
<i>Eozostrodon</i>	–	44%	Jenkins and Parrington, 1976
<i>Tachyglossus</i>	95°	48%	MNHN-1903-537
<i>Ornithorhynchus</i>	105°	54%	MNHN-1906-484
<i>Didelphis</i>	–	55%	MNHN-1878-538
<i>Canis</i>	–	41%	UFRGS-PV14Z

TABLE 3. Distal end width / humeral length ratio in cynodonts. The distal end width was measured between the two epicondyles, based on pictures of the humerus in anterior aspect.

Taxon	Distal end width	Source
<i>Procynosuchus</i>	49%	Abdala, 1999
<i>Galesaurus</i>	50%	UMZC-T823
<i>Thrinaxodon</i>	50%	Jenkins, 1971
<i>Cynognathus</i>	51%	NHMUK-R3772a
<i>Diademodon</i>	44%	UMZC-T492
<i>Cricodon</i>	42%	Crompton, 1954
<i>Scalenodon</i>	38%	UMZC-T925
<i>Massetognathus</i>	38–40%	Abdala, 1999; Jenkins, 1971
<i>Luangwa</i>	40%	OUMNH-TSK121
<i>Boreogomphodon</i>	60%	Sues and Hopson, 2010
<i>Exaeretodon</i>	49–57%	Abdala, 1999
<i>Pascualgnathus</i>	46%	Bonaparte, 1966
<i>Trucidocynodon</i>	30%	UFRGS-PV1051T
<i>Chiniquodon</i>	58–63%	Abdala, 1999
<i>Probainognathus</i>	34–37%	Abdala, 1999
<i>Prozostrodon</i>	58%	UFRGS-PV0248T
<i>Irajatherium</i>	55%	UFRGS-PV599T
<i>Tritylodon</i>	48–51%	Gaetano et al., 2017
<i>Oligokyphus</i>	42%	NHMUK-R7402
<i>Kayentatherium</i>	60%	Sues and Jenkins, 2006
<i>Brasilitherium</i>	43%	UFRGS-PV1043T
<i>Eozostrodon</i>	30%	Jenkins and Parrington, 1976
<i>Tachyglossus</i>	95%	MNHN-1903-537
<i>Ornithorhynchus</i>	83%	MNHN-1906-484
<i>Didelphis</i>	30%	MNHN-1878-538
<i>Canis</i>	20%	UFRGS-PV14Z

than the entepicondylar foramen and enclosed by a thin flange. This ectepicondylar foramen is lacking in tritylodontids (Young, 1947; Kühne, 1956; Sun et al., 1985; Maisch et al.,

2004; Sues and Jenkins, 2006; Gaetano et al., 2017), *Probainognathus* (Abdala, 1999), *Trucidocynodon*, *Brasilodon* (Bonaparte et al., 2012), and *Eozostrodon* (Jenkins and Parrington, 1976). According to Abdala (1999), it is also lacking in *Cynognathus* but an ectepicondylar foramen can be observed in the well-preserved sample NHMUK-R3772a. The lack of an ectepicondylar foramen is a synapomorphy of the most derived non-mammaliaform cynodonts (Hopson and Kitching, 2001).

The distal extremity is twice as wide transversally as the proximal extremity. The width across the two epicondyles represents about 58% of the estimated total proximodistal length of the bone (Table 3). An expanded distal end is a common feature in non-mammaliaform cynodonts and monotremes, contrasting with the narrow distal end seen in *Eozostrodon* and generalized living therians.

The distal articular surface is damaged and incomplete, represented by a bulbous condyle facing anteriorly. Bonaparte and Barberena (2001) considered this structure to be the capitulum, but the medial position of the condyle implies that it is the ulnar condyle and that the capitulum is not preserved in this specimen. A bulbous ulnar condyle is present in all non-mammaliaform cynodonts (Kemp, 1980a, 1980b; Abdala, 1999; Oliveira et al., 2010; Sues and Hopson, 2010; Bonaparte et al., 2012; Fedak et al., 2015) as well as in the mammaliaforms *Eozostrodon* and *Megazostrodon* (Jenkins and Parrington, 1976). This feature contrasts with the concave trochlea observed in extant eutherians (Fisher et al., 2007, 2009). A shallow olecranon fossa is present posteriorly. Well-marked striations are present in the dorsal aspects of the two condyles, and slight striations are also present on the ventral surface of the stout flange enclosing the entepicondylar foramen.

Pelvic Girdle and Hind Limb

The pelvis is known from the right ilium and both ischia, all displaced from their original position. Only a few fragments of the pubis are partially preserved, and no notable features can be described for this bone. The hind limb is known from the femora and tibiae, a possible left fibula, and a right hind foot. Only the ilium and the hind foot were previously described by Bonaparte and Barberena (2001).

Ilium—The most anterior part of the iliac blade is broken off and the edge of the posterior margin is slightly damaged, leaving the exact outline in doubt in these areas. The ilium of *P. brasiliensis* is formed by a thin and expanded blade separated from the base by a constricted neck (Fig. 5A). Although damaged, the edge of the posterior margin becomes very thin, suggesting that the ilium was not much more extended posteriorly. The postacetabular portion of the blade is reduced in *P. brasiliensis*, corresponding to a small prominence, a derived condition that is also observed in tritylodontids (Sues and Jenkins, 2006; Sullivan et al., 2013; the specimen NHMUK-R7445), although the prominence is smaller in this clade. In *Therioherpeton* and the early mammaliaforms (e.g., *Eozostrodon*, *Erythrotherium*; Jenkins and Parrington, 1976), the postacetabular portion is completely absent. In *Procynosuchus* (Brink and Kitching, 1953), *Menadon* (Kammerer et al., 2008), *Luangwa*, *Exaeretodon* (Bonaparte, 1963), *Trucidocynodon*, and *Aleodon* (Oliveira et al., 2009), the preacetabular portion of the ilium is longer than the postacetabular region. The opposite is the case in *Cynognathus* (Jenkins, 1971a) and *Andescynodon* (Liu and Powell, 2009). In *Galesaurus* (Parrington, 1934), *Pascualgnathus* (Bonaparte, 1966), *Massetognathus* (Jenkins, 1970), and *Probainognathus* (Romer and Lewis, 1973), the postacetabular and the preacetabular portions are equally developed in length.

As in *Galesaurus*, *Menadon* (Kammerer et al., 2008), *Chiniquodon* (Romer and Lewis, 1973), *Therioherpeton*, and tritylodontids (Maisch et al., 2004; Sues and Jenkins, 2006), the iliac blade of *P. brasiliensis* was projected anterodorsally from the acetabular region in life position, rather than anteriorly. This is the typical condition in living mammals, also present in *Eozostrodon* (Jenkins and Parrington, 1976). The lateral surface of the blade is slightly concave, but a ridge separates the blade into two fossae on the anteroposterior axis. The iliac blade of *P. brasiliensis* is dorsoventrally narrow, with straight and parallel dorsal and ventral edges. This ‘rod-like’ morphology is similar to that seen in several non-mammaliaform cynodonts such as *Therioherpeton*, *Luangwa*, tritylodontids (Maisch et al., 2004; Sues and Jenkins, 2006; Sullivan et al., 2013), the mammaliaform *Eozostrodon* (Jenkins and Parrington, 1976), and living mammals. However, the iliac blade of *P. brasiliensis* remains wider dorsoventrally than in the mammaliaforms, *Therioherpeton*, and tritylodontids. Other non-mammaliaform cynodonts have an ilium with a spatulate plate formed by a convex dorsal edge (Bonaparte, 1963; Jenkins, 1970, 1971a; Kemp, 1980a; Abdala, 1999; Butler, 2009; Liu and Powell, 2009; Oliveira et al., 2009). The medial surface of the blade is damaged, and no scars or other indications of sacral rib attachment can be observed.

Besides the facet for the acetabulum, the base of the ilium consists of the laterally directed supracetabular buttress, the posteriorly directed surface for the articulation with the ischium, and the anteroventrally directed process for the articulation with the pubis. The iliac facet of the acetabulum is semi-circular and facing laterally and posteroventrally rather than ventrally. The iliac facet of the acetabulum is facing mainly ventrally in basal cynodonts (Jenkins, 1971a; Kemp, 1980a; Butler, 2009) and *Trucidocynodon*.

The supracetabular buttress is projected laterally to the main plane of the pelvis. It is moderately developed and lies antero-dorsal, rather than dorsal, to the acetabulum, a condition found in *Aleodon* (Oliveira et al., 2009), traversodontids (Bonaparte, 1963; Jenkins, 1970; Kammerer et al., 2008), and tritylodontids (Sullivan et al., 2013). In contrast, the iliac buttress has a dorsal position in the basal cynodonts *Procynosuchus* (Kemp, 1980a), *Galesaurus*, and *Cynognathus*. In *Oligokyphus*, *Kayentatherium*, and *Eozostrodon*, there is no lateral projection of the superior margin on the acetabulum (Kühne, 1956; Jenkins and Parrington, 1976; Sues and Jenkins, 2006).

Ischium—Except for the partially damaged acetabular facet, the two ischia are well preserved. The ischium consists of one large and flat blade and a neck projected anteriorly (Fig. 5B). The head of the ischium is composed of one part of the acetabular surface, as well as surfaces for the ilium and the pubis. The acetabular facet of the ischium appears to be oval and is oriented anterolaterally. Dorsal to the acetabulum, there is a damaged facet for the articulation with the ilium, facing antero-dorsally. Another facet is present medioventrally to the acetabular facet and corresponds to the articulation with the pubis. This facet is rectangular and faces anteroventrally.

The thin ischial blade of *P. brasiliensis* is expanded transversally and is slightly concave medially. No ridge or groove is present on the surface of the blade. The posterior margin of the blade is slightly convex and is limited laterodorsally by the tuberosity of the ischium and the dorsal ramus and medioventrally by a straight symphyseal edge. The large angle (ca. 130°) between the posterior edge and the symphysis line gives a triangular shape to the ischium of *P. brasiliensis*. The dorsal ramus and posterior edge form an angle of ca. 65°. The morphology of the ischium of *P. brasiliensis* is similar to that seen in *Eozostrodon*, but in the latter the ischium is ‘L’-shaped, with the posterior and dorsal edges perpendicular to each other (Jenkins and Parrington, 1976). The ischia of *P. brasiliensis* are slightly scattered in preservation, suggesting that the symphysis was not fused in life. The ischium forms a semicircular margin for the obturator foramen.

Although no pubis is preserved and the exact size of the obturator foramen remains difficult to determine, the relatively long and narrow neck of the ischium and the curved margin for the obturator indicates an extended and oval foramen. In *Luangwa* (Kemp, 1980b), *Andescynodon* (Liu and Powell, 2009), *Menadon* (Kammerer et al., 2008), *Exaeretodon* (Bonaparte, 1963), *Chiniquodon* (Romer, 1969; Romer and Lewis, 1973), *Therioherpeton*, *Trucidocynodon*, tritylodontids (Kühne, 1956; Sullivan et al., 2013), and *Eozostrodon* (Jenkins and Parrington, 1976), the obturator is large, as seen in living mammals. Basal cynodonts such as *Cynognathus* and *Diademodon* have a smaller foramen, with the anteromedial margin of the ischium projected more medially, as in early therapsids (Jenkins, 1971a). Medially, the ischial plate becomes narrow and meets the posterior edge of the pubic plate antero-medially to the obturator foramen.

Femur—The two femora are nearly complete, but the distal epiphyses are missing. The proximal part of the right femur is damaged, with a fractured and slightly displaced greater trochanter. The following description is based on the better-preserved left femur and describes the femur with the shaft held vertically, in a mammalian orientation. The femur is 45.4 mm long (Fig. 5C–H).

The proximal part of the shaft is projected anteriorly in *P. brasiliensis*, which is a non-mammaliaform cynodont condition also observed in *Eozostrodon* (Jenkins, 1971a; Jenkins and Parrington, 1976). The proximal portion of the shaft is only slightly dorsally projected in living mammals (Jenkins, 1971a). The femoral head is projected medially, at an angle of about

45° relative to the longitudinal axis of the femur. Among prozostrodonians, the angle is variable. The femoral head is less projected medially in *Therioherpeton* and *Irajatherium* (ca. 20°), similarly projected in *Oligokyphus* and *Eozostrodon* (about 40°) and more medially projected in *Brasilodon* (ca. 60°). The medial projection of the femoral head of *P. brasiliensis* and other non-mammaliaform cynodonts contrasts with that of the femoral head of ‘pelycosaurs,’ located in line with the axis of the shaft (Jenkins, 1971a; Kemp, 1980b).

As in most non-mammaliaform cynodonts, the femoral head of *P. brasiliensis* is bulbous and nearly flattened. Most tritylodontids have a hemiovoid head elongated along the posterolateral-antemedial axis (Kühne, 1956; Sues and Jenkins, 2006; Sullivan et al., 2013). *Tritylodon* (Gaetano et al., 2017) and *Brasilodon* (Bonaparte et al., 2012) have a hemispherical head with morphology similar to *Eozostrodon* (Jenkins and Parrington, 1976) and most living mammals. The femoral head of *P. brasiliensis* is not set off from the shaft by a constriction and is confluent with the greater trochanter. This feature is observed in basal non-mammaliaform cynodonts (Crompton, 1954; Butler, 2009), traversodontids (Bonaparte, 1963; Jenkins, 1970; Liu and Powell, 2009; Sues and Hopson, 2010; Bertoni, 2014), *Trucidocynodon*, *Chiniquodon* (Romer, 1969; Romer and Lewis, 1963), *Therioherpeton*, and tritheledontids (Martinelli et al., 2005). The head is prominently set off from the shaft in the most derived non-mammaliaform cynodonts (e.g., tritylodontids, *Brasilodon*; Kühne, 1956; Sun et al., 1985; Bonaparte et al., 2012; Gaetano et al., 2017), the mammaliaform *Eozostrodon* (Jenkins and Parrington, 1976), and living mammals.

The well-developed greater trochanter is projected laterally, and its lateral extremity is slightly thicker than the ridge connecting it to the femoral head. The greater trochanter reaches the level of the femoral head proximally. The lesser trochanter is a tuberosity separated from the head and located near the trochanteric fossa. It is projected posteromedially and remains visible in anterior view (Fig. 5E). This is a derived feature found in several non-mammaliaform cynodonts (e.g., *Therioherpeton*, *Trucidocynodon*, *Irajatherium*, *Andescynodon*, tritylodontids; Kühne, 1956; Sues and Jenkins, 2006; Liu and Powell, 2009; Sullivan et al., 2013) and in *Eozostrodon* (Jenkins and Parrington, 1976). However, in *Eozostrodon*, the lesser trochanter has migrated proximally and reached the level of the greater trochanter (Jenkins and Parrington, 1976). In basal cynodonts such as *Procynosuchus* and *Cricodon*, the lesser trochanter is projected posteriorly (Crompton, 1954; Kemp, 1980a). In *Thrinaxodon*, *Diademodon*, *Chiniquodon* (Romer, 1969), the traversodontids *Boreogomphodon* (Sues and Hopson, 2010; Liu et al., 2017), *Menadon* (Bertoni, 2014), *Massetognathus* (Jenkins, 1970), *Exaeretodon* (Bonaparte, 1963), and *Santacruzodon* (Bertoni, 2014), the lesser trochanter has a posteromedial position but is not projected as far medially as in *P. brasiliensis* and is not visible in anterior view. This trochanter is a short tuberosity in *P. brasiliensis* like in *Irajatherium* (Martinelli et al., 2005), *Therioherpeton*, tritylodontids (Sullivan et al., 2013), and *Eozostrodon* (Jenkins and Parrington, 1976). In most non-mammaliaform cynodonts, the trochanter is a long and well-developed crest (Crompton, 1954; Bonaparte, 1963; Romer, 1969; Jenkins, 1970; Kemp, 1980a, 1980b; Bertoni, 2014; Liu et al., 2017; Gaetano et al., 2018). A third trochanter is absent.

The trochanteric fossa is located posteriorly, immediately distally to the femoral head. It is shallow and circular, a typical condition in non-mammaliaform cynodonts (Jenkins, 1971a; Butler, 2009; Liu and Powell, 2009; Bertoni, 2014). No intertrochanteric crest is present in *P. brasiliensis* as in other non-mammaliaform cynodonts, except in *Brasilodon* (Bonaparte

et al., 2012). However, the distal border of the trochanteric fossa connects the two trochanters and is certainly the homologue of the intertrochanteric crest of extant mammals, although this border remains poorly defined in non-mammaliaform cynodonts. Distal to the trochanteric fossa, the posterior surface of the proximal portion of the shaft is flat in *P. brasiliensis*, lacking the fossa for the adductor muscles, like that described by Jenkins (1971a). This fossa is also absent in tritylodontids such as *Tritylodon* (Gaetano et al., 2017) and *Oligokyphus*.

The shaft of the femur is straight. It is approximately square in cross-section but becomes more rectangular distally, being compressed anteroposteriorly. The distal extremity of the femur is gradually and symmetrically expanded transversally. This extremity reaches the same width as the proximal one. In *P. brasiliensis*, the popliteal fossa is wide and long, representing one-third of the bone. The condyles are incomplete in both femora. No patellar groove is present as in most non-mammaliaform cynodonts (Sues and Jenkins, 2006; Sues and Hopson, 2010), although the femur of one indeterminate species of tritylodontid shows a weakly developed patellar groove (Sullivan et al., 2013).

Tibia—Both tibiae are preserved but lack their proximal and distal epiphyses. The tibiae are approximately 42 mm long and are slightly shorter than the femur. The proximal end has a triangular shape for the left tibia but is enlarged transversally and flattened anteroposteriorly for the right tibia, probably due to the compression of this bone during preservation. The epiphysis is missing, and no other information is known about the articular surface in life. The cnemial crest arises from the anterolateral margin of the proximal end and reaches one-third of the tibia (Fig. 6A). Its prominence decreases progressively distally. A well-marked fossa is present on the lateral side of the crest, reaching one-fourth of the shaft.

The most characteristic feature is the straight shaft of *P. brasiliensis*, whereas other non-mammaliaform cynodonts have a medially bowed tibia (Bonaparte, 1963; Jenkins, 1970; Kemp, 1980a; Butler, 2009; Liu et al., 2017). The shaft is straight in *Bienotheroides* (Maisch et al., 2004) and *Brasilodon*. The shaft of the tibia of *P. brasiliensis* is moderately slender and flattened lateromedially. The diameter of the shaft decreases gradually distally before becoming wider at the distal end. The posterior surface of the shaft is flat proximally but becomes more convex after the midshaft.

Fibula—A poorly preserved, possible left fibula is recovered (Fig. 6A). Its epiphyses are not preserved, leaving the true surfaces of the articulation unknown. The fibula has approximately the same size as the tibia (39 mm) and is more slender than the latter. The shaft is rounded, but the proximal and distal extremities are transversally expanded and anteroposteriorly flattened. The proximal end is slightly projected medially, and the fibular crest on its lateral side is less developed than in *Trucidocynodon* (Oliveira et al., 2010). The fibula is bowed laterally in *Thrinaxodon* (Jenkins, 1971a), *Galesaurus* (Butler, 2009), *Cynognathus* (Jenkins, 1971a), *Trucidocynodon*, *Massetognathus* (Jenkins, 1970), *Boreogomphodon* (Liu et al., 2017), *Exaeretodon* (Bonaparte, 1963), and *Menadon* (Bertoni, 2014) but is straight in *P. brasiliensis*, *Eozostrodon* (Jenkins and Parrington, 1976), *Ornithorhynchus*, *Tachyglossus*, and didelphids. In *Procynosuchus*, the fibula differs markedly from that of other non-mammaliaform cynodonts, with a straight, robust, and flat shaft (Kemp, 1980a).

Foot—The right hind foot is present and almost integrally semiarticulated (Fig. 6C, D). The astragalus is a quadrangular bone. The bone is broken, so its orientation remains uncertain and no noteworthy features can be described. The calcaneum and the navicular are only represented by small fragments.

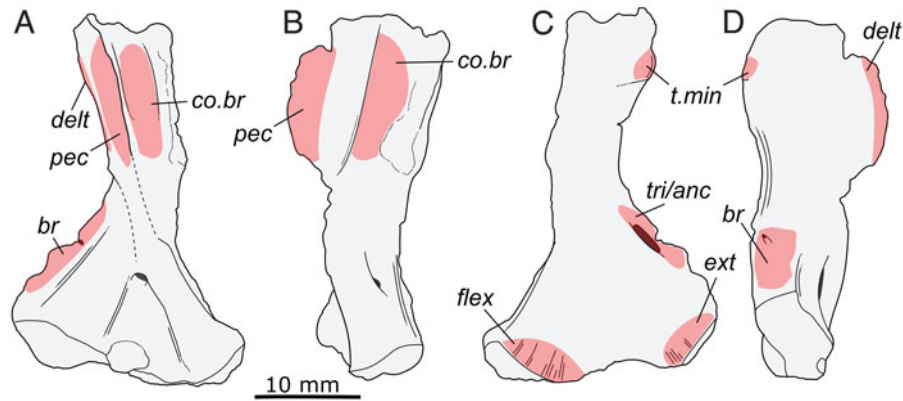


FIGURE 7. Humeral muscular origins and insertions of *P. brasiliensis*. Right humerus in **A**, anterior, **B**, medial, **C**, posterior, and **D**, lateral views. **Abbreviations:** **br**, origin of the *M. brachioradialis*; **co.br**, insertion of the *M. coracobrachialis*; **delt**, insertion of the *M. deltoideus*; **ext**, origin of extensor muscles of the wrist joint and digits; **flex**, origin of flexor muscles of the wrist joint and digits; **pec**, insertion of the *M. pectoralis*; **t.min**, insertion of the *M. teres minor*; **tri/anc**, origin of the *M. triceps brachii* and *M. anconeus*.

Three small bones, probably cuneiforms, are present between the proximal tarsals and the metatarsals.

All metatarsals and phalanges are preserved except for the ungual phalanx of digit V. The pedal phalangeal formula is 2-3-3-3-3. This formula is the advanced mammalian condition also observed in *Kayentatherium* (Lewis, 1986), whereas the exact phalangeal formula remains in doubt in basal cynodonts (Jenkins, 1971a). The metatarsals are symmetrical. Metatarsals III, IV, and V are approximately the same size (about 8.5 mm), whereas metatarsal I is shorter (6.5 mm); the length of metatarsal II cannot be determined clearly due to its poor preservation. On metatarsals III, IV, and V, the proximal end is moderately expanded lateromedially but has a dorsoplantar expansion. The distal end is more broadly expanded lateromedially than the proximal end, to form the metatarsal phalangeal articulations. Metatarsal I is the widest metatarsal, and its proximal end is greatly expanded lateromedially, with a width greater than that of the distal end. The lack of epiphyses suggests the presence of a cartilaginous cover on the proximal and distal joints.

The anterior and posterior ends of the proximal phalanges are wide, whereas the distal ends of the intermediate phalanges are less broadly expanded. The proximal ends of the phalanges consist of a concave surface and two prominent posteroproximal projections located on the posterior edge. The distal articular facet of the proximal and intermediate phalanges is a wide trochlea that extends plantarly and dorsally. The unguals are slightly curved and short.

Muscular Reconstruction of the Appendicular Skeleton of *P. brasiliensis*

Muscles of the Shoulder Joint—In all tetrapods, the deltoid muscle is present as a clavicular division (*M. deltoideus clavicularis*) and a scapular division (*M. deltoideus scapularis*), with an additional division from the acromion (*M. deltoideus acromialis*) in mammals (e.g., Gambaryan et al., 2015). The lateral margin of the deltopectoral crest of *P. brasiliensis* was the area of insertion of the *M. deltoideus* (Fig. 7), as seen in living tetrapods (e.g., Stein, 1981; Jenkins and Goslow, 1983; Meers, 2003; Walthall and Ashley-Ross, 2006). The *M. deltoideus* protracted the forelimb and was also able to abduct the glenohumeral joint, as in living reptiles and therians.

In mammals, the *M. teres minor* derives from the *M. deltoideus scapularis* (Abdala and Diogo, 2010). It originates from

the ventral half of the posterior border of the scapula in therians and inserts on the posterolateral surface of the humerus, distal to the greater tuberosity. In *P. brasiliensis* and most non-mammaliaform cynodonts, a tuberosity is present on the proximal portion of the posterolateral ridge of the humerus, near the greater tuberosity. This structure is interpreted to be the area of insertion of the *M. teres minor* (Jenkins, 1970, 1971a; Kemp, 1980b; Butler, 2009). The *M. teres minor* would assist in abduction of the humerus.

In all living tetrapods, the *M. coracobrachialis* originates from the coracoid, with a second portion originating from the anterior part of the scapular base in crocodylians. This muscle inserts on the anteromedial surface (equivalent to the posteroventral surface in reptiles) of the humerus in most living tetrapods (Meers, 2003; Fisher et al., 2007, 2009). In *P. brasiliensis* and non-mammaliaform cynodonts, the large bicapital groove present on the anteromedial surface of the humerus was the area of insertion of the *M. coracobrachialis*. The muscle possibly extended until the entepicondylar ridge, as seen in monotremes and some therians (Fisher et al., 2009; Gambaryan et al., 2015), but no osteological evidence supports this assumption. Its function was mainly to adduct the humerus, as in living crocodylians or therians.

The *M. pectoralis* complex originates mainly from the sternum in therians, crocodylians, and amphibians, and from the interclavicle and sternal ribs in monotremes and squamates. In *P. brasiliensis* and other non-mammaliaform cynodonts, the origin of this muscle was certainly on the posterior ramus of the interclavicle, as in living monotremes (Jenkins, 1971a; Gambaryan et al., 2015). The *M. pectoralis* ran proximodistally along the medial margin of the deltopectoral crest, as seen in other tetrapods. Its function was to retract and adduct the limb.

Muscles of the Elbow Joint—The *M. triceps brachii* consists of four divisions in urodelans, squamates, and mammals, and five in crocodylians (Abdala and Diogo, 2010). On the scapula, the *M. triceps brachii* scapularis originates from a scar located on the posterior border, above the glenoid, in squamates, crocodylians, and mammals. The humeral portions originate from the posteromedial and posterolateral surfaces of the humeral shaft in all tetrapods possessing them (e.g., Jenkins and Weijss, 1979; Walter, 1988; Zaaf et al., 1999; Walthall and Ashley-Ross, 2006; Fisher et al., 2007, 2009). In *P. brasiliensis*, the ectepicondylar crest provides a wide area of origin for the extensor muscles of the elbow joint, such as the *M. triceps brachii* caput

laterale, as seen in didelphid marsupials (Argot, 2001). In living tetrapods, all the divisions of the *M. triceps brachii* insert on the olecranon process of the ulna, retracting the humerus, extending the elbow, and supporting the body off the ground against gravity.

The *M. brachioradialis*, flexor of the elbow joint, originated from the anterior side of the ectepicondylar crest, as seen in didelphid marsupials (Argot, 2001).

Muscles of the Wrist Joint and Digits—Marked striations are present on the posterior and distal margins of the entepicondyle and ectepicondyle of *P. brasiliensis* and indicate, respectively, the areas of origin of digits and wrist flexor and extensor muscles, as seen in living mammals and reptiles (Meers, 2003; Fisher et al., 2009).

Muscles of the Hip Joint—In squamates and crocodylians, the *M. iliofemoralis* (homologue of the *M. glutei* in mammals) originates from the lateral surface of the iliac blade (Zaaf et al., 1999; Otero et al., 2010). In mammals, the origin is limited to the preacetabular portion of the iliac blade, because the postacetabular region is extremely reduced or absent. The postacetabular portion of the ilium of *P. brasiliensis* is greatly reduced, indicating that the area of origin of the *M. glutei* was limited to the preacetabular portion of the blade. The longitudinal crest on the lateral side of the iliac blade of *P. brasiliensis* is slightly marked but could already separate the *M. glutei* (superior part of the blade) from the *M. iliopsoas* (inferior part) origins as in monotremes and many therians (Jenkins and Parrington, 1976). In *P. brasiliensis*, the *M. glutei* inserted on the apex and lateral aspect of the greater trochanter, as in most living tetrapods. This muscle abducted and retracted the leg. The retractor function of the *M. glutei* is discussed in detail below.

In *P. brasiliensis* and other non-mammaliaform cynodonts, the *M. obturator internus* and the *M. gemelli* (homologue of the *M. ischio-trochantericus* in non-mammalian tetrapods) probably had their origins on the dorsal surface and the prominent tuberosity of the ischium, as seen in some therians (Fisher et al., 2008). The anterior reflection of the greater trochanter seen in other non-mammaliaform cynodonts provides a laterally projected surface for the insertion of the *M. obturator internus* and *M. gemelli*. This reflection is not visible in *P. brasiliensis*, but the *M. glutei* probably retained its insertion on the anterior aspect of the greater trochanter, because the circular trochanteric fossa was occupied by the *M. obturator externus*. From these areas of origin and insertion, the muscle could retract the femur, working in tandem with the *M. glutei*.

In *P. brasiliensis* and non-mammaliaform cynodonts, the *M. obturator externus* (homologue of the *M. pubo-ischio-femoralis externus* in non-mammalian tetrapods) originated from the lateral surface of the pubis and the ischial plate, as seen in living reptiles and therians (Romer, 1922; Otero et al., 2010). This muscle inserts on the proximal region of the posterior femoral surface in living tetrapods, including the lesser trochanter in urodelans and squamates, but is restricted to the trochanteric fossa in therians. The lesser trochanter of *P. brasiliensis* is a short tuberosity, located more medially than posteriorly and suggesting that the insertion *M. obturator externus* was already restricted to the trochanteric fossa, leaving the trochanter for the insertion of the *M. iliopsoas*, as in therians. The *M. obturator externus* had retractor and adductor functions.

In urodelans, the *M. pubo-ischio-femoralis internus* (homologue of the *M. iliopsoas* in mammals) originates from the ventromedial surface of the puboischial plate. Although the pubis of *P. brasiliensis* remains unknown, it is probable that no part of this bone was projected anteriorly to the acetabulum, as seen in other probainognathians (Bonaparte and Barberena, 2001; Oliveira et al., 2010). As a matter of fact, the *M. iliopsoas*

originated from the ventral part of the lateral surface of the well-developed preacetabular portion of the ilium, as seen in therians (Argot, 2002). It could also originate further forward than the ilium, on the lumbar or thoracic vertebrae, but no osteological evidence supports this assumption. In therians, the distal part of the *M. iliopsoas* originates from the preacetabular portion of the ilium and fuses with the *M. psoas major*, arising from the transverse processes of dorsal and thoracic vertebrae (Fisher et al., 2008, 2010), to form the *M. iliopsoas*. As in therians, the lesser trochanter of *P. brasiliensis* is located medially and its apex is facing proximally instead of posteriorly, providing an area of insertion for the *M. iliopsoas*. This muscle was a protractor of the hind limb.

There is no fourth trochanter for the insertion of the *M. gluteofemoralis* (homologue of the *M. caudifemoralis* in non-mammalian tetrapods) on the femur of *P. brasiliensis*. The size of the tail of *P. brasiliensis* is unknown, but it is relatively reduced in other non-mammaliaform cynodonts compared with ‘pelycosaurs’ (Bonaparte, 1963; Jenkins, 1971a), suggesting a reduction in importance of this muscle in cynodonts.

DISCUSSION

The pectoral girdle and humerus of *P. brasiliensis* bear a combination of plesiomorphic and derived features among cynodonts. For example, the robust clavicles and interclavicle, the flat humeral head, the long deltopectoral crest, the expanded humeral distal end, and the presence of an ectepicondylar foramen are features seen in basal non-mammaliaform cynodonts. On the other hand, the lateral extensions of the interclavicle, the absence of significant long-axis torsion of the humerus, and the perpendicularly projected deltopectoral crest are traits similar to those seen in more derived members of prozostroodontians (e.g., *Brasilodon*) and mammaliaformes. The pelvic girdle and the femur of *P. brasiliensis* reveal derived features such as a reduced postacetabular portion and an anterodorsally projected preacetabular portion of the ilium, a large obturator foramen, and the short and medially projected lesser trochanter, similar to those of the derived prozostroodontians (e.g., tritylodontids, *Brasilodon*), early mammaliaforms (e.g., *Eozostrodon*), and living therians. However, *P. brasiliensis* also bears distinctive features such as the bulbous femoral head without a constricted neck and confluent with the greater trochanter, similar to those of more basal non-mammaliaform cynodonts.

Postural and Functional Inferences

An important functional shift in early synapsids was the transition from a sprawling posture, shared with early amniotes and living reptiles in general, to an erect or semierect posture, shared essentially by therians (e.g., Romer, 1922; Kemp, 2005) amongst the synapsid lineage. The sprawling posture is mainly characterized by the lateral undulation of the vertebral column, the horizontal retraction and protraction of the limbs, the rotation of the stylopods, and the extension of the elbow and the knee to improve the stride length (Jenkins, 1971a). In living therians, the lateral undulation of the vertebral column and the rotation of the stylopods were lost, whereas the retraction and protraction of the limbs and the flexion and extension of the elbow and the knee were developed. Moreover, the dorsoventral undulation of the column and the move of the shoulder girdle on the thoracic cage were added (Jenkins, 1971b).

Within cynodonts, previously proposed models describe an evolutionary trend toward a more erect hind limb posture, whereas the forelimb retains a sprawling posture (Jenkins,

1971a; Kemp, 1980b). The independent acquisition of a parasagittal gait of the hind limb has been proposed for a number of terrestrial tetrapod lineages, including dinocephalians, anomodonts, and theriodonts within synapsids (Blob, 2001; Fröbisch, 2006; Ray, 2006), and rauisuchians, ornithosuchids, early crocodylomorphs, pterosaurs, and dinosauromorphs within sauropsids (e.g., Bonaparte, 1984; Kubo and Benton, 2007).

Pectoral Girdle—The function of the pectoral girdle is to resist the compressive and transverse force transmitted by the limb and exerted on the thorax (Jenkins, 1971a). This force is more important in animals with sprawling posture and gait than in erect animals, such as generalized therians. In these mammals, only minor transverse forces are generated on the thorax because the scapula is located above the limb, approximately in a parasagittal plane. As a matter of fact, Monotremata is the only group of extant mammals to retain the interclavicle and the procoracoid-coracoid complex because they have a sprawling posture (Howell, 1937a). In therians, the interclavicle and procoracoid are lost, the clavicles are reduced in size or lost, and the coracoid is reduced to a small process located on the anterior part of the glenoid (e.g., Howell, 1937b). The robust pectoral girdle of *P. brasiliensis* suggests that important compressive forces were still generated by the forelimb on the thorax; thus, a sprawling or semisprawling posture for this cynodont is proposed. As in most non-mammaliaform cynodonts, the posterior ramus of the interclavicle in *P. brasiliensis* is broader than in ‘pelycosaurian’ synapsids (Jenkins, 1971a), indicating better fixation of the *M. pectoralis* and thus permitting powerful humeral adduction to sustain the body above ground.

The clavo-interclavicular articulation of *P. brasiliensis* is relatively similar to that of tritylodontids, early mammaliaforms, and monotremes, consisting of rigid clavicular processes of the interclavicle overlapping the medial end of the clavicle. Although this configuration is a derived condition compared with the concave articular facets observed in most non-mammaliaform cynodonts, the planar morphology of the processes and the medial end of the clavicle limited the elevation, depression, and long-axis rotation of this bone. Moreover, in monotremes, the clavicle and the clavicular processes of the interclavicle are bound by ligaments and no clavo-interclavicular mobility is present in this group (e.g., Luo, 2015). Eutriconodontians are the first basal-most group of Mesozoic mammals that developed a mobile clavo-interclavicular articulation, with a single point of contact between the two bones, as seen in living therians (Ji et al., 1999).

Torsion of the Humeral Shaft—Torsion of the humerus occurs in terrestrial tetrapods that have a sprawling posture. The weak torsion measured on the humerus of *P. brasiliensis* could suggest a more erect posture of the forelimb, compared with basal non-mammaliaform cynodonts. However, a lack of torsion is not necessarily indicative of a parasagittal gait. Indeed, there is no humeral torsion in fossorial therians, such as talpids, spalacids, and myospalacids, which secondarily acquired sprawling or semisprawling posture due to adaptations to fossoriality (Gambaryan and Kielan-Jaworowska, 1997).

Importance of the Adductor Musculature—A long deltopectoral crest can increase the efficiency of the *M. pectoralis*. In basal tetrapods and reptiles, the *M. pectoralis* plays a substantial role in the maintenance of limb posture, elevating the body from the ground in animals that have an abducted humerus (Jenkins, 1971a; Walker, 1987; Meers, 2003). In contrast, the adductor function is limited to the *M. pectoralis superficialis* in generalized mammals, and the *M. pectoralis profundus* is a powerful retractor, with a reduced role in posture (Hildebrand, et al., 1995; Fisher et al., 2007, 2009). The length of the crest

and its great anterior projection seen in *P. brasiliensis* and all non-mammaliaform cynodonts indicate that the adductor function of the *M. pectoralis* had an important role in posture and that the humerus was held in a sprawling or semisprawling position. The bicipital groove of the humerus is well marked and broad in *P. brasiliensis* and non-mammaliaform cynodonts, providing a wide area for the *M. coracobrachialis*. This muscle could assist the *M. pectoralis* to adduct the humerus, and sustain the body. According to Abdala (1999), the reduced angle of the deltopectoral crest found in *P. brasiliensis* and other small non-mammaliaform cynodonts can be correlated to a relatively reduced *M. pectoralis* compared with larger cynodonts, because the latter needed more powerful adductor muscles to sustain their weight.

Musculature of the Forearm—According to Romer (1922), the development of the elbow extensor and flexor muscles is necessary to maintain the elevated position of the body when the forearm is inclined. Romer (1922) suggested that these muscles are less developed in mammals because the sustentation is maintained by the vertical position of the radius rather than by muscle. Thus, the development of the condyles and their associated muscles in *P. brasiliensis* could be correlated to an inclined position of the forearm. However, this inclination is not necessarily associated with a sprawling posture. Indeed, arboreal mammals have well-developed elbow extensor and flexor muscles to bring the body close to the substrate with an inclined forearm (Argot, 2001, 2004).

Femoral Head—The femoral head of *P. brasiliensis* is bulbous, permitting a greater range of motion than the flattened head of ‘pelycosaurian’ synapsids. However, it did not provide the same range of motion as the hemispherical head of the most derived non-mammaliaform cynodonts, early mammaliaforms, and living therians. The articular area for the acetabulum is not located in line with the axis of the shaft as in ‘pelycosaurs’ (Romer and Price, 1940) but is oriented more medially, at an angle of 45° to the shaft, as in living therians. The position of the femoral head of *P. brasiliensis* indicates that the shaft was held close to the parasagittal plane in a shift toward a more erect hind limb posture.

Hip Muscular Evolution in Basal Synapsids and Non-mammaliaform Cynodonts

The transition to a more erect hind limb posture in mammals was associated with the evolution of muscular organization and a new mode of hip retraction within the Synapsida, which occurred independently in multiple lineages of Permian–Triassic therapsids. In ‘pelycosaurian’ synapsids, the retraction was driven mainly by the *M. caudifemoralis*, which was assisted also by the posterior part of the *M. obturator externus*, as in early amniotes and reptiles (Romer, 1922; Gatesy, 1995). In ‘pelycosaurs’ and other basal synapsids, the *M. glutei* originated on the lateral surface of the posterior and middle parts of the iliac blade (Fig. 8), as seen in living squamates and urodelans (Romer, 1922). These areas were the most appropriate for the function of abduction and rotation of the femur about its long axis during sprawling locomotion (Kemp, 1980b). In basal non-mammaliaform cynodonts such as *Cynognathus*, the preacetabular portion of the iliac blade is extended anteriorly, permitting the reorientation of the gluteal musculature, making it more similar to that in mammals than that in ‘pelycosaurs.’ The posterior fibers of the *M. glutei* retained an abductor function, but the most anterior fibers can pass dorsally and posteriorly to the center of rotation of the hip joint to insert on the greater trochanter, permitting the gluteus musculature to retract the hind limb. The most anterior fibers could permit increasing the extent to which the femur

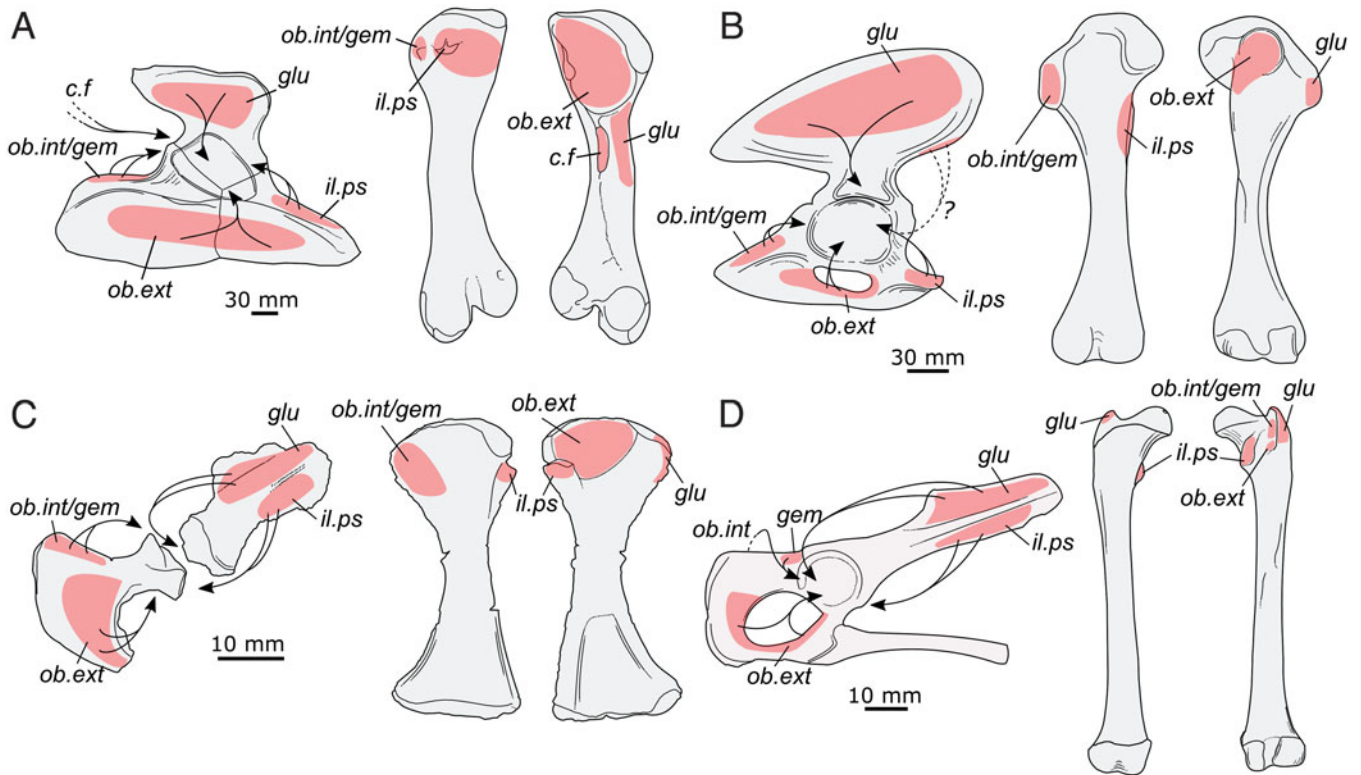


FIGURE 8. Hip muscular origins and insertions for right side of pelvis and right femur in synapsids. **A**, the ‘pelycosaur’ *Dimetrodon*; **B**, the basal cynognathian *Cynognathus*; **C**, *P. brasiliensis*; **D**, the therian *Didelphis*. **Abbreviations:** **c.f.**, origin and insertion of the *M. caudifemoralis*; **glu**, origin and insertion of the *M. glutei* (= *M. iliofemoralis*); **il.ps**, origin of the *M. iliopsoas* and insertion of the *M. iliopsoas* (= *M. pubo-ischio-femoralis internus*); **ob.ext**, origin and insertion of the *M. obturator externus* (= *M. pubo-ischio-femoralis externus*); **ob.int/gem**, origin and insertion of the *M. obturator internus* and *M. gemelli* (= *M. ischio-trochantericus*).

could retract posteriorly compared with that of basal synapsids (Kemp, 1980a). The anteriorly extended blade and prominent greater trochanter observed in other derived non-mammaliaform cynodonts suggest that the mechanism of gluteus-driven retraction may have been widespread in traversodontids, tritylodontids, and other probainognathians (Kemp, 1980b; Sullivan et al., 2013) and progressively replaced the reptilian *M. caudifemoralis* as the main retractor muscle of the leg. The ilium of *P. brasiliensis* is more similar to derived non-mammaliaform cynodonts and mammals than to the basal non-mammaliaform cynodont morphology (Figs. 5, 8), having a rod-like iliac blade with a reduced postacetabular portion. As a matter of fact, the area of origin of the *M. glutei* was limited to the preacetabular portion of the blade in *P. brasiliensis*. This morphology indicates that the main function of this muscle was to retract the limb, as seen in therians (Fisher et al., 2008, 2010).

In basal synapsids and non-mammaliaform cynodonts, the *M. obturator externus* originated from the lateral surface of the pubis and the ischial plate, as seen in living reptiles and therians (Romer, 1922; Otero et al., 2010). In ‘pelycosaurs’ and basal non-mammaliaform cynodonts, this muscle inserted in the trochanteric fossa and on the apex of the lesser trochanter, because this trochanter is a crest located near the fossa and posteriorly projected (Crompton, 1954; Jenkins, 1971a; Kemp, 1980a). In ‘pelycosaurs,’ this muscle was probably able to retract the femur, but its main function was adduction, to elevate the body from the ground during locomotion, as seen in living reptiles (Romer, 1922; Otero et al., 2010). In mammals, the *M. obturator externus* is restricted to the trochanteric fossa because the apex of the lesser trochanter is medially located

and used for the insertion of the *M. iliopsoas*. The morphology and position of the lesser trochanter suggest that this was also the case in *P. brasiliensis* and other basal prozostrodonians (e.g., *Therioherpeton*, *Irajatherium*). Because the femur of non-mammaliaform prozostrodonians was oriented in a nearly parasagittal plane, the adductor musculature plays a less important postural role to elevate the body from the ground and the *M. obturator externus* can be restricted to the trochanteric fossa.

In ‘pelycosaurs,’ the homologue of the *M. iliopsoas* originated from the anterodorsal portion of the puboischial plate, as seen in basal amniotes (Romer, 1922; Walthall and Ashley-Ross, 2006). The *M. iliopsoas* could not insert on the internal trochanter given the posterior position of this trochanter. The insertion of the *M. iliopsoas* was more likely located on the anterior surface of the femur, as in basal amniotes (Jenkins, 1971a; Kemp, 1982). According to Kemp (1980b), the *M. iliopsoas* inserted on the anterior surface of the femur in the traversodontid *Luangwa*, because the lesser trochanter still had a posterior position and remained inaccessible from the anterior surface. The posterior position of the lesser trochanter is observed in *Procynosuchus*, *Galesaurus*, *Diademodon*, and *Cynognathus*, which indicates that basal cynodonts had similar muscular configuration to ‘pelycosaurian’ synapsids. In *P. brasiliensis* and tritylodontids, the *M. iliopsoas* originated from the ventral part of the lateral surface of the well-developed preacetabular portion of the iliac blade, as seen in *Didelphis* (Argot, 2002). The dorsal migration of the origin of the *M. iliopsoas* was accentuated by the projection of the iliac blade, which is more anterodorsal than anterior in prozostrodonians. In therians,

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LITERATURE CITED

- the *M. iliopsoas* inserts on the lesser trochanter (Argot, 2002; Fisher et al., 2008, 2010), which protrudes medially. Jenkins (1971a) proposed that the *M. iliopsoas* progressively gained its insertion on the apex of the lesser trochanter during early mammaliaform evolution. The lesser trochanter of *P. brasiliensis* is located medially, and its apex is facing proximally instead of posteriorly, providing an area of insertion for the *M. iliopsoas* (Fig. 8C). This condition supports the hypothesis of Jenkins (1971a) but suggests that the new insertion for the *M. iliopsoas* evolved in basal prozostrodonians, before the origin of Mammaliaformes. This muscle is a protractor of the hind limb in many tetrapods, including amphibians, reptiles, and mammals. However, the new origin and insertion of the *M. iliopsoas* seen in *P. brasiliensis* indicate an important shift of the movement generated. Indeed, the origin and insertion of this muscle are approximately at the same horizontal level as in ‘pelycosaurs.’ With this disposition, the muscle protracted the femur in a horizontal arc, instead of parasagittally. In *P. brasiliensis*, with its new area of origin and insertion, the *M. iliopsoas* was protracting the femur in a nearly parasagittal plane, as in living therians.
- The hip muscular organization changed considerably during the evolution of non-mammaliaform cynodonts. The *M. obturator externus* progressively replaced the *M. caudifemoralis*, providing the main locomotory force during the initial phase of retraction. Because the femur progressively swung backward and the trochanter major had a more dorsal position, the most anterior fibers of the *M. glutei* were able to retract the femur during the latter half of the propulsive phase. In *P. brasiliensis*, the rotational and abductor functions of the *M. glutei* became less important, whereas the retraction function became more developed. Finally, the *M. iliopsoas* shifted its origin from the pubis to the ventral part of the preacetabular portion and its insertion from the anteroventral part of the femur to the apex of the lesser trochanter, permitting the swinging of the femur in a nearly parasagittal plane. This muscular reorientation indicates an erect or semierect position and locomotion for the hind limb of *P. brasiliensis*, similar to that of generalized mammals.
- ### CONCLUSIONS
- The postcranium of *P. brasiliensis* bears plesiomorphic and derived features reflecting the nonlinearity of probainognathian evolution. Although the scapula-humeral articulation is not preserved, the presence of a robust and rigid pectoral girdle, the long deltopectoral crest, and the large bicapital groove of *P. brasiliensis* indicate that the forelimb was held in a sprawling or semisprawling position. In contrast, the pelvis and hind limb of *P. brasiliensis* show several derived features, such as the well-developed preacetabular portion of the iliac blade, the reduced postacetabular portion, and the medial position of the lesser trochanter, that indicate a muscular reorientation compared with early synsids and basal non-mammaliaform cynodonts. In cynodonts, this new muscular orientation of the hip occurred before the appearance of the clade Mammaliaformes, during the evolution of non-mammaliaform probainognathians, and refers to a more therian-like erect posture and parasagittal locomotion for the hind limb of *P. brasiliensis*. Detailed studies of more derived probainognathians such as *Brasilodon* would be a great opportunity to provide a complete picture of the postcranial evolution of prozostrodonians and to fill in the gap in our knowledge regarding the mode of locomotion of this group.
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