# Functional morphology and biomechanics of the cynodont *Trucidocynodon riograndensis* from the Triassic of Southern Brazil: Pectoral girdle and forelimb

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Non-mammalian cynodonts provide insights on several points about mammalian evolution, such as the postural change and locomotory advances within the group. Unfortunately, complete skeletons of Triassic cynodonts are rather uncommon and where more complete specimens are found they can offer a global vision on some traits not available from partial specimens. This is the case of the cynodont *Trucidocynodon riograndensis*, from the Triassic of Brazil, that has preserved its forelimbs providing some insights into locomotory properties. The movements between interclavicle and clavicle must have been limited, as such as those occurring between the latter and the scapulocoracoid although the long acromion process of this should have permitted a greater degree of freedom. Some of the more significant movements were those on the shoulder joint, in which the maximum adduction should have been ca. 35º relative to the parasagittal plane and the greater abduction ca. 55º. The maximum adduction occurred when the humerus was in the more retracted position during stride and the variation in the adduction/abduction should have been significant to the limb posture during its recovery stroke. The long olecranon and the distal overlapping between radius and ulna suggest the predominance of simple flexion/extension on the forearm without significant pronation/supination. The poorly preserved hand suggests that *Trucidocynodon* could have evolved a slight semidigitigrad condition in its forelimbs. All these features give to this cynodont an important role in the evolution of the mammalian locomotory properties indicating that some features, such as the possibility of greater humeral adduction, evolved early in cynodont lineage.

Key words: Cynodontia, *Trucidocynodon*, limb posture, biomechanics, Triassic, Carnian, Brazil.

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## Introduction

The understanding of the relationships between skeletal morphology and function permits attribute to a given animal, with relatively high accuracy, its capability (or incapability) in effectuate some activity. Obviously, more consistent results are those obtained due to direct observation of the animal behavior, followed by further comparison of this with a detailed anatomical analysis correlating the structural peculiarities and their functions (Gans 1969; Alexander 1983; Lauder 1991; Carter and Beaupré 2001).

Consequently, the direct observation of morphofunctional and biomechanical data is restricted to the extant taxa. In the strictly fossil taxa, the most common source of information, but not the exclusive one, is the comparison between them and extant animals, which could lead to the formulation of useful hypotheses (Lauder 1991). Nonetheless, some fundamental questions arise during these analyses, such as: what are the useful extant taxa? Or how can we distinguish these taxa from those only apparently useful? Sometimes, these questions are hard to answer and the better situations are those where the extinct and extant species are closely related and morphologically similar, although less related taxa sharing similar morphologies could be very valuable too (even comparing taxa so far related as mammals and dinosaurs, as seen in Sander et al. 2011 and Xu et al. 2015), do not invalidating the results although making them less precise.

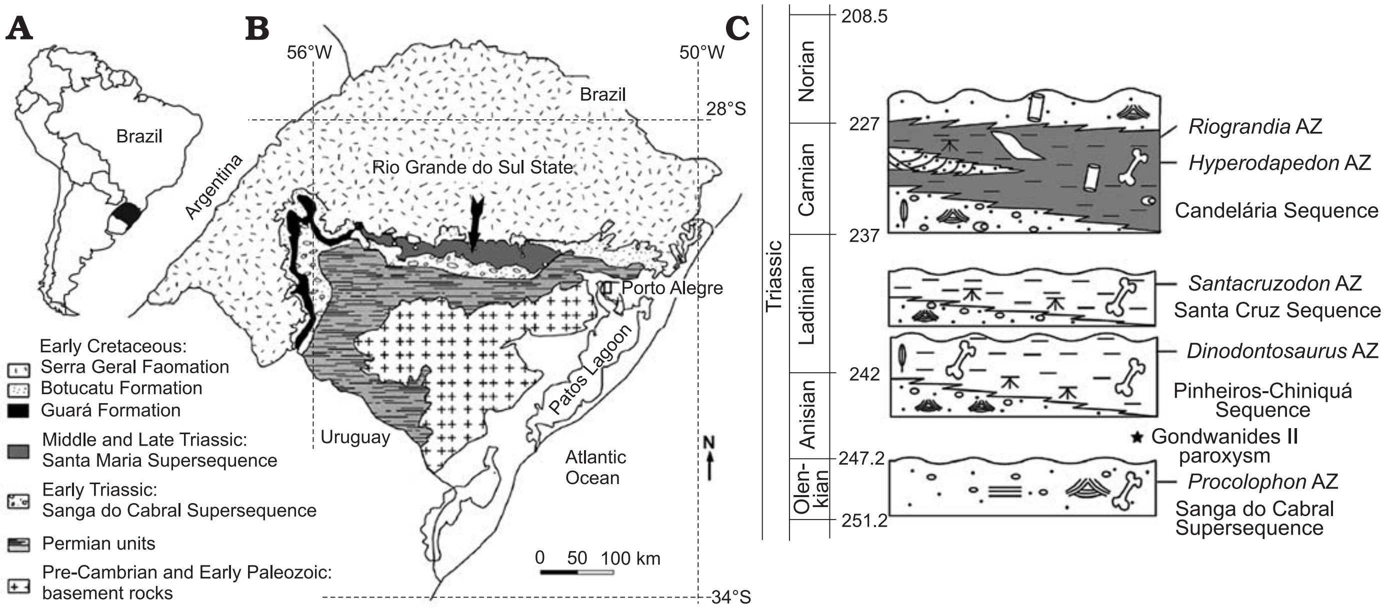

Fig. 1. **A**. Map of South America with the state of Rio Grande do Sul shaded. **B**. Location of the Agudo municipality (arrow) in the state of Rio Grande do Sul, where Middle and Upper Triassic rocks crop out. **C**. Sequence stratigraphy of Brazilian rocks containing Triassic vertebrates, with the *Hyperodapedon* Assemblage Zone highlighted (modified from Horn et al. 2014).

A notorious example of this shaded matter is the evolution of the mammalian locomotory properties, especially the acquisition of a parasagittal limb posture. This history began with several lineages of non-mammaliaform cynodonts (sensu Abdala 2007) or even with more basal synapsids, where modifications towards the mammalian condition are seen (e.g., Crompton and Jenkins 1973; Kemp 2005). The extinction of all non-mammalian synapsid lineages makes the comparison with extant analogues difficult, so each specimen must be carefully analyzed and interpreted, especially the once, which are more complete.

The first known synapsids are a paraphyletic assemblage of animals traditionally named "pelycosaurs" that lived in Carboniferous and Permian (perhaps also Triassic; see Piñeiro et al. 2003) mainly in Laurasia (Rubidge and Sidor 2001; Kemp 2005). These animals are typically treated as "reptilian" in their overall morphology and physiology, what includes their locomotory behavior based in sprawled fore and hind limbs, an ancestral condition since basal amniotes (Kemp 2005).

The more advanced synapsids, the Therapsida, are known since the Carboniferous (though the record of *Tetraceratops* [Matthew 1908; Laurin and Reisz 1996] has been recently reinterpreted by Amson and Laurin [2011] as Permian). Therefore, the earliest doubtless record is from Permian (Rubidge and Sidor 2001; Kemp 2005). The first evidences of a modified limb posture and locomotory skills relative to the "pelycosaurs" appear within this group; several dinocephalians, gorgonopsians, therocephalians, anomodonts (notably the dicynodonts), and non-mammalian cynodonts show advances in their morphology suggesting a more upright posture in their limbs (Kemp 2005). These changes in the limb posture and the consequent increment in the locomotion probably were not the only causes for the geographic spreading of the therapsids and their dominance throughout the late Paleozoic and early Mesozoic times, but they were certainly important.

Within the Cynodontia, the diverse lineage that includes the mammals, the parasagittalization of the limbs occurred many times independently. The most primitive cynodonts, such as the Permian *Procynosuchus*, had sprawled limbs and must have walked in a primitive way (Kemp 1980). The progressively more advanced cynodonts evolved a series of anatomical adaptations related to a more upright limb posture and "efficient" locomotion (i.e., more "mammal-like"), as a slender humerus and femur, the reduction and loss of the coracoidal plate, and several modifications in the pelvic girdle. These modifications can be observed e.g., in traversodontids and chiniquodontids, with some non-mammaliaform cynodonts reaching a virtually mammalian condition, as in the very advanced tritylodontids and tritheledontids (Kemp 2005).

The acquisition of advanced characters towards an upright limb-based locomotion was not uniform or linear within the group and each cynodont is a unique source of information about this particular point on the mammalian evolution. The more valuable taxa to solve some questions on this issue are certainly those with more complete known postcranial skeleton, as *Trucidocynodon riograndensis* Oliveira, Soares, and Schultz, 2010, a cynodont from the Brazilian Upper Triassic (Fig. 1) with the almost complete skeleton preserved (Fig. 2). This species can contribute as much as the Argentine *Massetognathus* (Jenkins 1970b) or the African *Thrinaxodon* and *Cynognathus* (Jenkins 1971b), which also have very informative postcranial material known.

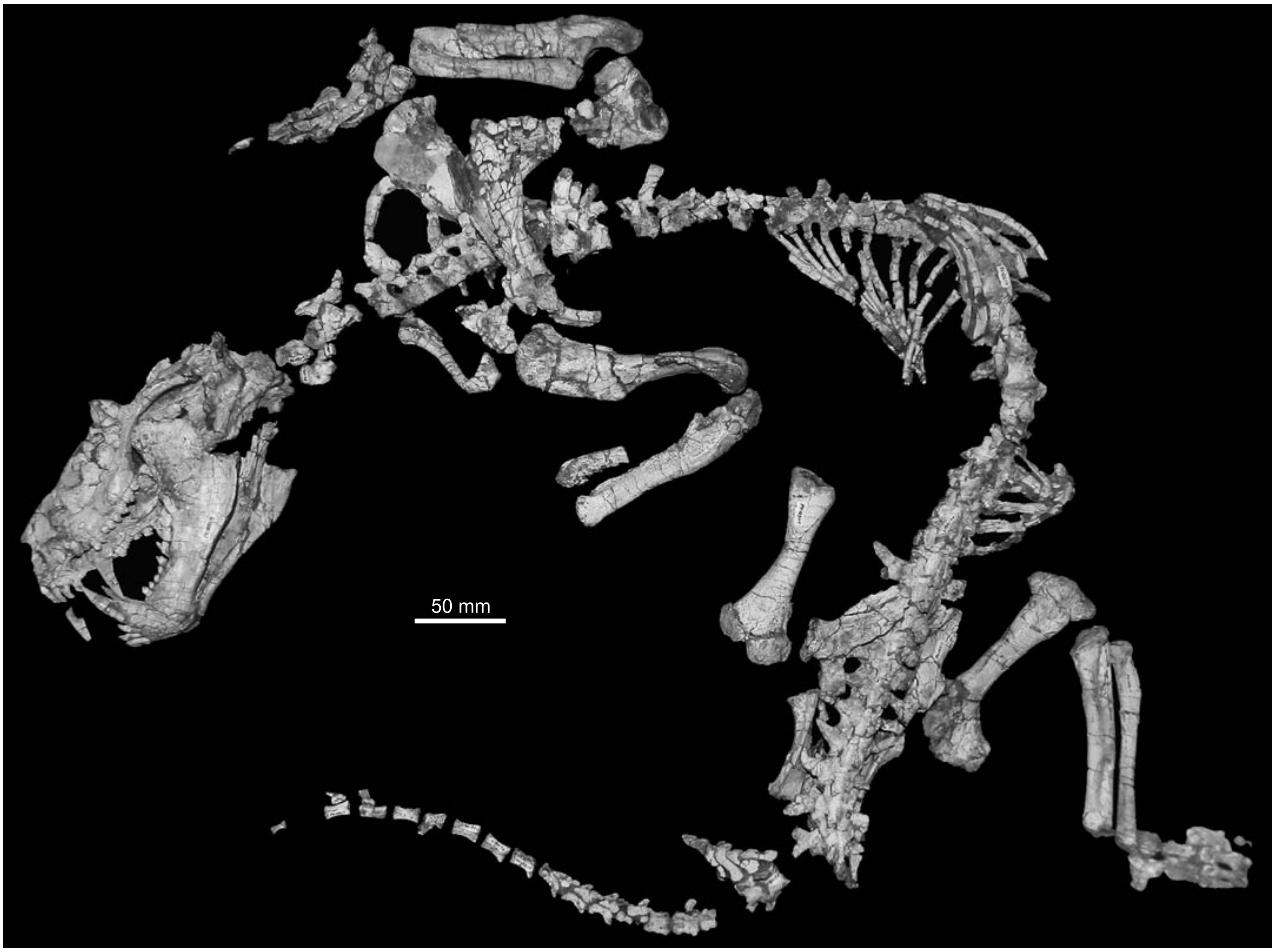

Fig. 2. The holotype of the non-mammalian cynodont *Trucidocynodon riograndensis* Oliveira, Soares, and Schultz, 2010 (UFRGS PV-1051-T) from Carnian (Upper Triassic) of Agudo municipality, state of Rio Grande do Sul, Brazil.

Specimens like the holotype of *T. riograndensis* allow understanding some features of a given species in a more global way permitting to reconstruct the muscular anatomy, the articular movements, and, thus, its postural and locomotory properties (and understand other uses of the limbs too, such as their digging abilities, see e.g., Luo and Wible 2005).

*Institutional abbreviations.*—UFRGS PV, Universidade Federal do Rio Grande do Sul, Vertebrate Paleontology, Porto Alegre, Brazil.

# Material and methods

The specimen referred throughout this paper is the holotype of *Trucidocynodon riograndensis* (UFRGS PV-1051-T), an ecteniniid eucynodont (sensu Martínez et al. 2013). The taxon is recorded in the Upper Triassic rocks from the Candelária Sequence (*Hyperodapedon* Assemblage Zone) outcropping in the state of Rio Grande do Sul, Brazil (Fig. 1; Soares et al. 2011; Horn et al. 2014).

The pectoral girdle and limb bones of *Trucidocynodon* were three-dimensionally scanned in the Engineering School of the Universidade Federal do Rio Grande do Sul, with a Laser Point Digimill 3D® scanner (resolution 0.05 mm). The information was manipulated in the software Rhinoceros® to build 3D models of the individual bones (stereolithography file format or STL). The STL models were manipulated in a 3D environment in Autodesk® Maya® software, version 8.5. The angles between each pair of bones were measured in the 3D environment and in the bidimensional images derived from it.

The musculature was reconstructed searching the origin and insertion sites on the bones using the few homology models including non-mammalian therapsids and primitive mammals (as prototherians) already published (e.g., Gregory and Camp 1918) and also papers, books, or atlas dealing with mammalian anatomy (e.g., Jenkins and Weijs 1979; Schaller 1992; Abdala et al. 2006; Diogo and Abdala 2010). The inferred condition of the muscles and the skeleton anatomy, as well as the manipulation of the three-dimensional models,

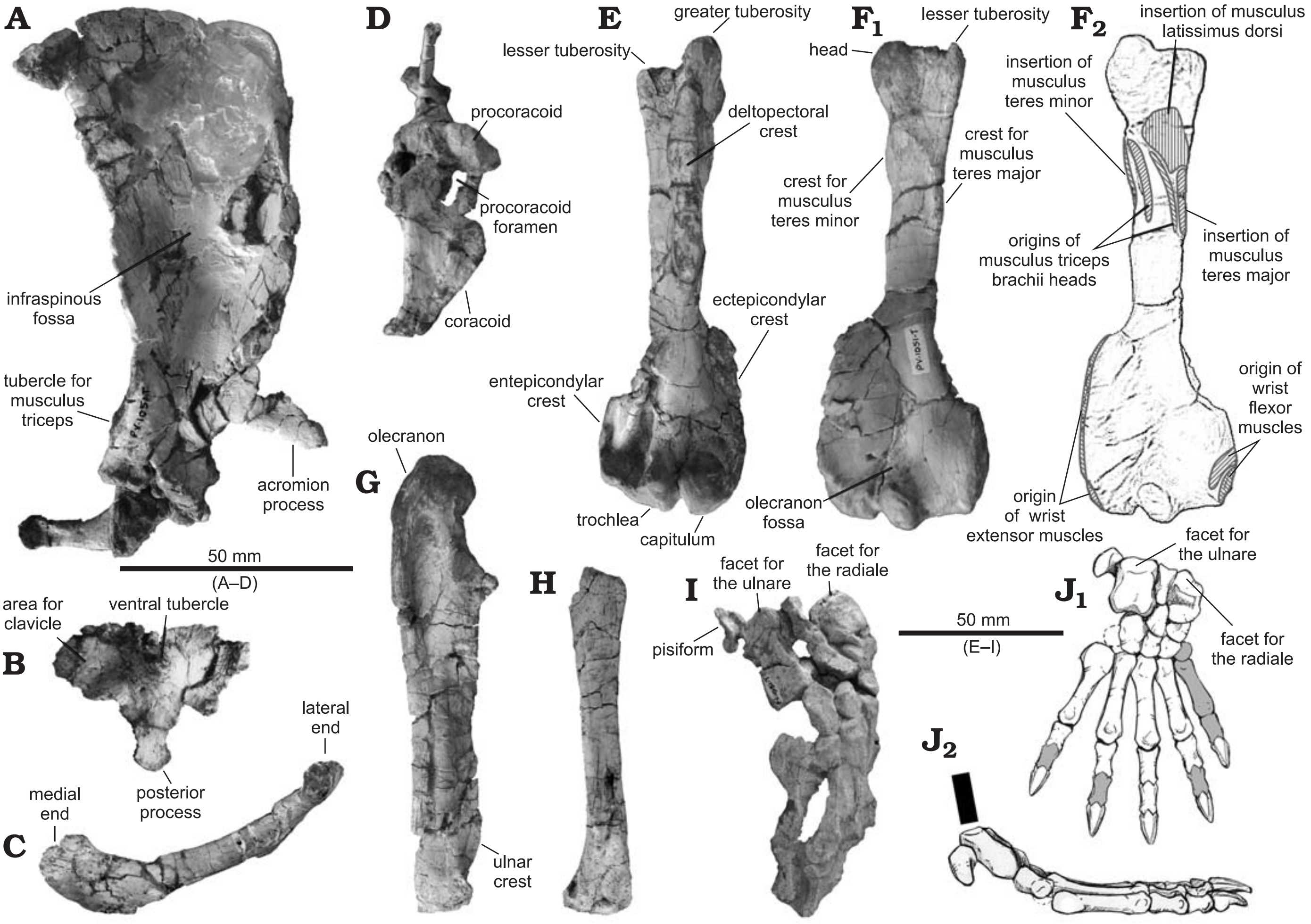

Fig. 3. Pectoral appendicular skeleton of non-mammalian cynodont *Trucidocynodon riograndensis* Oliveira, Soares, and Schultz, 2010 (UFRGS PV-1051-T) from Carnian (Upper Triassic) of Agudo municipality, state of Rio Grande do Sul, Brazil. **A**–**D**. Pectoral girdle; right scapulocoracoid in lateral (**A**) and ventral (**D**) views; right clavicle in dorsal view (**C**); interclavicle in ventral view (**B**). **E**–**J**. Forelimb; left humerus in anterior (**E**) and posterior (**F**) views ($F_1$, photograph; $F_2$, interpretation of the attachment areas of some muscles); right ulna (**G**) and right radius (**H**) in lateral view; right hand in dorsal view (**I**). **J**. Reconstruction of the hand in dorsal ($J_1$) and lateral ($J_2$) views (gray-shaded bones were not preserved; the black bar in $J_2$ represents the potential orientation of the forearm bones).

were used to infer the movements in the articulations. This allowed to reconstruct the functioning of the forelimb during the locomotion.

# Results

**The morphology of *Trucidocynodon riograndensis* pectoral girdle and forelimb**.—The detailed morphology of the pectoral girdle and forelimb of *T. riograndensis* as well the comparison of its skeleton to several cynodonts was described in Oliveira et al. (2010), thus only its functional aspects are presented here.

The scapular blade is tall and laterally occupied by a relatively deep infraspinous fossa (origin of the musculus infraspinatus; Fig. 3A); a supraspinous fossa (for the m. supraspinatus) is not developed. The acromion is very long and the coracoidal plate is still large and contributes greatly for the pectoral glenoid fossa (Fig. 3A, D). The interclavicle (Fig. 3B) is anteroposteriorly short, with a median ventral tubercle and two lateral areas to receive the clavicles.

The humerus (Fig. 3E, F) is moderately slender, with a slightly hemispheric and dorsoposteriorly displaced head. The deltopectoral crest is long, extending up to the half-length of the diaphysis; it is almost perpendicular to the lateromedial axis of the bone (although its exact condition must be slightly taphonomically distorted). The ectepicondylar and entepicondylar crests are well developed, although the former is longer. The trochlea and the capitulum for articulation with ulna and radius, respectively, are rounded.

The ulna (Fig. 3G) and the radius (Fig. 3H) are slender; the ulna has a well developed crest in its distal half. The olecranon process is considerably large. The hand of *T. riograndensis* (Fig. 3I) is poorly preserved, but it is possible to observe the caudal displacement of the articular facets for radius and ulna in the radiale and ulnare bones, respectively. Another remarkable feature is the moderately large pisiform.

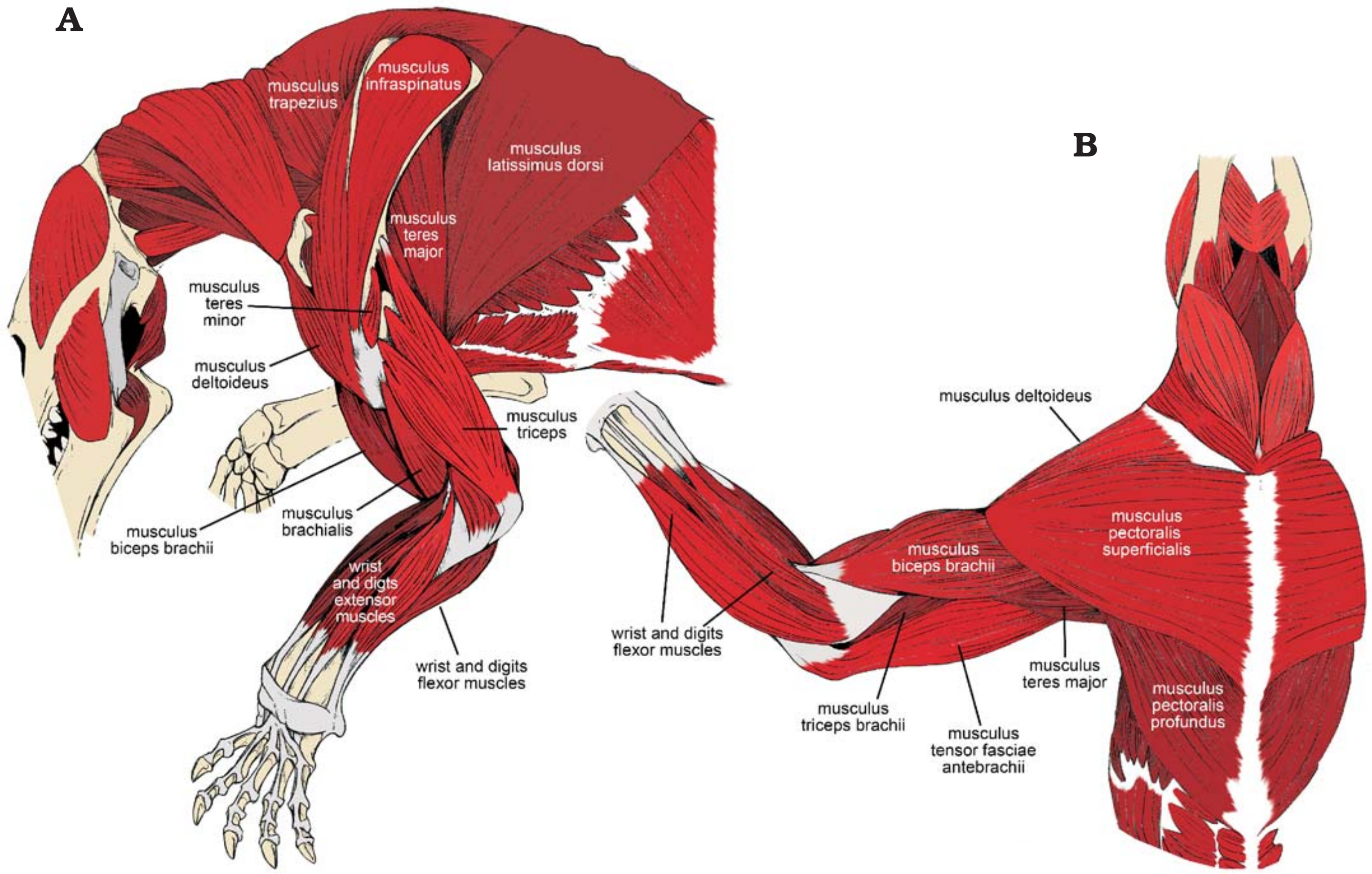

Fig. 4. Muscular reconstruction of pectoral region and forelimb of *Trucidocynodon riograndensis* in lateral (**A**) and ventral (**B**) views (only the muscles discussed in the text are labeled).

**The musculature associated to the pectoral girdle and forelimb of *Trucidocynodon riograndensis*.**—Some of the morphological features cited above are significant for a precise interpretation of muscle anatomy and they were important to build the reconstruction presented in the Fig. 4. The first one is the well-developed tubercle in the caudal margin of the scapular blade just dorsal to the glenoid region (Fig. 3A); this was the origin site of the m. triceps brachii long head (the remaining heads of the triceps had their origins in the humerus; Figs. 3F, 4). The long acromion (Fig. 3A) was the insertion area for the m. trapezius (Fig. 4A) and origin of the m. deltoideus (Fig. 4).

On the deltopectoral crest of the humerus, a ridge (Fig. 3F) is visible in its anterolateral surface, representing probably the insertion of the m. teres minor (Fig. 4A). The deltopectoral crest itself was the most significant area for insertion of mm. deltoideus and pectoralis superficialis (Fig. 4); the m. pectoralis profundus (Fig. 4B) inserted in the lesser tuberosity of the humerus. In the posterior surface of the humerus there are two longitudinal low crests, the lateral one (Fig. 3F) was the origin of another head of the m. triceps brachii and the edge of the insertion of the m. latissimus dorsi (Figs. 3F, 4A); the medial crest, larger (Fig. 3F), was the insertion of the m. teres major (Figs. 3F, 4). The adjacent areas to the deltopectoral crest were occupied by the mm. biceps brachii (Fig. 4) and brachialis (Fig. 4A).

The well-developed ectepicondylar crest of the humerus (Fig. 3E) was the main area for wrist and digital extensor musculature (Figs. 3F, 4A); in the medial side of the humerus, the entepicondylar crest (Fig. 3E) was occupied mainly by wrist and digital flexor muscles (Figs. 3F, 4). Part of these latter muscles inserted in the pisiform bone (Fig. 3I).

The heavily built and moderately long olecranon process of the ulna (Fig. 3G) suggests the robustness of the mm. triceps and tensor fasciae antebrachii that inserted in it (Fig. 4).

**The articular movements in the pectoral girdle and forelimb of *Trucidocynodon riograndensis*.**—The individual joints between pectoral girdle and limb are important to define the posture acquired by the limb and the behavior of the whole limb during locomotion. The first analyzed joint was that between the interclavicle and clavicle where the medial plate of the latter was attached to the ventral surface of the interclavicle probably by means of fibrous tissue as indicated by the markedly striated surface. The properties of this probable fibrous interposed material should have restricted the movements to a slight anteroposterior translation of the clavicle, with a total range of ca. 25° from the more retracted to the more protracted position (Fig. 5A).

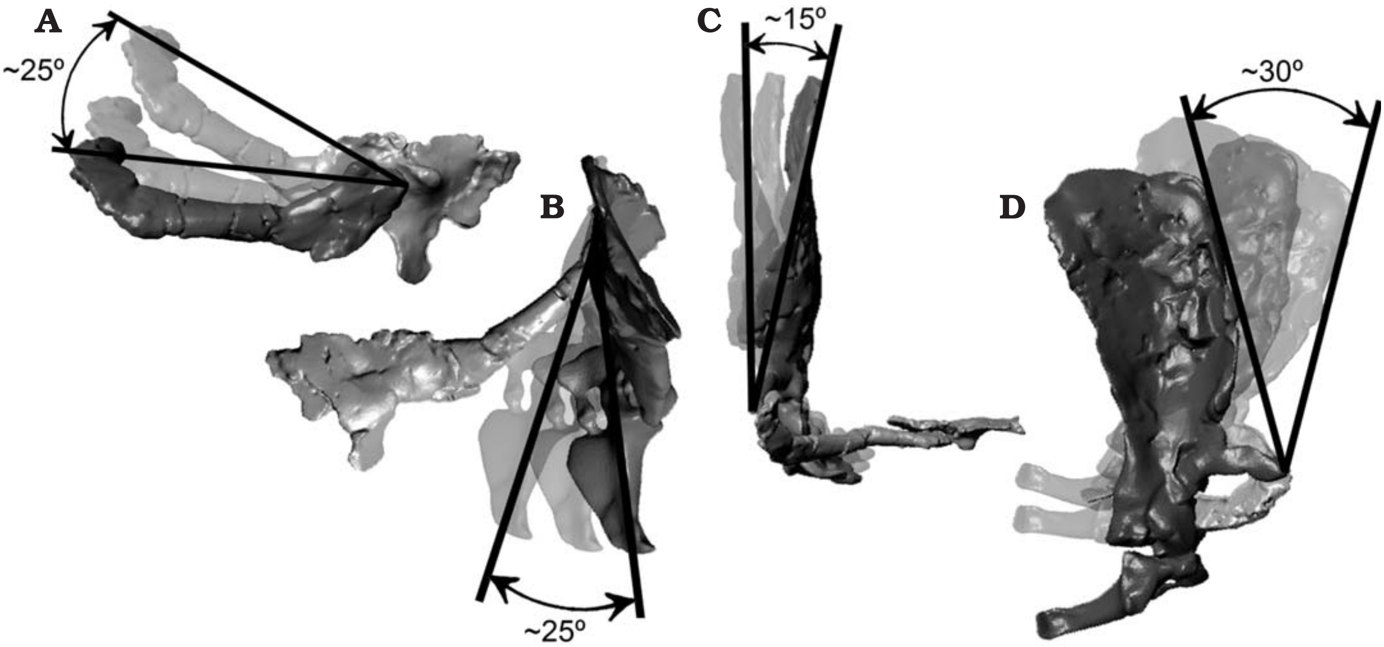

Fig. 5. Movements in the pectoral girdle of *Trucidocynodon riograndensis*. Right clavicle/interclavicle articulation, in ventral view, front upward (**A**); right clavicle/scapulocoracoid articulation, in dorsal (**B**), anterior (**C**), and lateral (**D**) views.

The joint between clavicle and scapulocoracoid consists in the contact between a shallow groove in distal end of the clavicle and the acromion of the scapula and should have been a more complex behavior. The first movement (Fig. 5B) occurred around a vertical axis causing a change in the orientation of the lateral surface of scapulocoracoid, with the coracoidal plate getting closer to the midline (and the scapula facing more lateroposteriorly) or moving away from this (when the scapula faced more laterally). The second movement (Fig. 5C) was around a horizontal axis in a frontal plane, placing the scapular blade closer or farther to the midline (it is possible to consider these movements as adduction and abduction of the scapular blade). These movements, probably, were the less significant during locomotion, promoting fine adjustments on the position of the scapulocoracoid and forelimb throughout the stride.

The third movement (Fig. 5D) in this joint occurred in a parasagittal plane, with the scapulocoracoid oscillating forward (protraction) or backward (retraction); this movement was, probably, the more developed in this joint and could have contributed significantly to increase the step length in *T. riograndensis*.

The shoulder articulation, between scapulocoracoid and humerus, was a key to the acquisition of mammalian forelimb posture. Several modifications involved in the parasagittalization of the forelimb appear in this joint, as summarized, for example, by Howell (1937a, b) and Jenkins (1971b).

The shape of pectoral glenoid fossa, the reduction of the coracoids size, and the almost hemispherical head of humerus suggest a semi-upright posture for *T. riograndensis*, with the maximum adduction of humerus ca. 35–40° from the parasagittal plane and the minimum ca. 55° (Fig. 6A, B). A more upright posture was not possible due to the morphology of the lesser tuberosity of the humerus (Fig. 6A) that does not permits greater adduction.

In the shoulder was possible to infer three main movements, probably occurring simultaneously during stride. The first one comprises the protraction and retraction of the humerus (Fig. 6C), the anteroposterior translation of the bone, occurring in an almost vertical plane and around a horizontal axis; this was the most significant for increasing the step length. For the correct accommodation of the humeral head on the pectoral glenoid fossa during this movement, the arm must have been fully adducted (during retraction; Fig. 6A) and then abducted (in the protracted phase; Fig. 6B). The third movement was a simple rotation of the humerus along its long axis (Fig. 6D); in this, the axis of the distal end of the humerus changed its orientation from an almost transversal condition in the fully retracted position to a more oblique orientation in the protracted phase.

Given the hemispherical morphology of humeral capitulum and trochlea and the condition of the radius/ulna when articulated to the humerus, the elbow of *T. riograndensis* must have been almost restricted to the flexion/extension movements (Fig. 6E) and the extension could have been quite significant to increase the step length. But a slight translation of radius/ulna towards the sagittal plane (Fig. 6F) could have occurred when the limb was not supporting weight, once it was not possible to move this pair of bones in a strictly parasagittal plane.

The overlapping of the distal ends of the radius by the ulnar crest must have constrained considerably the pronation/supination and these movements must have been insignificant. The preservation of the hand does not permit to infer the detailed mechanics of this region, but the position of the articular facets for the radius/ulna suggest that the hand of

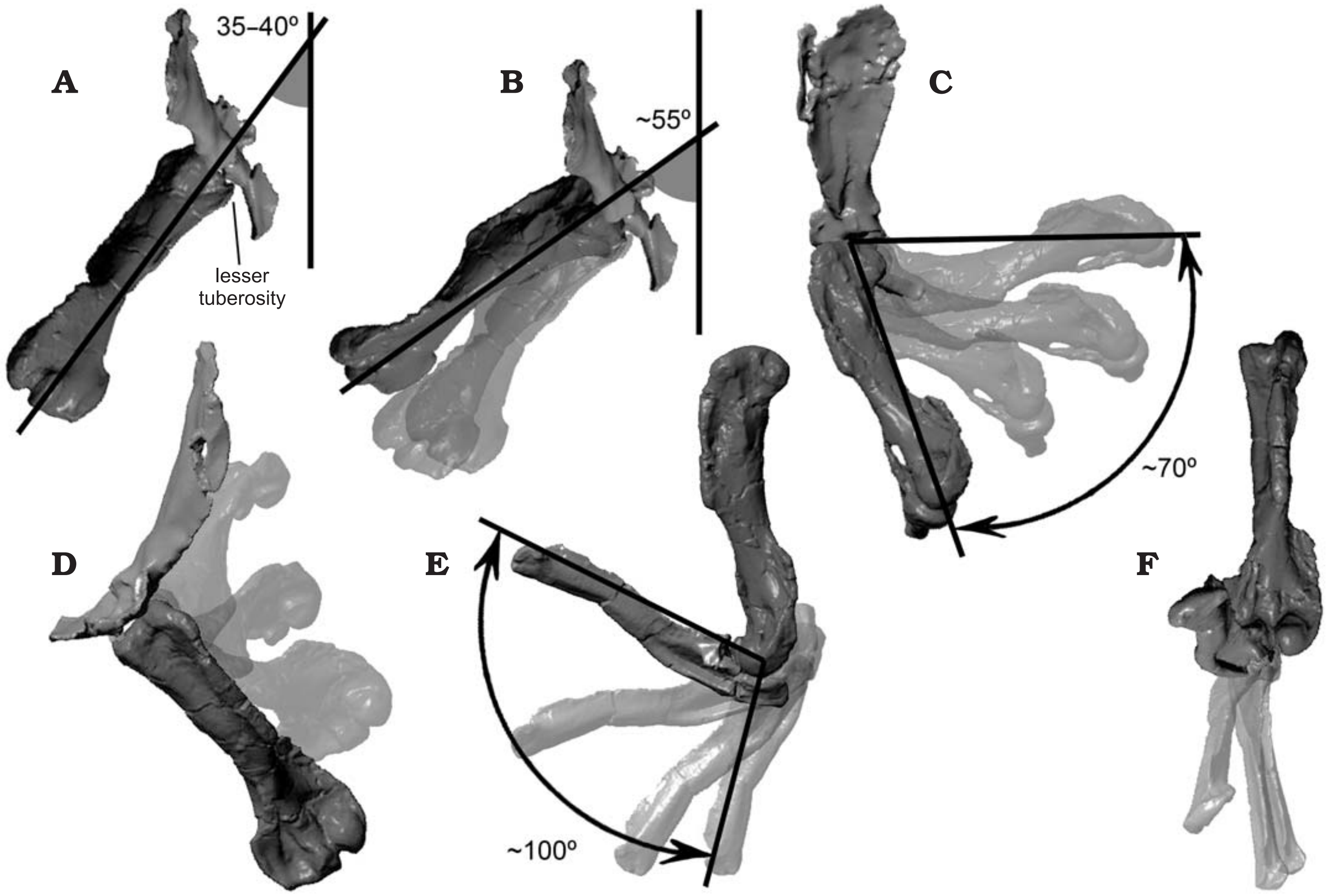

Fig. 6. Movements in the left shoulder and elbow of *Trucidocynodon riograndensis*. Maximal (**A**) and minimal (**B**) humeral adduction, in dorsal view; humeral protraction in lateral view (**C**), humeral rotation in anterior view (**D**); elbow flexion in lateral view (**E**), medial translation of ulna during elbow flexion in anterior view (**F**). Darker shaded steps, in E and F the radius was not figured.

this cynodont was not plantigrade in a strict sense (Fig. $3J_2$), maybe in a condition analogue to that of mammals as the Tasmanian wolf *Thylacynus* (see Freeman 2007) but not as advanced as e.g., in canids or felids.

# Discussion

**The forelimb mechanics during the locomotion of *Trucidocynodon riograndensis*.**—Elftman (1929) divided the locomotory cycle of an animal in two moments or phases (slightly modified here): (1), the stance phase (marked by the propulsive stroke) and (2), the swing phase (that includes the recovery stroke). The stance phase can be divided in other two intervals: (1a), the touchdown (from the moment when the hand touch the substrate until the limb be vertically aligned with the pectoral glenoid fossa) and (1b), the remaining time until the limb losing the contact with the substrate, the lift-off. In its turn, the swing phase can be divided into: (2a), a first half that begins at the end of the stance phase and extends to the moment of maximum retraction of the humerus; and (2b), which begins with the humeral protraction and ends when the hand touches the substrate once more (Fig. 7).

The semi-upright posture proposed for *T. riograndensis* shows the significance of the elbow flexion/extension to step length, especially in the swing phase (Fig. 7A) typical of animals with this kind of posture, as presented by Jenkins (1970a, 1971a). The opposite situation is that in animals with a sprawled forelimb posture, as the prototherian mammals (see Jenkins 1970a), where the step length is mainly regulated by the magnitude of the axial undulations. The large olecranon also suggests that the propulsive force generated by the action of the main elbow extensors (the already mentioned mm. triceps brachii and tensor fasciae antebrachii; Fig. 4) was very important in the phase 1b of the cycle pushing the animal forward. The propulsive stroke could be yet increased by the action of the mm. latissimus dorsi and teres major, probably well-developed given their well-marked insertion sites in the humerus (Fig. 3F).

One of the movements at the clavicle/interclavicle can have occurred during this propulsive stroke: the retraction of the clavicle can have been a result of the contraction of the m. latissimus dorsi (Fig. 4A) when the limb was pulled backward. It is possible also that the clavicular retraction occurred passively, at least partially, for example where the forelimb was touching the substrate and the hind limb

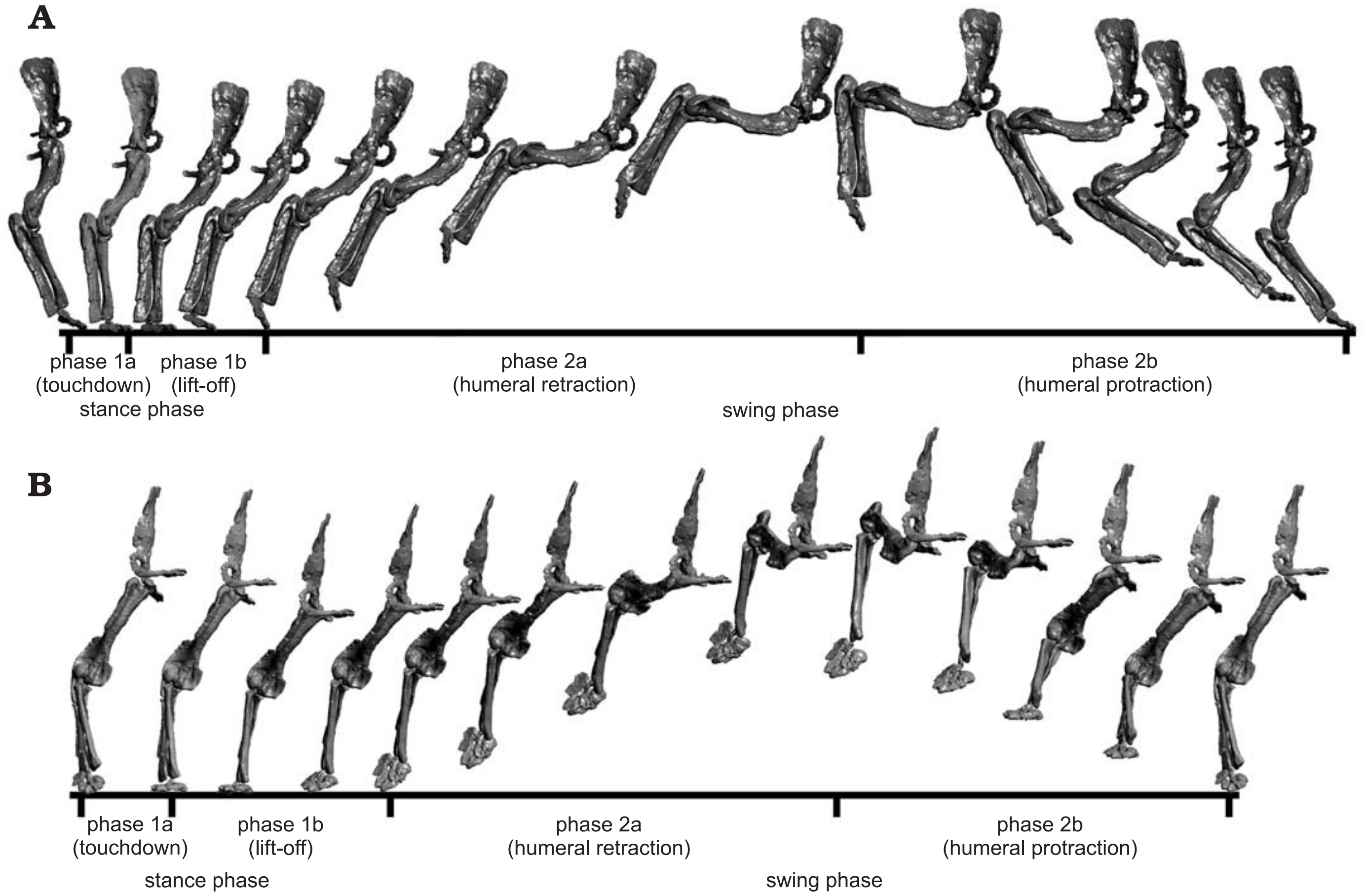

Fig. 7. Locomotory cycle of the right forelimb of *Trucidocynodon riograndensis*, in lateral (**A**) and anterior (**B**) views. The cycle begins with the leftmost image and its phases are those described in the text.

pushed the body forward. On the other hand, the clavicle protraction can have been caused by the action of muscles as the trapezius and deltoideus (and other muscles originated in the neck, not mentioned here, Fig. 4A), which contraction would have pulled the scapulocoracoid and forelimb forward during the swing phase when the limb was being prepared to the next touchdown (phase 2b; Fig. 7).

During the end of the phase 1b and the beginning of the phase 2a, the scapulocoracoid is inclined forward (the opposite condition than in Fig. 5D), maybe by the action of muscles originated in the head and neck and inserted in the scapula. The retraction of the scapulocoracoid (Fig. 5D) seen in the phase 2b (Fig. 7) when the limb is being prepared for the touchdown must have been carried out by the action of muscles originated in the trunk and inserted in the posterior region of the girdle or even by anterior muscles inserted ventrally to the articular pivot (as the m. deltoideus). The range of movement was, very probably, increased by the presence of the long acromion, once it loosens the contact between clavicle and scapula, differently than in cynodonts where the acromion was shorter and the articulation was less mobile (Jenkins 1971b; Kemp 1980; Sues and Jenkins 2006).

As mentioned above, the humerus of *T. riograndensis* could have been placed in a quite adducted position, ca. 35° from parasagittal plane (Fig. 6A), similar to some modern rodents and carnivores (Jenkins 1971a), but also in a more abducted orientation, approximately 55° relative to midline (Fig. 6B), a condition common in several non-mammalian cynodonts (Jenkins 1971b). Analyzing the Fig. 7B, it is possible to observe that during the whole stance phase the humerus acted in the more adducted condition achieved by this cynodont; the abduction of the limb, occurred just in the swing phase when the limb was moved away from the substrate, thus being not significant for the locomotion in a strict sense.

Relative to the forearm behavior during the locomotion, the morphology of the articular surfaces between humerus and radius/ulna strongly suggest the predominance of flexion/extension movements (Fig. 6E). The pronation/supination in the forearm was probably very constrained by the ulnar crest (Fig. 3G) mentioned in the anatomical description. These two functional features are concordant with the locomotion based in semi-upright forelimbs, once supination/pronation are movements very important in animal with more abducted limbs, as reptiles (Landsmeer 1981, 1983) and primitive mammals (Jenkins 1970a). *Trucidocynodon riograndensis*, however, was not a very specialized cursor as some advanced mammals as ungulates where the forearm pronation/supination is avoided by the fusion of radius and ulna (Hildebrand and Goslow 2001) unless these movements are useful for the animal, as the grappling abilities of the felids (Andersson 2003).

Concerning to the hand posture and a possible semi-digitigrady, *T. riograndensis* can have represented a slight advance towards a more agile locomotion when compared with strictly plantigrade cynodonts. In spite of the difficulties in including all animals (specially the mammals) in the three postural categories, plantigrade, digitigrade, and unguligrade (see Carrano 1997), it is clear that the latter two types generally include more agile and fast animals when compared with the former one (Hildebrand and Goslow 2001).

# Conclusion

All the traits mentioned above indicate a semi-upright posture in the forelimbs of *Trucidocynodon riograndensis*. This permits to infer a more agile locomotion for this carnivorous cynodont as pointed in several papers (e.g., Biewener 1989; Blob 2001; Day and Jayne 2007) where the limb posture appears as the most constraining factor to the limb movement patterns, the muscular functionality, and the stresses dispersion along the limb. When the limb is adducted, the displacement of the articulations towards the sagittal plane reduces the muscular efforts to prevent the limb collapse as well as the bending and torsional stresses, at least in animals where the sprawled posture is unusual, as the case of *T. riograndensis* (Blob 2001; Blob and Biewener 2001).

*Trucidocynodon riograndensis* shows several advanced features in its posture and locomotory status. The forelimb function, as presented here, shows that this cynodont reached a locomotory grade close to some advanced non-mammalian cynodonts and even some mammals. This is corroborated by some morphological traits of other parts of its skeleton, as the probable parasagittal functioning of its column, the lumbarization of some vertebrae and posterior presacral ribs (see Oliveira et al. 2010), and the even more upright hind limbs (OTV unpublished material).

Given the far related condition of *T. riograndensis* relative to Mammaliamorpha (Oliveira et al. 2010; Martinez et al. 2013), this animal is an example of the nonlinear locomotory evolution within the cynodont clade, showing that mammals were not the only animals to reach an advanced condition. Unfortunately, the cynodonts rarely were the subjects of detailed studies about synapsis locomotion (e.g., Fröbisch 2006 presented a thorough analysis of the function of the hind limb during the locomotion, but focused in a dicynodont). Once several cynodonts are known only from fragmentary skeletons (see e.g., Sullivan et al. 2013), several aspects of the evolution of the "mammalian" posture and locomotion among the cynodonts could be misinterpreted. A discovery of more informative material or detailed evaluation of the known complete specimens is necessary to fill the gaps in our knowledge on locomotion in this group.

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