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NÁDIA MARIA FREITAS EDUARDO

**ANÁLISE FUNCIONAL DO ESQUELETO APENDICULAR DE UM MARSUPIAL
AUSTRALIANO DO MIOCENO**

FORTALEZA

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NÁDIA MARIA FREITAS EDUARDO

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AUSTRALIANO DO MIOCENO**

**Monografia apresentada ao Curso de
Ciências Biológicas do Departamento de
Biologia da Universidade Federal do Ceará,
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Co-orientador: Dr. Michael Archer.

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Aos meus pais, Eduardo e Kátia.

**Ao Grupo de Discussão sobre Mamíferos e
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RESUMO

Estudos sobre a funcionalidade do esqueleto pós-cranial de mamíferos fornecem uma nova visão sobre a ecologia da mastofauna extinta. Neste contexto, o fóssil do tilacínídeo *Nimbacinus dicksoni* (Marsupialia, Thylacinidae) é um dos fósseis mais completos da fauna de marsupiais carnívoros do Mioceno Australiano. O esqueleto pós-cranial apendicular deste marsupial foi analisado e funcionalmente comparado com um borhyaenídeo do Mioceno da América do Sul, *Lycopsis longirostris*. Este último foi escolhido para comparação porque ambos foram contemporâneos e tiveram tamanhos corporais similares. *N. dicksoni* tem uma combinação de características morfológicas sugestivas à arborealidade. Características dos membros anteriores são as seguintes: (1) a crista deltopectoral e o epicôndilo lateral do úmero são bem desenvolvidos; (2) a epífise distal do úmero é assimétrica; (3) o olecrano da ulna é curto; (4) e a diáfise do rádio é curva. Isso sugere que *N. dicksoni* era capaz de usar seus membros anteriores para manipulação e escalada. As seguintes características dos membros posteriores reforçam essa hipótese: (1) o acetábulo orientado lateralmente; (2) a assimetria da epífise distal do fêmur e dos côndilos tibiais; (3) a fíbula robusta; (4) o facete astragalonavicular mais largo transversalmente; (5) e o facete calcaneocuboidal côncavo, indicam a realização eficiente de movimentos de abdução dos pés. Concluindo, *N. dicksoni* era primariamente um marsupial escansorial, com grande capacidade para manipulação de alimentos.

Palavras-chave: Análise Funcional. Esqueleto Pós-cranial. Fóssil. Marsupial. Mastofauna Australiana. Locomoção.

ABSTRACT

Studies on the functionality of the postcranial skeleton of mammals provide insights on the ecology of extinct mammals. In this context, the fossil of the thylacine *Nimbacinus dicksoni* (Marsupialia, Thylacinidae) is one of the most completed fossil from the carnivorous marsupial fauna of the Australian Miocene. The appendicular postcranial skeleton of this fossil specimen was analysed and functionally compared to a borhyaenoid from the South American Miocene, *Lycopsis longirostris*. The latter was selected for comparison because they were contemporary and had similar body sizes. *N. dicksoni* has a combination of features suggestive of arboreality. Forelimb characteristics are as follows: (1) the deltopectoral crest and the lateral epicondyle of the humerus are well developed; (2) the distal epiphysis of the humerus is asymmetrical; (3) the olecranon of the ulna is short; and (4) the diaphysis of the radius is curved. These suggest that *N. dicksoni* was able of using its forelimbs for manipulation and climbing. Moreover, on the hindlimbs indicate an efficient performance of abductive movies of the feet. The following hind limbs features reinforce this hypothesis: (1) the laterally oriented acetabulum; (2) the asymmetry of the distal epiphysis of the femur and of the tibial condyles; (3) the robust fibula; (4) the transversally wider astragalonavicular facet and the concave calcaneocuboid facet. In conclusion, *N. dicksoni* was mainly a scansorial marsupial, with great hability of manipulating food.

Key-words: Functional Analysis. Postcranial skeleton. Fossil. Marsupial Australian Mammal Fauna. Locomotion.

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1. INTRODUCTION

Analysis of postcranial skeletons have historically been neglected, since the skull contains the most important information to Mammalia phylogenetic studies (WROE & MUSSER, 2001). However, more recent studies on postcranial features have brought insights on the locomotor behaviour and habits of extinct mammals (ARGOT, 2001; ARGOT, 2002; ARGOT, 2003A; ARGOT, 2003B; ARGOT, 2003C; ARGOT, 2004A; ARGOT, 2004B; ARGOT, 2004C; ARGOT & BARBOT, 2011; ERCOLI *et al.*, 2012, SAMUELS *et al.*, 2013).

A great number of these researches have focused on extinct marsupials from South America (ARGOT & BARBOT, 2011). For this, postcranial analysis of living species are an essential tool to understand the functional meaning of fossil skeleton features. In addition, comparative studies between fossils from different areas can highlight the adaptations of these species, as well as assess whether there is evolutionary convergence between the taxa. In this context, Argot (2003b) published a study comparing the postcranial morphology of two Miocene borhyaenoids, *Borhyaena* e *Prothylacinus*. Both of them coexisted in South America, had similar body sizes and were highly carnivorous species. As a result of the study, many adaptive features relative to their ecology were revealed, been an example of how much information is hid underneath the fossil bones of vertebrates.

Australia, as South America, has a huge marsupial fossil record that has been well studied (WROE, 2003). Nevertheless, these studies are concentrated on the morphology of the skull. Only few ones focus on the postcranial skeleton morphology. In this context, the fossil specimen of *Nimbacinus dicksoni* QMF36357 (Queensland Museum Fossil 36357) brings a great potential for postcranial skeleton analysis since its skeleton is almost complete and most of the bones are well preserved. This fossil was found at the Riverleigh Fossil Deposit, Northern Queensland, Australia, and belongs to one of the 11 extinct species of the Thylacinidae family (WROE & MUSSER, 2001).

This family was composed by species that were small or medium sized and that were specialized predators (WROE, 2003). They were morphologically very similar to each other and the main differences are found on the dentition of these species (ATTARD *et al.*, 2014). In the case of *N. dicksoni*, if compared to its modern relative *Thylacinus cynocephalus*, it had an unspecialized dentition, suggesting a more generalist feeding behaviour. It was also smaller, with a body size around 50cm including the tail and estimated weight of 5kg. This species also had a strong bite relative to its size, allowing it to pray on frogs, lizards, snakes, small birds and even other marsupials (ARCHER *et al.*, 2006). Nevertheless, its diet may had been restricted by competition with other Miocene carnivorous marsupials and by fluctuation on pray abundance (ATTARD *et al.*, 2014).

Australian and South American marsupials were under relatively similar natural selection pressures (YU *et al.*, 2012). It may led to the selection of similar morphological traits among the marsupial species of these two continents. Thus, comparisons between the Miocene *N. dicksoni* fossil from Australia with a Miocene marsupial from South America would be useful. For this comparison, the fossil specimen of *Lycopsis longirostris*, that was found at the La Ventan Fossil Deposit, in Colombia, was used. This is because this specimen belongs to a Miocene species that also inhabited South American Miocene rainforest (ARGOT,

2004a). The present study aimed to undertake functional analysis of the appendicular postcranial skeleton of *N. dicksoni* and associate this to its locomotor behaviour.

2. MATERIAL AND METHODS

The specimen of *Nimbacinus dicksoni* (QMF36357) was discovered at the fossil deposit of Riversleigh, in Queensland, Australia. It was described by Muirhead & Archer (1990). The specimen is constituted by a complete skull (WROE & MUSSER, 2001), and its postcranial skeleton associated. We analysed the appendicular postcranial skeleton, formed by (1) both left and right scapula; (2) left and right humerus; (3) right radius and ulna; (4) complete pelvic girdle; (5) right femur, tibia, fibula; (6) astragalus and calcaneous; and (7) the distal epiphysis of the left femur and proximal epiphysis of the left tibia.

This specimen had its skull described by Wroe & Musser (2001) but its postcranial skeleton has not been described in detail. I described only the appendicular skeleton, which includes the pectoral and pelvic girdle, as well as the forelimbs and hind limbs. As Argot (2004a), we assumed that the scars found in bones of *N. dicksoni* indicate the insertions of muscles as in living marsupial species. In this way, we analysed the function of the *N. dicksoni* bones on its locomotor behaviour.

The bones were analysed using a stereoscopic microscope and the features of each bone were related to probable miological aspects. The bones were photographed in different anatomical views. I compared the *N. dicksoni* specimen QMF36357 with *Lycopsis longirostris* (MARSHALL, 1977), a species of borhyaenoid (Borhyaenidae, Metatheria) that lived in the forests of South America during the Miocene. For our comparison, we used the description of the specimen UCMP38061 that was functionally described by Argot (2004a). These comparisons allowed to assessing the functional meaning of the osteological features of *N. dicksoni* and its probable locomotor behaviour.

3. RESULTS

3.1. Scapula and Shoulder Joint

Both left and right scapula are found in the postcranial skeleton of *Nimbacinus dicksoni*, specimen, but the left one is better preserved. The scapula is approximately rectangular shaped in outline (Figure 1.A.), but less than in *Lycopsis longirostris* specimen (ARGOT, 2004a). Although the scapula of *L. longirostris* has a triangular infraspinous fossa (ARGOT, 2004a), as in *N. dicksoni*, the latter has a more rounded supraspinous fossa. Even though the cranial border is not totally preserved, the *N. dicksoni* supraspinous fossa is clearly larger than the infraspinous fossa.

The anterior surface of the scapula has a large subscapular fossa and it elevates by a slight gradient posterior to the neck of the scapula. On the caudal surface, a prominent and high scapular spine, which is perpendicular to the vertebral border, separates both supraspinous and infraspinous fossa (Figures 1.A; 1.C.). The distal part of the spine is inclined caudally and the acromion process of the spine is preserved. The acromion is larger than in *L. longirostris* (ARGOT, 2004a) and it does not overhangs the coracoid process. However, it does overhang the glenoid cavity and it bends anteriorly. The neck of the scapula is large and thick anteroposteriorly (Figure 1.A).

In distal view, the glenoid cavity is oval shaped and it is larger craniocaudally than anteroposteriorly. The distal part of the supraglenoid tuberosity is evident and the coracoid process is prominent ventrally (Figure 1.D.). The head of the humerus is convex and oval shaped proximally (Figure 2.C.), which is compatible with the shape of the glenoid cavity of the scapula. The greater tubercle has a hemispherical shape and it is slightly higher than the head. The lesser tubercle is more prominent than the greater tubercle and it is not pressed to the head. Both tubercles are divided by an evident intertubercular groove (Figure 2.B.).

3.2. Humerus and Elbow Joint

The proximal epiphysis of the humerus is separated from the diaphysis by a well-defined neck. The deltopectoral crest is well developed and it extends further distally for more than half of the diaphysis. However, the deltopectoral crest ends up before the proximal tip of the lateral epicondylar crest. The shaft is roughly twisted and the distal extremity of the

deltopectoral crest is sharp and prominent. The lateral epicondylar crest is also developed along the distal third of the diaphysis and its proximal tip has a hook-like shape (Figure 2.C.).

The distal extremity of the humerus is well conserved, but there is no evident radial fossa (Figure 2.D.). On the other hand, the olecranon fossa, on the caudal surface, is present and has a medial position. This fossa also has an elliptical shape and it is wider than deeper. The distal epiphysis of the humerus is less symmetrical in distal view, due to its well-developed medial condyle. The distance between the medial ridge of the trochlea and the medial extremity of the medial condyle is approximately 36% of the total size of the humerus distal epiphysis, which differs from the percentage in *L. longirostris* (28%) (ARGOT, 2004a). In distal view, the epiphysis of the *N. dicksoni* humerus has a medial epicondyle that is prominent medially and is elongated proximal-distally. It causes the asymmetry of the distal extremity of the humerus. A constricted ridge separates the trochlea and the capitulum while a wide deep area divides the trochlea to the medial epicondyle. The entepicondylar foramen is long proximodistally and evident and has an ellipse shape. The capitulum is developed and distally has a hemispherical shape.

On the ulna, the olecranon represents approximately 16% of the total ulna length, which is relatively shorter than in *L. longirostris* (20%) (ARGOT, 2004a). The *N. dicksoni* anconeal process is very prominent anteriorly and its lateral lip is better developed than the medial one. The anconeal and the coronoid processes project both anteriorly for approximately the same distance. The coronoid process is slightly longer anteroposteriorly than wide transversally. The radial notch is small, rounded and slightly concave. It forms an obtuse angle with the lateral side of the coronoid process in anterodistal view (Figure 3.A.; 3.B).

3.3. Ulna and Radius

The ulna is compressed transversally and its anteroposterior width is slightly larger in the proximal third of the body. The diaphysis is straight and does not have a convex posterior border. However, its distal posterior border is slightly concave. On the medial side of the ulna, the fossa where the muscle *flexor digitorum profundus* originates is deep and wide. Moreover, it extends from the olecranon until the beginning of the diaphysis. On the lateral side, the fossa where the muscle *abductor pollicis longus* originated is shallow. It extends from the radial notch along the proximal half of the diaphysis. The insertion of the muscle *anconeus* is shallow and short (Figures 3.C.; 3.D.).

The proximal extremity of the radius is oval-shaped, and its cranio-lateral border is slightly larger than the caudomedial border (Figure 4.A.). The articular fovea is thick and concave, slightly higher than the articular circumference, which is also concave. The ulnar proximal facet on the radius is convex and evident. The radial diaphysis bowed in an anteroposterior plane and it is less straight than in *L. longirostris* (ARGOT, 2004a). In addition, the bicipital tuberosity on the caudal surface of the radius is oval shaped and longer than in *L. longirostris* (ARGOT, 2004a). The cranial border of the ulna and the caudal border of the radius are sharp, suggesting the presence of a strong interosseous membrane. The radius is approximately triangular in cross section at mid-shaft diameter (Figures 4.B.; 4.C.; 4.D.).

The radial distal extremity is massive and wider than the proximal extremity (Figure 4.F.). It is also wider than the distal extremity of the ulna. The medial and lateral surfaces of the radius are damaged. However, it seems that there is a fossa where the muscle *abductor pollicis longus* originates. The ulnar distal facet is prominent and slightly rounded. The distal facet of the radius articulating with the scaphoid is flat, and the styloid process is very prominent.

3.4. Pelvic girdle and Hip Joint

The pelvic girdle of *N. dicksoni* is preserved, except for the distal portion of the ischium (Figure 5.A.). Consequently, it is not possible to obtain some important information from the ischium. Moreover, the left side is better preserved than the right one.

The iliac blade is expanded, quadrangular and anteroventrally deflected outwards. The gluteal fossa is oriented medially and it is shallow and short. In contrast, the fossa from where the muscle *iliacus* originates is deeper and longer. It ends on the posterior edge of the sacral articulation. The pubic tubercle is well developed and expanded. The acetabulum is poorly preserved, with its dorsal-caudal edge damaged. Dorsally, the dorsal border of the acetabulum seems to be slightly concave. The acetabulum is more laterally than ventrally oriented (Figures 5.A.; 5.B.).

The right femur is poorly preserved and it is broken close to its distal epiphysis. The head of the femur has a hemispherical shape and it is circular proximally (Figure 6.A.). It is also high and it protrudes more proximally than medially. The *fovea femoralis* is not evident. The greater trochanter, where the muscle *gluteus medius* inserts, is lower than the head and its apex is shallow and has a pyramidal shape. The trochanteric fossa is deep dorsalanteriorly and long proximally. It is also more vertically orientated and laterally positioned. The lesser

trochanter is well developed since it protrudes medial-caudally and it is elongated proximal-distally. The distance between the lesser trochanter and the neck is short in *N. dicksoni*. The third trochanter is small, little prominent and ellipse-shaped. It is also laterally orientated. The neck of the femur is poor preserved (Figures 6.A.; 6.B.).

3.5. Femur and Knee Joint

The diaphysis of the femur is poor preserved, since there are many little broken pieces lost. Instead, the distal epiphysis of the femur is well preserved. It has a quadrangular shape and it is slightly wider than deeper in distal view, due to the well-developed femoral medial epicondyle (Figure 6.B.). The femoral trochlea is deeper than in *L. longirostris* (ARGOT, 2004a) and the medial ridge is slightly higher than the lateral ridge, in distal view (Figure 6.C.). There is a shallow fossa on the *N. dicksoni* femur diaphysis, above the trochlea groove. Caudally, the lateral femoral condyle is wider than the medial one. The extensor fossa of the lateral condyle is shallow, while the popliteal fossa is shorter, oval and very deep. The latter is located caudally and distally to the extensor fossa and it is well marked.

The right tibia is well preserved and its proximal surface has a triangular shape. The anterior tuberosity is robust and prominent, and it has a more rounded anterior border. However, it is lower than the tibial proximal condyles. Furthermore, the lateral tibial condyle is higher and more robust than the medial one. The tibial tuberosity is quadrangular and evident (Figure 7.A.).

3.6. Tibia and Fibula

The diaphysis of the tibia is straight and its cross section is triangular along the whole shaft (Figure 7.B.; 7.C.). The proximal part of the diaphysis is larger than the distal one. On the diaphysis, the fossa where the muscle *flexor digitorum tibialis* originates is long and deep, and it is proximal located. Moreover, it is oval shaped and caudally laterally oriented. The lateral fossa where the muscle *tibialis anterior* originates is also oval. However, it is shorter and deeper than the fossa of muscle *flexor digitorum tibialis*. The fossa where the muscle *semimembranosus* inserts is small and shallow. In addition, it is very proximal and located more caudal on the medial surface. The anterior crest is well developed and sharp (Figure 7.B.; 7.C.; 7.D.).

The distal extremity of the tibia is shorter than the proximal one. The articular facet is slightly convex and the distal tip is proximal. It is larger anteroposteriorly than transversally. The tibial medial malleolus is evident, thick, long anteroposteriorly and protrudes distally. In contrast, the lateral malleolus of the tibia is slightly helical. The medial malleolus is large, with one third of the size of the distal epiphysis of the tibia (Figure 7.E.).

The fibula of *N. dicksoni* specimen is well preserved, except for its distal epiphysis, which is not present. The diaphysis of the fibula is robust and slightly curved towards the tibia. It is proximally elliptical and distally quadrangular in cross-section. The lateral surface of the diaphysis is flattened and concave. The head of the fibula is less expanded anteroposteriorly than in arboreal species. Laterally, the head of the fibula presents an elliptical shape and it is inclined medially, while it is flattened transversally. Medially, the muscle *facies articularis capites fibulae* protrudes medially, towards to the lateral condyle of the tibia. The distal epiphysis of the fibula has not been found (Figure 8).

3.7. Ankle Joint

The right astragalus is well conserved. In outline, it is shorter and broader than in *L. longirostris*. The *N. dicksoni* astragalotibial medial facet is short and shallow while the astragalofibular facet is large. It suggests that there is not an articulation between the fibula and the calcaneum. However, it is not possible to assess this question since the distal epiphysis of the fibula is absent (Figure 9.A.). The head of the astragalus is convex, and its astragalonaviclar articular surface is transversely wider (Figure 9.B.).

The right calcaneum is also well preserved. On the calcaneum, the sustentacular surface is concave and longer anteroposteriorly than transversely. The calcaneoastagalar facet is convex, well developed and dorsally oriented. Both facets are almost parallel and the calcaneoastagalar facet is aligned with the tuber calcanei. Moreover, the sustentacular surface reaches the calcaneocuboid facet distally. When articulated with the calcaneum, the astragalar head is located more dorsally than medially to the calcaneocuboid facet (Figure 10.A.). The calcaneocuboid facet is very concave and its lateral border is more distal than the medial one. It has a roughly oval shape and it is laterodorsally to medialplantar oriented. The lateral border of the ectal facet is also well developed. The peroneal tubercle is present and very well developed, compared with some arboreal taxa (Figure 10.A.).



Figure 1. Left Scapula of *Nimbacinus dicksoni*. 1.A. Lateral View. 1.B. Cranial View. 1.C. Caudal View. 1.D. Gleneoid Cavity. Not to scale.

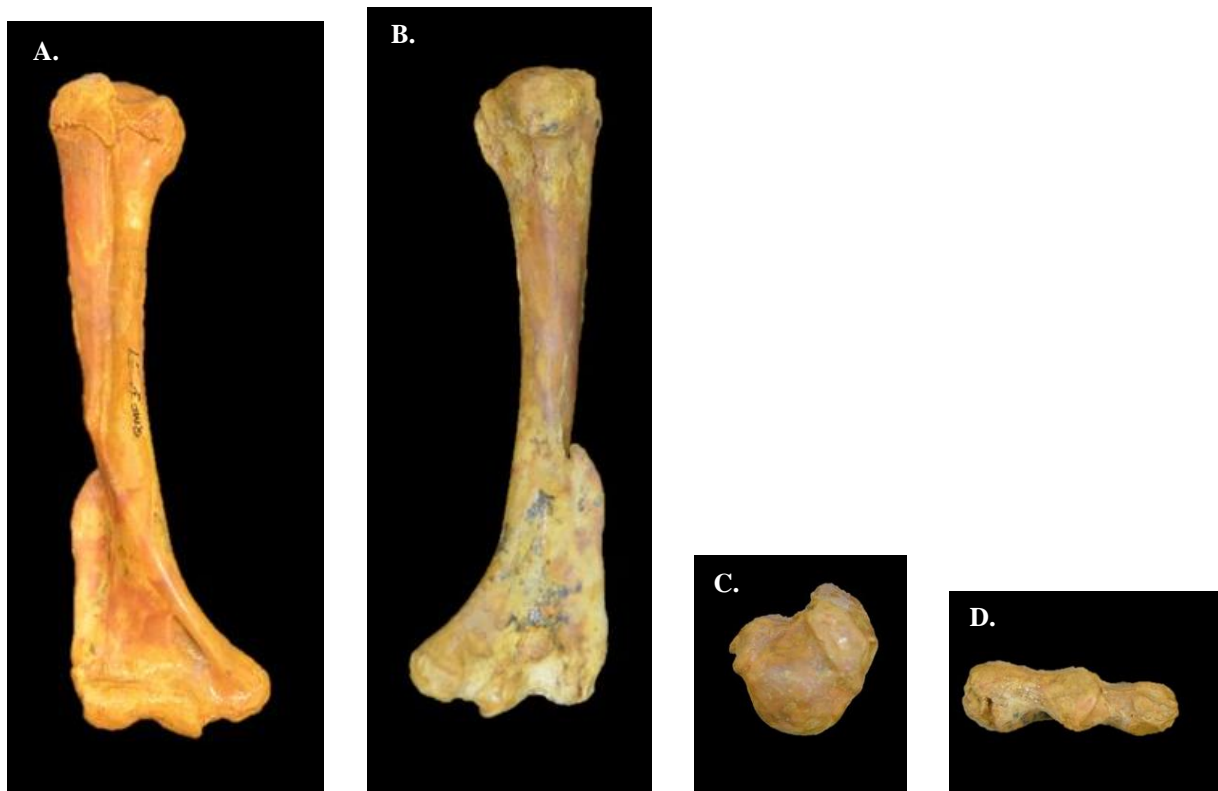


Figure 2. Right Humerus of *N. dicksoni* . 2.A. Anterior View. 2.B. Posterior View. 2.C. Head in Proximal View. 2.D. Distal Epiphysis in Distal View. Not to scale.

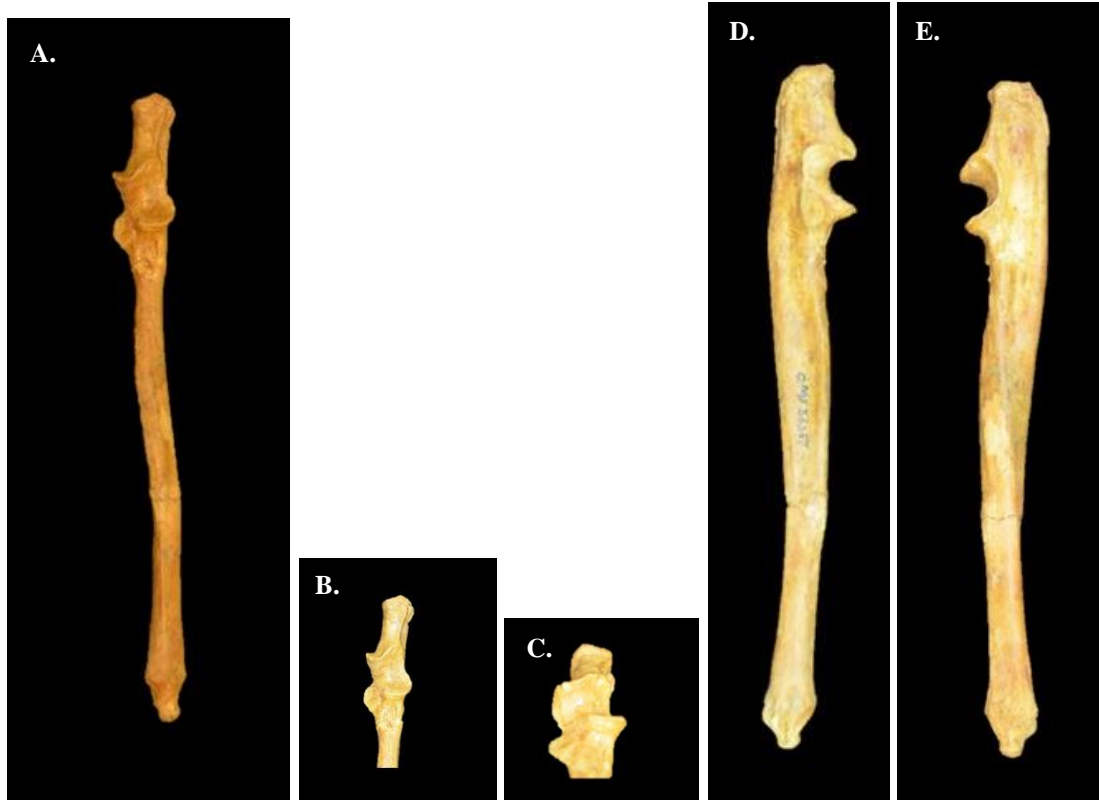
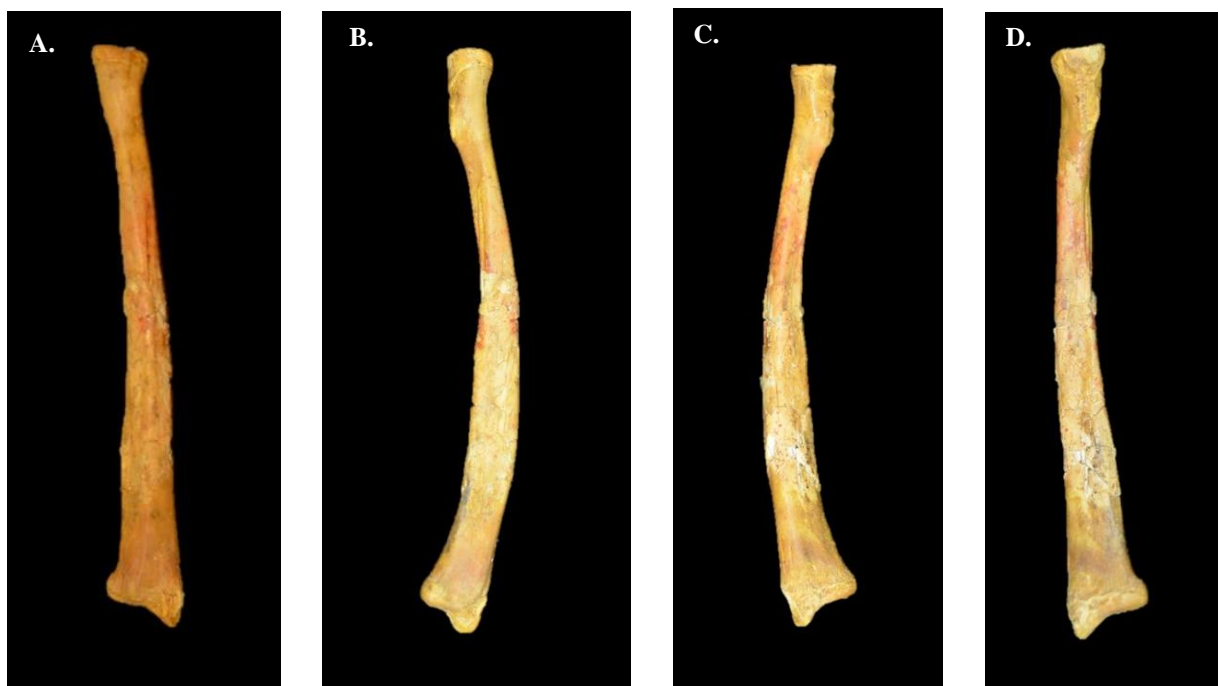


Figure 3. Right Ulna of *N. dicksoni*. 3.A. Anterior View . 3.B. Proximal Epiphysis in Anterior View. 3.C. Proximal Epiphysis in Anterodistal (Bottom) View. 3.D. Lateral View. 3.E. Medial View. Not to scale.



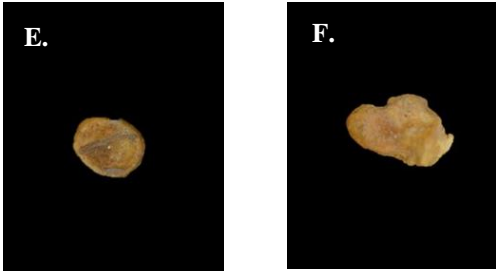


Figure 4. Right Radius of *N. dicksoni*. 4.A. Anterior View. 4.B. Lateral View. 4.C. Medial View. 4.D. Posterior View. 4.E. Head in Proximal View. 4.F. Distal Epiphysis in Distal View. Not to scale.

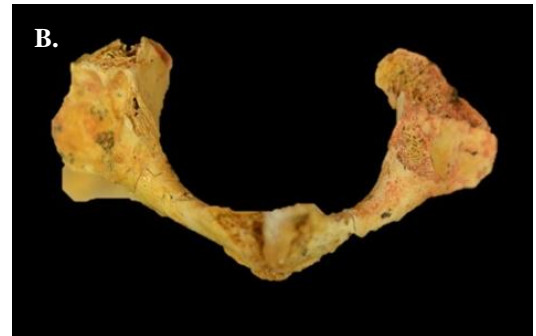


Figure 5. Pelvic girdle of *N. dicksoni*. 5.A. Caudal View. 5.B. Proximal View. 5.C. Lateral View. Not to scale.

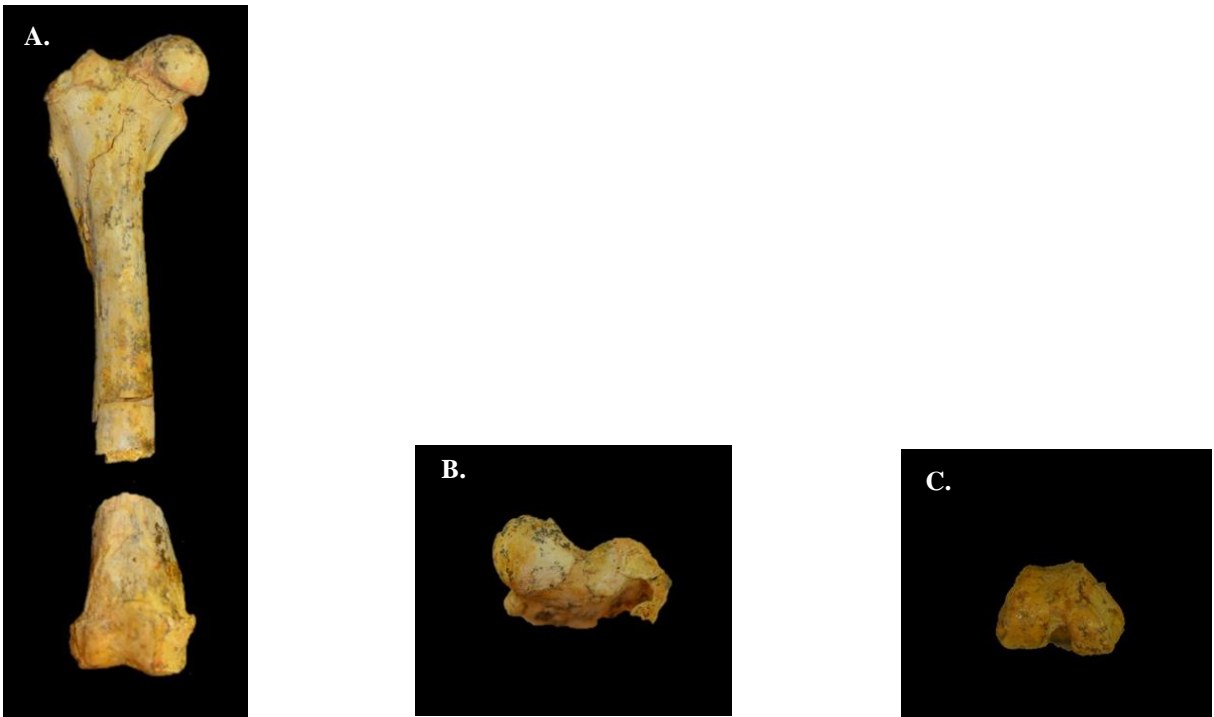


Figure 6. Right Femur of *N. dicksoni*. 6.A. Anterior View. 6.B. Head in Proximal View. 6.C. Distal Epiphysis in Distal View.



Figure 7. Tibia of *N. dicksoni*. 7.A Anterior View (Stereo Photo). 7.B. Head in Proximal View. 7.C. Lateral View. 7.D. Medial View. 7.E. Distal Epiphysis in Distal View. Not to scale.



Figure 8. Right Fibula of *N. dicksoni* in Anterior View. Not to scale.

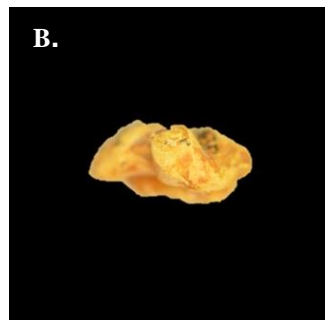
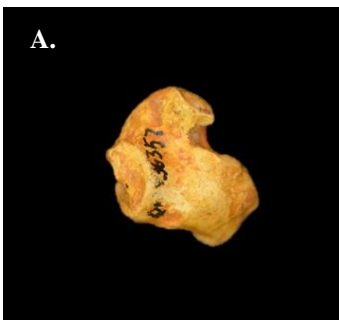


Figure 9. Right Astragalus of *N. dicksoni*. 9.A. Superior View. 9.B. Head in Anterior View. Not to scale.



Figure 10. Right Calcaneus of *N. dicksoni*. 10.A. Superior View. 10.B. Proximal Extremity in Proximal View. Not to scale.

4. DISCUSSION

4.1. Pectoral Girdle and Forelimbs

The scapula of *Nimbacinus dicksoni* resembles that of *Lycopsis longirostris* and suggests a tendency to cursoriality. This more rectangular shape of the scapula together with its shorter vertebral border, found in both species, indicates a more cursorial habit. This is because these anatomical features are related to forelimb forward and backward movement (ARGOT, 2001). This is based on the following aspects: (1) the supraspinous fossa is larger than the infraspinous one, which indicates a well-developed muscle *supraspinatus*; (2) the greater tubercle of the proximal epiphysis on the humerus, where the muscle *supraspinatus* inserts, is higher than the head; and (3) the muscle *supraspinatus* indicates that the shoulder joint is stabilized, especially during movements such as protraction and abduction of the forelimb (ARGOT, 2001).

On the other hand, the shoulder joint of *N. dicksoni* suggests an arboreal habit. This is because the acromion of the scapula has a large hamatus process and the humerus has a salient and large deltopectoral crest. These features indicate a well-developed muscle *deltoideus pars acromialis*. This muscle empowers adduction and rotation movements of the humerus and proportionates efficient manipulative capabilities (ARGOT, 2001). Moreover, it has a shallower glenoid cavity of the scapula than *L. longirostris*. This indicates that *N. dicksoni* had a free shoulder articulation and forelimb motion.

Adding to this arboreal evidence, the elements of the elbow joint and forearm reinforce the climbing capabilities of *N. dicksoni*. This is based on several aspects as follows. First, a well-developed lateral epicondylar crest on the humerus suggests a strong muscle *brachioradialis*, responsible for the flexion and supination of the forelimb (ARGOT, 2004a; CANDELA & PICASSO, 2008). Secondly, the distal epiphysis of the humerus is asymmetrical due to a large separation between the medial epicondyle and the trochlea. Thirdly, the asymmetry of the distal epiphysis of the humerus indicates a well-developed muscle *flexor digitorum profundus*, a flexor of the digits (JENKINS, 1973; ARGOT, 2001; ARGOT, 2004a). A fourth reason is that the olecranon is shorter than in *L. longirostris*, indicating a strong insertion of the caput longum of the triceps, responsible for ulna flexion (SZALAY & SARGIS, 2001). Another reason is that the radio diaphysis is bowed, increasing the mechanical forces of

the muscles responsible for pronation and supination movements (ARGOT, 2001). Finally, a wide distal facet of the radius indicates a larger range of flexion movements of the manus (ARGOT, 2001).

The forelimbs indicate that *N. dicksoni* was a scansorial marsupial. This is because the humerus rounded head and the ulna straight diaphysis seem to limit rapid forelimb movements, typical of specialized arboreal species (VALKENBURGH, 1987; SARGIS, 2002).

4.2. Pelvic Girdle and Hind limbs

The pelvic girdle of *N. dicksoni* resembles the pattern found among marsupials, where the iliac blades are expanded and deflected outwards. This similar pattern between thylacinids and borhyaenids indicates the constraints on the development of the pelvic girdle. This pattern may be related to the development of the marsupia in these mammals (SZALAY & SARGIS, 2001; ARGOT, 2004a). Moreover, the shape of iliac blades suggest well-developed epaxial musculature. This feature indicates stabilized lateral bend of the pelvic girdle, important for cursorial species (ARGOT, 2003b; SCHILLING & CARRIER, 2010).

The hip joint of *N. dicksoni* differs from the one of *L. longirostris*, because it has many features related to arboreality. The acetabulum is more laterally than ventrally oriented, a similar condition to the one found in more arboreal species (SZALAY & SARGIS, 2001), such as *Prothylacinus*. This position indicates a large range of hind limb abductive movements (ARGOT, 2001; ARGOT, 2003b). Moreover, the femur head is high and protrudes more proximally, indicating a high mobility of the hip joint.

Furthermore, the knee joint, the tibia and the radius suggest climbing and grasping capabilities of the hind limb. This is because the femur distal epiphysis is asymmetrical, as well as the tibial condyles, indicating a high capacity of abductive movements. Moreover, the origin of the muscle *tibialis anterior*, on the tibial diaphysis, is short. This means that there is a less capacity of adduction of the foot (ARGOT, 2002). On the fibula, the thick diaphysis indicates a strong muscle. *flexor digitorum fibularis*. It is responsible for foot grasping movement. Finally, the tibia distal epiphysis has a helicoidally shaped lateral epicondyle, also involved in grasping movements.

The ankle joint also reinforces the grasping capability of the *N. dicksoni* foot. This is because of the following aspects: (1) the large tibial facet that suggest an absence of articulation between the fibular distal epiphysis and the astragalus; (2) the astragalonavicular

facet is wider transversally and the calcaneocuboid facet is concave; suggesting efficient transversal mobility of the foot; and (3) the well-developed peroneal process, indicating a strong muscle peroneus longus, involved in grasping movement of the foot.

5. CONCLUSIONS

The thylacine *Nimbacinus dicksoni* was primally scansorial.

It also had manipulative and grasping capabilities.

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