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Morphological Studies of the Forelimb Skeleton of the Orange Rumped Agouti (*Dasyprocta leporina* Linnaeus, 1758)

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Authors' contributions

This work was carried out in collaboration between all authors and all authors contributed equally. All authors read and approved the final manuscript.

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ABSTRACT

The aim of the study is to document the morphological details of the forelimb bones of the orange rumped agouti (*Dasyprocta leporina*). The bones were collected from 12 adult animals of both sexes. Each limb comprised of 47 bones (30 bones, 17 sesamoid bones). The clavicle was poorly developed while the metacromion process of the scapula was very well developed. The humerus was peculiar, displaying poorly developed deltoid tuberosity, teres tubercle and the crest of the humerus and complete absence of the musculospiral groove. The distal extremity of the humerus was wide and presented a well-developed lateral epicondyle. The radius and ulna were separated and the ulna was larger and longer. The radial tuberosity was absent and semilunar notch of the ulna was deeper. The proximal row of carpals comprised of only two bones viz., radio-intermediate and ulnar carpal along two sesamoid bones viz., radial and accessory sesamoid bones on the

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palmar face. The manus presented five long, relatively thin metacarpal bones and five digits. The first digit was shorter with two phalanges whereas the other digits presented three phalanges. In conclusion, the features in the forelimb bones of the *D. leporina* reflected a wide functional spectrum, which include fast running, digging and shoveling. However, predominant features of the forelimb typified the *D. leporina* as cursorial rodents.

Keywords: Agouti; macro-anatomy; bones; forelimb.

1. INTRODUCTION

Rodents represent the most specialized order of mammals and show an astonishing adaptation of the appendicular skeleton according to limb use and behaviour [1,2]. Caviomorph rodents are a typical group of mammals found in Neotropical America and are fairly numerous in South America [3]. The orange rumped agoutis (*Dasyprocta leporina*) is a large, principally frugivorous rodent, inhabit mainly forested habitats in tropical and subtropical areas [4]. It is found in the northeastern part of South America, as well as Trinidad and Tobago. The *D. leporina* moves with remarkable speed and agility and showing the ability to trot, gallop jump vertically and resembles small ungulates in its locomotor behavior [5,6]. It often builds burrows in riverbanks or under the roots of trees [1] and caches excess food in shallow pits [4,7].

The *D. leporina*, is very popular as an exotic meat in Trinidad and Tobago [8,9] with an estimate of 90000 agoutis being harvested from the forest of Trinidad and Tobago during each hunting season, from October to February [10]. These large extractions together with the depletion of habitat may result in the survival of this species being threatened. In recent years, there are a growing number of wildlife farmers [9] in Trinidad and Tobago who are domesticating this animal through breeding to meet the dietary demand for meat. Domestication also brought about the idea of using them as good laboratory models based on four main reasons viz., size (3.2 – 5 kg), longevity (18 – 20 years), maintenance in captivity and resistance to zoonotic diseases [11].

The domestication of *D. leporina* in Trinidad and Tobago evoked an interest on musculoskeletal system due to their wide range of functional spectrum like fast running, leaping, digging and shoveling [5,6,7,1]. The *D. leporina* relies on the speed and acceleration to escape from predators like other terrestrial quadrupeds [5,12]. Since the forelimb carry 60% of static body weight and are designed to catch body weight as it is thrown forward by pelvic limbs. Forelimbs improve gait efficiency by minimizing wasteful up/down energy expenditure (they absorb kinetic energy of downward movement, store it as potential energy in stretched ligaments, and in turn convert that to upward kinetic energy). So the study of anatomy of the forelimb limb will be more useful in understanding locomotor behaviour of this animal.

Though few studies on the appendicular system of caviomorphs [12,13,14,15] were done, the musculoskeletal system of the *D. leporina* was not studied so far. Considering the greater anatomical diversity of the caviomorph rodents, it will be inappropriate to extrapolate the information from other caviomorph rodents to the *D. leporina*. In addition, study of locomotor behaviour in the *D. leporina* is considered as very important in the domestication process of this animal. So it is necessary to carry an independent work on fore limb skeleton of *D. leporina* from the structural and functional point of view. A detailed study on the morphology of the forelimb limb skeleton of the *D. leporina* was carried out in the present work. The main forelimb traits of the *D. leporina* are also analyzed from a structural and functional perspective. It is expected that this study will be useful in future ecomorphologic, evolutionary studies and the domestication process on these rodents.

2. MATERIALS AND METHODS

A total of 12 adult orange rumped agoutis of both sexes (more than 2 years old) were purchased from the wild life farmers in Trinidad. The animals were euthanized by the use of a mixture of ketamine (35 mg/kg body weight) and xylazine (5 mg/ kg body weight). The Institutional Ethical Committee, Faculty of Medical Sciences, The University of the West Indies, Trinidad and Tobago, approved the research project. The forelimb is dissected out from the trunk. The muscles of the forelimb were carefully dissected and teased from the bones to leave the bones with minimal soft tissue attachments, then submerged into different plastic cups containing 3% sodium hydroxide. The plastic cups were then covered and placed under the sun and checked every 30 minutes to carefully remove the bones freed of flesh [16]. The bones were then rinsed in running water and then air-dried. The total number of bones recovered were counted and recorded. Photographs of the long bones were taken individually while that of the manus was taken together. The bones were measured for length and gross anatomical observations were made.

3. RESULTS

The general pattern of the forelimb bones in the *D. leporina* was found to be similar to other rodents, but the bones presented differences in their morphology and number. There was no sexual dimorphism in length or morphology of the bones observed in the present study. There were 47 bones (30 bones, 17 sesamoid bones) found in the each forelimb (Table 1).

Table 1. Number of bones that make up the pectoral limb of *D. Leporina*

Name of the bones	Number per forelimb
Scapula	1
Clavicle	1
Humerus	1
Radius	1
Ulna	1
Carpals	6
Metacarpals	5
First Phalanx	5
Second phalanx	4
Third phalanx	5
Sesamoid bones	
Carpal sesamoid -2	
Proximal sesamoids -10	17
Distal sesamoids -5	
Total	47

3.1 Pectoral Girdle

The pectoral girdle consisted of a scapula and a clavicle (Fig. 1).

3.1.1 Clavicle

The clavicles were very short, curved, rod-like bones with an average length of 1.5 cm. The acromion end was slightly broader than the sternal end (Fig. 1).

3.1.2 Scapula

The scapula had a triangular outline with an average length of 5.6 cm. The vertebral border of the scapula curved downwards towards the supraspinous fossa of the cranial border. The scapular spine arose gradually on the lateral surface and extended from the dorsal 1/3rd to roughly the distal 2/3rd where it continued distally as, acromion process. The acromion process then laterally flattened to form a distinct metacromion or hamate process at the distal end. The metacromion process had an average length of 1 cm and projected caudally. The supraspinous fossa was larger than the infraspinous fossa and bore a slight depression mid sagittally, which appeared as a distinct crest on the costal surface. The cranial border was strongly convex in profile whereas the caudal border was nearly straight except at its proximal end. The neck was distinct. The distal extremity presented the glenoid cavity and the tuber scapulaeD and was separated by a distinct glenoid notch. The tuber scapulae presented a less pronounced coracoid process medially and supraglenoid tubercle laterally. The medial surface was concave cranially and convex caudally (Fig. 1).

3.2 Humerus

The humerus was long, curved bone with expanded proximal and distal ends. The average length was 7.2 cm. The greater and lesser tubercles on the proximal end were positioned in front and to the side of the ovoid articular head and were separated by an intertuberal groove. The shaft presented an underdeveloped deltoid tuberosity on the lateral side and on the medial side, teres tubercle and the crest of the humerus was indistinct. The musculospiral groove was absent. The muscular ridges for the muscle attachment were less prominent. The distal extremity was wide and presented two condyles, two epicondyles, a supracondylar fossa, a trochlea, an olecranon fossa and a supratrochlear foramen. The lateral epicondyles were better developed than the medial epicondyles (Fig. 2).

3.3 Antebrachium

The antebrachium consisted of two separated bones, radius and ulna. They articulated only at their extremities leaving an interosseous space between their shafts (Fig. 3).

Fig. 1. The lateral (A) and medial (B) views of the clavicle and lateral (C) and medial (D) views of the scapula of the *D. leporina*. 1. Sternal end of clavicle 2. Acromion end of clavicle 3. Supraspinous fossa 4. Scapular spine 5.Infraspinous fossa 6.Acromion process 7. Metacromion Process 8.Glenoid cavity 9.Subscapular fossa 10. Coracoid process 11.Tuber scapulae

Fig. 2. The lateral (A) and medial (B) views of the humerus of the *D. leporina.* 1. Greater tubercle 2. Deltoid tuberosity 3. Supra trochlear foramen 4. Lateral epicondyle 5. Condyle 6. Supracondylar fossa 7. Head 8. Lesser tubercle 9. Trochlea

3.3.1 Radius

The radius was a simple, curved rod like bone with an average length of 6 cm and it was slightly more slender than the ulna. The proximal extremity presented an ovoid articular surface with a groove in the middle to articulate with the humerus. The groove ended in a notch on both the cranial and the caudal margin of the articular surface. The radial tuberosity was indistinct. The shaft was craniocaudally compressed and slightly bowed in its length. The distal part of the shaft was grooved cranially for the passage of the tendons and roughed caudally for muscular attachment. The distal extremity was expanded and the articular surface for the carpal bones was concave and somewhat ovoid presenting a less prominent styloid process on the lateral side (Figs. 3A and B).

3.3.2 Ulna

The ulna was longer and stronger than the radius. The proximal extremity presented an olecranon process, an anconeal process, medial and lateral coronoid processes and a semilunar notch. The shaft presented grooves on both medial and lateral surface indicating a deeper lateral groove. The distal extremity ended distally in a conical, blunt well-developed styloid process (Figs. 3C and D).

3.4 Carpus

The carpal bones were short and rigid, arranged in two rows with an average length of 0.69 cm. The proximal row comprised of a fused radio-intermediate carpal and ulnar carpal bones in a mediolateral sequence. The distal row presented four bones namely, first carpal, second carpal, third carpal and fourth carpal, ascending in size with the first carpal being the smallest bone while the fourth carpal IV was the largest in the distal row. Two sesamoid bones, a radial sesamoid on the medial side and an ulnar (accessory) sesamoid on the lateral side were present (Fig. 4).

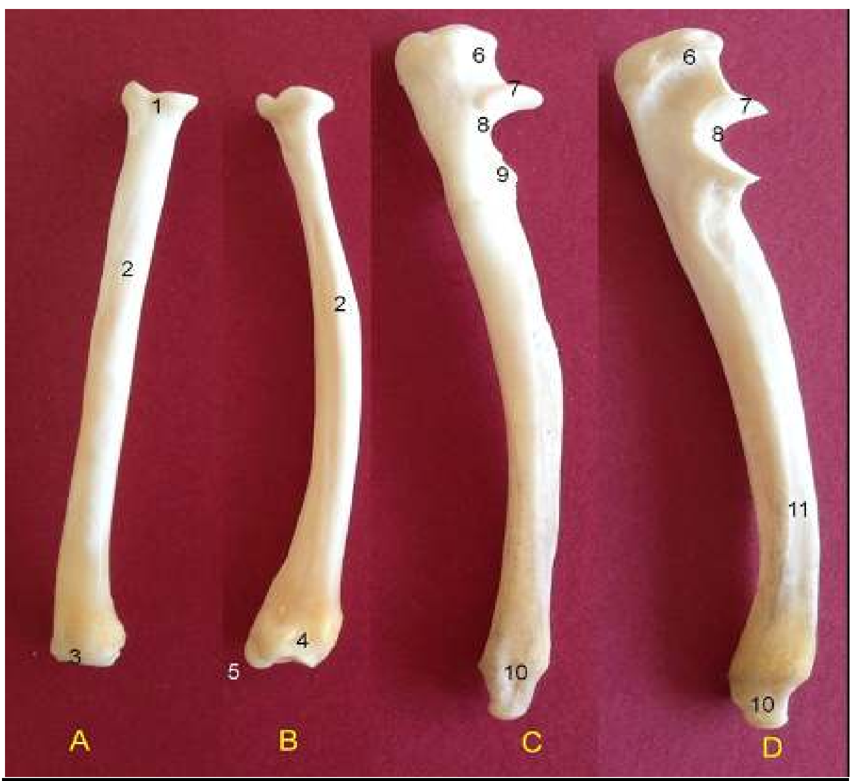

Fig. 3. The cranial (A) and caudal (B) views of the radius and medial (C) and lateral (D) views of the ulna of the *D. leporina*. 1. Articular notch 2.Shaft 3, 4. Articular facet for the carpals 5. Styloid process of the radius 6. Olecranon process 7. Anconeus process 8. Semilunar notch 9. Medial coronoid process 10. Lateral groove 11.Styloid process of the ulna

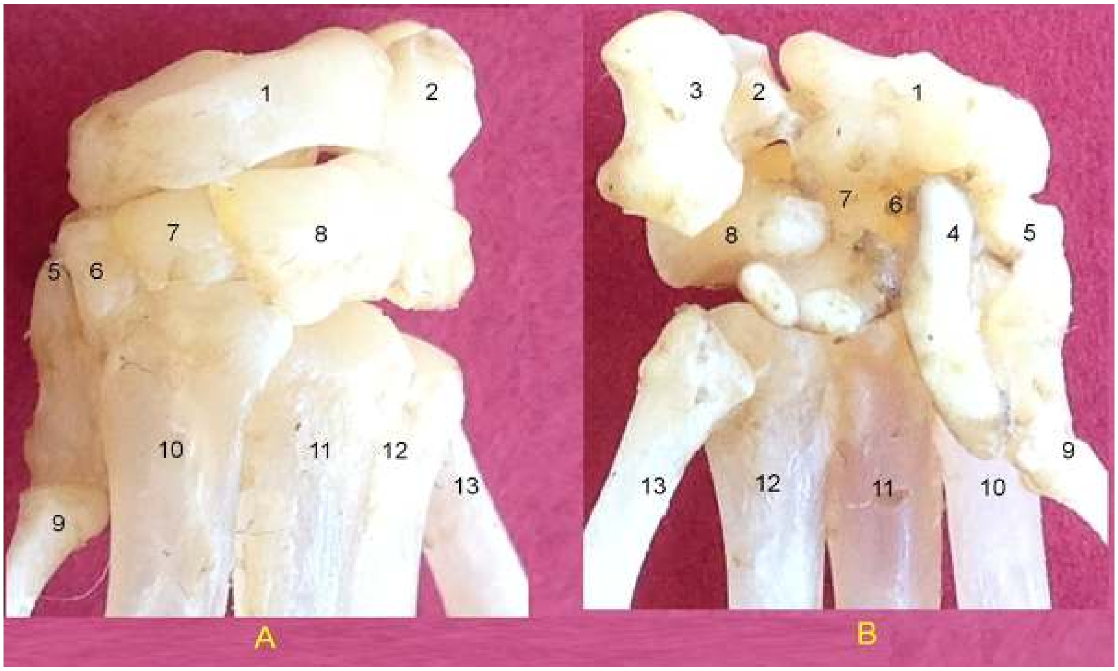

Fig. 4. The dorsal (A) and palmar (B) views of the carpus of the *D. leporina.* 1. Intermedio-radial carpal. 2. Ulnar carpal 3. Ulnar sesamoid 4. Radial sesamoid 5. First carpal 6. Second carpal 7. Third carpal 8. Fourth carpal 9. First metacarpal 10. Second metacarpal 11. Third metacarpal 12. Fourth metacarpal 13. Fifth metacarpal

3.5 Manus

The manus was complete with five metacarpal bones and five digits (Fig. 5).

3.5.1 Metacarpals

The metacarpal bones were relatively long and thin. The metacarpal lengths, in ascending order, were first metacarpal, fifth metacarpal, second metacarpal, fourth metacarpal and third metacarpal. The first metacarpal was shortest with an average length of 0.6 cm while the third metacarpal was longest with an average length of 2.3 cm. (Figs. 5A and B).

3.5.2 Digits

The first digit had two phalanges whereas all other digits had 3 phalanges. The digit lengths, in ascending order, were first digit, fifth digit, second digit, fourth digit and third digit. The average length of the first and the third digit was 0.3 cm and 1.9 cm respectively. The third phalanx was slightly arched and pointed. There were two proximal sesamoid bones present in each metacarpo-phalangeal joint on the flexor surface and one distal sesamoid bone presented at the distal end of the second phalanx. Since the first digit had only 2 phalanges, the distal sesamoid was placed at the base of the terminal phalanx (Figs. 5A and B).

4. DISCUSSION

The clavicles act as both a strut and a spoke to stabilize the lower end of the scapula during locomotion. The 'strut effect' prevents the scapular motion towards the median plane whereas the 'spoke effect' maintains a fixed distance between the acromion and sternum to assure an arcuate movement [17]. The clavicles of the *D. leporina* are very thin, curved, rod like bones as reported in the guinea pig [18], the rabbit [19] and the mole rat [20]. However, the clavicles in the present study are much smaller with an average length of 1.5 cm in comparison with the clavicle length of 2.5 cm reported in the African giant rats [21] an animal that has a similar size as the *D. leporina*. The shorter clavicle in *D. leporina* may suggest that it provides more spoke effect than strut effect resulting *D. leporina* being able to perform forelimb excursions closer to the median plane. A shorter clavicle therefore may be interpreted as a cursorial adaptation.

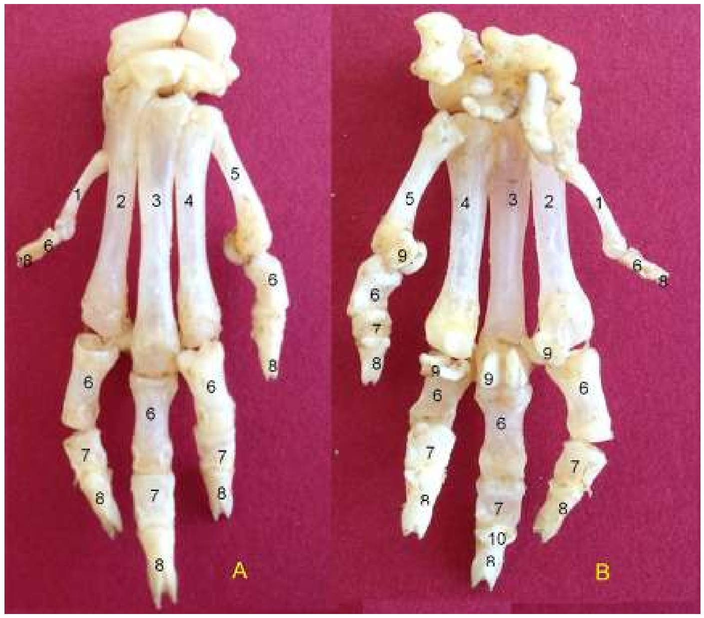

Fig. 5. The dorsal (A) and palmar (B) views of the manus of the *D. leporina*. 1. First metacarpal 2. Second metacarpal 3. Third metacarpal 4. Fourth metacarpal 5. Fifth metacarpal V 6. First phalanx 7. Second phalanx 8. Third phalanx 9. Proximal sesamoid bones 10. Distal sesamoid bones

The presence of acromion and metacromion processes in the scapula of the *D. leporina* is similar to the reports in other rodents such as Wister rats [22], guinea pigs and rabbits [23] as well as carnivores [24]. The metacromion process acts as the insertion for the levator scapulae ventralis and the acromiotrapezius muscles unlike the acromion process in other mammals, which an act as the insertion point for these muscles since the metacromion process is absent [25]. The well developed metacromion process in the *D. leporina* provides an extended insertion for the muscles, which can be correlated to an adaptation to maintain a highly flexed shoulder joint throughout the locomotor cycle and to resist ground reaction forces during fast running [25]. A dorsal projection on the metacromion process called suprahamate process, another adaptation for fast running in cats [24] and lions [26] but not observed in this study.

The humerus is short, and robust with well-developed tuberosities and wider distal extremity in digging rodents [20,21,27] whereas the humerus is long with less muscular attachment sites in the cursorial South American caviomorph rodents [28]. The relatively long humerus with less pronounced muscular attachment sites like deltoid tuberosity, teres tubercle, and the crest of the humerus and absence of musculospiral groove in the *D. leporina* are suggested as adaptations for fast running. The ovoid shape of the humeral head of the *D. leporina* indicates an increase in the possible range of movement in the anterio-posterior plane and a decrease in the lateral movement, which is similar to the reports in subterranean rodents [29]. However, the presence of a wider distal extremity and well-developed lateral epicondyles, an indication of well developed extensor muscles may be attributed to the digging capacity of the *D. leporina*.

The separated radius and ulna in the present study is in contrast to the reports on African giant pouched rats [30]. The separated radius and ulna make the antebrachium more flexible and the presence of a well-developed lateral epicondyle of the humerus indicates that the supination is more pronounced than the pronation in the *D. leporina*. The ovoid articular surface at the proximal extremity of the radius and the deep semi-lunar notch of the ulna may suggest a pronounced articulation with the humerus, which may strengthen and maintain the integrity of the elbow joint despite the increased pressure on their forelimb while burrowing as reported in subterranean animals [29]. The deep groove on the lateral surface of the shaft of the ulna in the present study is an indication of the well-developed extensor muscles, which are important for the digging function in the *D. leporina.*

The arrangement of the carpal bones in *D. leporina* followed the basic structural plan of rodents [31]. The short and rigid carpal bones, fused radio-intermediate carpal and the presence of two sesamoid bones in the proximal row in the present study are similar to the reports in rodents [27]. The short and rigid carpal bones with well-developed sesamoid bones in the carpal region, indicates that the *D. leporina* are scratch-digging animals. The presence of radial and ulnar sesamoid bones in the present study is similar to the findings in the mole rats [27], the African giant rat [21] and subterranean rodents [29]. The well-developed sesamoid bones in the *D. leporina* increase the breadth of the hand, which in turn increases the efficiency of shoveling the earth. The presence of four bones in the distal row of *D .leporina* is similar as in porcupines [32] and in other rodents [27]; but contrary to the reports in some burrowing rodents [14], where a fifth carpal bone, namely the central carpal, is found in the distal row.

The manus is relatively elongated and thin in the *D. leporina,* which is in contrast to reports in burrowing rodents [14], where the metacarpals are short and robust. In the present study, the elongation of the metacarpal bones may be considered as a cursorial adaptation.

The observation of five digits in the *D. leporina* is consistent with reports in other rodent species [27]. The arched and pointed shapes of the distal phalanges are adaptations for burrowing and shoveling [29]. In the present study, the pointed shapes of the distal phalanges are present but the curvature of the distal phalanges is not prominent. This feature may reduce the digging efficiency of the *D. leporina*.

5. CONCLUSION

The features in the forelimb bones of the *D. leporina* reflect a wide functional spectrum, which includes fast running, digging and shoveling. However, predominant features of the forelimb typified the *D. leporina* primarily as cursorial rodents.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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