

# Hind foot drumming: Morphofunctional analysis of the hind limb osteology in three species of African mole-rats (Bathyergidae)

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Running Title: Hind limb osteology in mole-rats

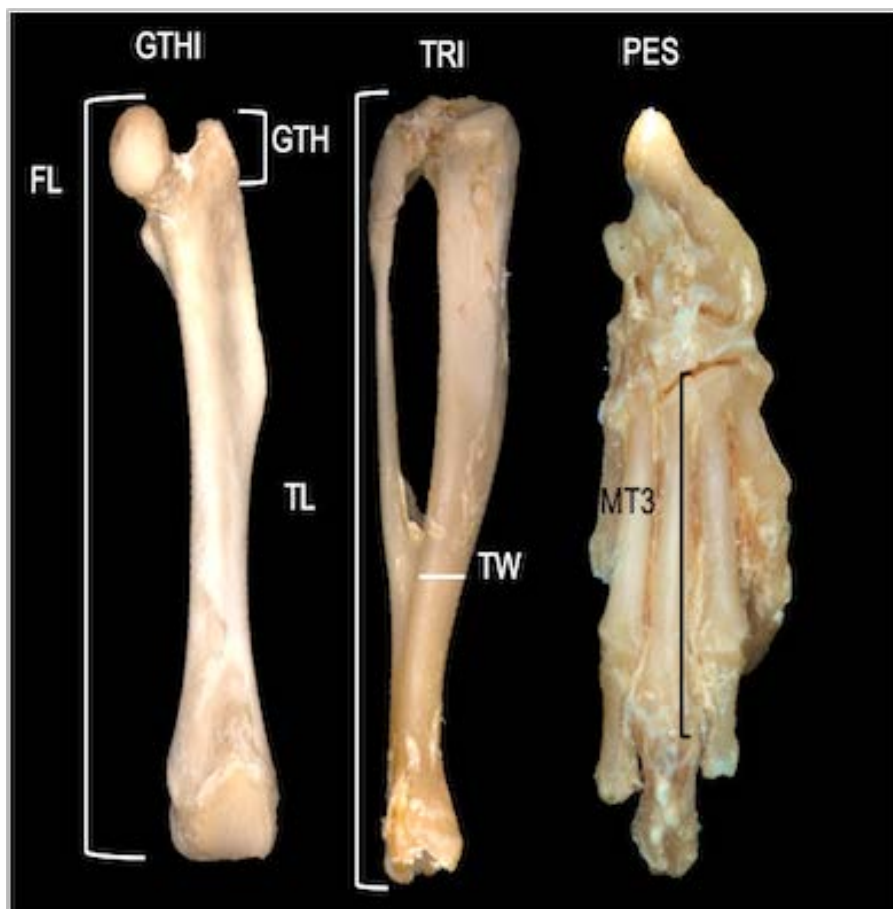
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## Graphical abstract



## ABSTRACT

Hind foot drumming is a form of seismic signaling that plays a vital role in the communication of several Bathyergidae species. Hind foot drumming is initiated by the rapid movement of the whole hind limb by flexion and extension of the hip and knee. This study aimed to determine if morphological adaptations of the hind limb osteology were measurable using established morphometric analyses in two drumming (*Bathyergus suillus* and *Georchus capensis*) and one non-drumming (*Cryptomys hottentotus natalensis*) African mole-rat species. Forty-three linear measurements of the hind limb were taken in 48 limbs (n=16 limbs per species) and 32 indices were calculated. Mixed model analysis of variance was used to compare the three species and sexes within a species. Fourteen indices had significant differences between species. Eleven indices had significant differences between sexes within a species. Significant differences between the drumming (*B. suillus* and *G. capensis*) and the non-drumming species were observed in three indices. The femoral greater trochanter was relatively shorter in the drumming species compared to the non-drumming species which is proposed to allow for increased hip joint mobility thereby permitting drummers to move their limbs at the rapid speed required to generate seismic signals. Furthermore, the small in-lever (shorter greater trochanter) may increase the velocity of limb motion. The robust tibias in the drumming species, as indicated by the tibial robustness index, are likely to counter the additional biomechanical load caused by the muscles involved in hind foot drumming. The relatively small hind feet seen in the drumming species allows for reduced limb weight needed for the rapid extension and flexion motion required during hind foot drumming. The significant differences reflected in the hind limb osteological indices between *B. suillus* and *G. capensis*, and the non-drumming species are indicative of adaptations for hind foot drumming.

### Keywords:

Seismic signaling; morphological adaptations; African mole-rats

### Research highlights

Adaptations to the hind limb for hind foot drumming as indicated by the osteological indices include a small femoral greater trochanter for increased hip mobility, robust tibias for muscle attachment and small hind feet to reduce limb weight.

## 1. INTRODUCTION

Hind foot drumming is a form of seismic signaling, which plays a crucial role in the communication of several bathyergid species (Bennett & Faulkes, 2000). Foot drums in these species are produced as a result of flexion and extension of the hip and knee joints causing the whole hind limb to rapidly move up and down (Bennett & Jarvis 1988; Narins, Reichman, Jarvis & Lewis, 1992). The rate and frequency of the seismic signals generated by hind foot drumming varies depending on the species as well as the sex of the individual (Randall, 2010). Seismic signals are used during courtship behavior and to convey territorial signals to both conspecific and heterospecific species (Bennett & Jarvis, 1988; Hill, 2009; Randall, 2001; 2010).

The family Bathyergidae (African mole-rats) is a group of subterranean rodents that are specifically adapted for their ecological niche. This study focuses on two solitary drumming species and one social non-drumming species found in South Africa. Firstly, the solitary Cape dune mole-rat, *Bathyergus suillus*, is the largest species in the family with males weighing up to two kilograms. While the drumming rate in this species has yet to be described, they use foot drumming in territorial displays (Hart, O’Riain, Jarvis & Bennett, 2006). During courtship *B. suillus* males and females drum messages to each other with increasing frequency and speed to the point where males drum very fast (Jarvis & Bennett, 1991). Secondly, the Cape mole-rat, *Georychus capensis*, also uses foot drumming as part of territorial and courtship behavior (Bennett & Jarvis, 1988; Sherman, Jarvis & Alexander, 1991; Bennett, Maree & Faulkes, 2006) with males drumming at a speed of 26 beats (drums) per second, and females around 15 beats per second (Bennett & Jarvis 1988; Narins *et al.*, 1992; van Sandwyk & Bennett, 2005). While *Cryptomys hottentotus natalensis* is regarded as a non-drumming, social species, intermittent foot thumping has been reported in other subspecies of *Cryptomys hottentotus* (Lacey, Patton & Cameron 2000).

Osteological morphometric analysis of the limbs has been used to evaluate the locomotor habits of a variety of mammalian species in the past. Various indices have been created using linear measurements (Sargis, 2002; Elissamburu & Vizcaino, 2004; Samuels & Van Valkenburgh, 2008; Salton & Sargis, 2009; Echeverria, Becerra & Vassallo, 2014) however, to our knowledge these indices have not been used to determine specializations for specific behaviors such as hind foot drumming.

Osteological indices can reflect four main characteristics of bones namely, robustness, proportions and shapes, as well as functional attributes of the morphology, such as mechanical advantage (Elissamburu & Vizcaino, 2004; Chen & Wilson, 2015).

Previous studies using morphometric analyses of the postcranial skeleton to infer locomotor modes have included small numbers of *B. suillus*, *G. capensis* and unspecified *C. hottentotus* subspecies. However, these studies grouped several species together and no individual species comparisons were performed (Samuels & Van Valkenburgh, 2008; Chen & Wilson, 2015; Wilson & Geiger, 2015). More recently Montoya-Sanchueza, Wilson & Chinsamy (2019) used similar methods to analyze the long bones of *B. suillus* at different ages to determine how these morpho-functional indices change with the age of the animal. The purpose of the present study was to determine if adaptations for a specialized behavior such as hind foot drumming can be detected by using previously established osteological indices of the pelvis, femur, tibia and third metatarsal, in three species of African mole-rats.

## **2. MATERIALS AND METHODS**

### **2.1 Sample**

Hind limbs fixed in 10% buffered formalin of 24 animals (N=48 limbs), consisting of three species (n=16 each), were obtained from previous ethically cleared unrelated studies (Table 1). The species included *Bathyergus suillus* (Schreber, 1782), *Georchus capensis* (Pallas, 1778) and *Cryptomys hottentotus natalensis* (Roberts, 1913). Ethical approval for the use of the specimens was obtained from the Stellenbosch University Research Ethics Committee: Animal Care and Use (REC: ACU; SU-ACUM 16-00005). The muscles of limbs were dissected after which the origin and insertion sites of the muscles were determined (Sahd, Bennett & Kotzé, 2019). Any remaining soft tissue was macerated as described in Sahd *et al.* (2019) in order to clean the bones.

**Table 1.** Species information including ethical approval, capture information and mean body mass. ( $\pm$  Standard deviation)

Species	Ethical approval	n	Capture site	Mean body mass (g)
<i>Bathyergus suillus</i>	University of Cape Town: 200/V7/JOR	8	ACSA Cape Town, Western Cape	922.25 $\pm$ 233.47
<i>Georchus capensis</i>	University of Johannesburg: 215086650- 10/09/15	8	Darling, Western Cape	213.89 $\pm$ 60.82
<i>Cryptomys hottentotus natalensis</i>	University of Pretoria: ECO0070-14	8	Glengarry, Kwa-Zulu Natal	118.96 $\pm$ 30.63

## 2.2 Morpho-functional analysis of bones

Forty-three linear measurements (Table 2) of the pelvis, femur, tibia and third metatarsal in all 48 limbs ( $n=16$  per species) were taken using a digital sliding caliper to the nearest 0.01 mm. These measurements were used in the 32 indices described in Table 3 to compare the three species. The measurements and indices were based on previous studies by Sargis (2002); Samuels & Van Valkenburgh, (2008); Salton & Sargis (2009) and Wilson & Geiger (2015).

## 2.3 Statistical Analysis

Descriptive statistics including the mean and standard deviation were calculated using the raw osteological indices per species and per sex. The osteological indices were  $\log_{10}$  transformed before undergoing statistical analysis. Mixed model analysis of variance (ANOVA) tests were used to determine significant differences between species as well sex differences within species. Fischer's Least Significant Difference (LSD) post-hoc test was used to determine the p-values. Statistically significant results were determined with a  $p < 0.05$ . All statistical analysis was performed using Statistica 13.5 (TIBCO software, Palo Alto, California, USA).

**Table 2.** Osteological measurements used in analysis based on the measurements used in Sargis (2002); Samuels & Van Valkenburgh, (2008); Salton & Sargis (2009) and Wilson & Geiger (2015).

<b>Measurement</b>	<b>Description</b>
<b>Innominate length</b>	Iliac crest to the caudal edge of the ischium
<b>Ilium length</b>	Iliac crest to cranial border of the acetabulum
<b>Ilium width</b>	Medial to lateral edge of the iliac crest
<b>Pubis length</b>	Ventral border of the acetabulum to the medial edge of the pubis
<b>Ischium length</b>	Caudal border of the acetabulum to the caudal edge of the ischium
<b>Ischium width</b>	Ischial tuberosity to the attachment site of <i>m. semimembranosus</i>
<b>Acetabulum length</b>	Cranial to caudal border of the acetabulum
<b>Acetabulum width</b>	Dorsal to ventral border of the acetabulum
<b>Obturator foramen length</b>	Cranial to caudal border of the obturator foramen
<b>Obturator foramen width</b>	Dorsal to ventral border of the obturator foramen
<b>Femur length</b>	Head of the femur to distal end of the femur
<b>Femoral head length</b>	Proximal to distal border of the femoral head
<b>Femoral head width</b>	Medial to lateral border of the femoral head
<b>Femoral neck mediolateral width</b>	Medial to lateral border of the femoral neck
<b>Femoral neck craniocaudal width</b>	Caudal to cranial border of the femoral neck
<b>Proximal femur width</b>	Most proximal point of the femoral head to the most lateral point of the greater trochanter
<b>Greater trochanter height</b>	From the most proximal point of the greater trochanter to the point where the greater trochanter meets the femoral neck
<b>Midshaft mediolateral width of femur</b>	Medial to lateral border of the femur
<b>Midshaft craniocaudal width of femur</b>	Cranial to caudal aspects of the femur
<b>Medial extension of lesser trochanter</b>	Medial border of the lesser trochanter to the medial border of the femur
<b>Distance of lesser trochanter from proximal femur</b>	Midpoint of the lesser trochanter to the head of femur
<b>Distance of lesser trochanter from distal femur</b>	Midpoint of the lesser trochanter to the distal end of the femur
<b>Lateral extension of third trochanter</b>	Lateral border of the third trochanter to the lateral border of the femur
<b>Distance of third trochanter from proximal femur</b>	Midpoint of the third trochanter to the head of the femur
<b>Distance of third trochanter from distal femur</b>	Midpoint of the third trochanter to the distal end of the femur

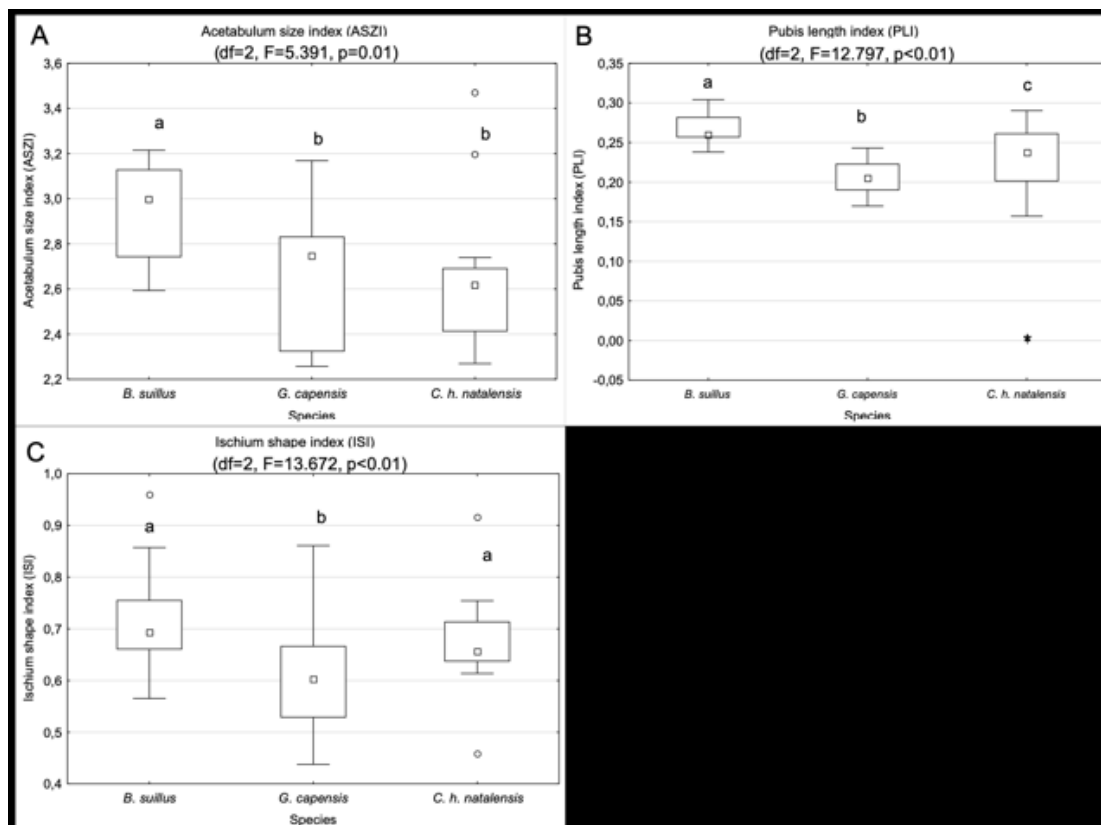
<b>Proximodistal length of patellar groove</b>	Proximal to distal border of the patellar groove
<b>Mediolateral width of patellar groove</b>	Medial to lateral border of the patellar groove
<b>Proximodistal length of medial femoral condyle</b>	Proximal to distal border of the medial condyle on the caudal aspect of the femur
<b>Mediolateral width of medial femoral condyle</b>	Medial to lateral border of the medial condyle on the caudal aspect of the femur
<b>Craniocaudal depth of medial femoral condyle</b>	Caudal border of the medial condyle to the cranial border of the medial patellar ridge
<b>Proximodistal length of lateral femoral condyle</b>	Proximal to distal border of the lateral condyle on the caudal aspect of the femur
<b>Mediolateral width of lateral femoral condyle</b>	Medial to lateral border of the lateral condyle on the caudal aspect of the femur
<b>Craniocaudal depth of lateral femoral condyle</b>	Caudal border of the lateral condyle to the cranial border of the lateral patellar ridge
<b>Femoral epiphysis mediolateral width</b>	Medial to lateral border of the condyles of the femur
<b>Tibia length</b>	Proximal border of the tibia to the medial malleolus
<b>Midshaft mediolateral width of tibia</b>	Medial to lateral border of the tibia just distal to the fusion of the tibia and fibula
<b>Length of tibial tuberosity</b>	Proximal border of the lateral tibial condyle to the distal extent of the tibial tuberosity
<b>Length of proximal tibia</b>	Proximal border of the lateral tibial condyle to the point of fusion between the tibia and fibula
<b>Medial tibial condyle width</b>	Medial to lateral border of the medial tibial condyle
<b>Lateral tibial condyle width</b>	Medial to lateral border of the lateral tibial condyle
<b>Length of proximal tibial end</b>	Border of the tibial tuberosity to the most distal point of the tibial plateau
<b>Width of proximal tibial end</b>	Medial border of the medial tibial condyle to the lateral border of the lateral tibial condyle
<b>Length of third metatarsal</b>	Proximal to distal end of the third metatarsal

### 3. RESULTS

Fourteen of the 33 morpho-functional indices had significant differences ( $p < 0.05$ ) between species (Table 4). Eleven indices had significant differences with regards to sex differences within species.

#### 3.1 Pelvic osteological indices

The relative acetabulum size index (ASZI) of *B. suillus* was significantly larger compared to the two other species ( $df=2$ ,  $F=5.392$ ,  $p=0.011$ ; Figure 1A). The LSD test showed that the difference in the ASZI between *B. suillus* and *G. capensis* had a  $p$ -value of  $p=0.019$  and  $p < 0.01$  when compared to *C. h. natalensis* respectively. A sex difference was found in the acetabulum shape index (ASHI) in *G. capensis* ( $p=0.022$ ) where females had more elliptically shaped acetabula than the males and the inverse was observed in *C. h. natalensis* ( $p=0.043$ ; Table 4).



**Figure 1.** Box and whisker plots (with median, interquartile range, non-outlier range, and outliers) showing the three significant pelvic osteological indices. A. *B. suillus* (a) had a significantly larger acetabulum size index (ASZI) compared to both *G. capensis* and *C. h. natalensis* (b). B. All three species had significantly different pubis length index (PLI) values. C. *G. capensis* (a) had a significantly smaller ischium shape index (ISI) compared to both *B. suillus* and *C. h. natalensis* (b). Differing superscript letters (a, b, c) indicate significant differences between species with  $p < 0.05$ .



**Table 3.** Osteological indices used for morphometric analysis of the hind limb, their calculation and functional significance (adapted from Sargis, 2002, Samuels & Van Valkenburgh, 2008; Salton & Sargis, 2009; Echeverria et al., 2014; Wilson & Geiger, 2015)

<b>INDEX</b>	<b>CALCULATION</b>	<b>FUNCTIONAL SIGNIFICANCE</b>
<b>Ilium length index (ILI)</b>	Ilium length / innominate length	Provides an estimate to the proportions of the ilium to the pelvis
<b>Ilium shape index (ILSI)</b>	Ilium width / length	Provides an estimate to the robustness of the ilium
<b>Acetabulum shape index (ASHI)</b>	Acetabulum width / length	Provides an estimate of the shape of the acetabulum
<b>Acetabulum size index (ASZI)</b>	(Ilium length + width) / (Acetabulum length + width)	Provides an estimate to depth and proportion of the acetabulum to the pelvis
<b>Pubis length index (PLI)</b>	Pubis length/ innominate length	Provides an estimate to the proportions of the pubis to the pelvis
<b>Ischium length index (ISLI)</b>	Ischium length / innominate length	Provides an estimate to the proportions of the ischium to the pelvis
<b>Ischium shape index (ISI)</b>	Ischium width / length	Provides an estimate to the robustness of the ischium
<b>Obturator foramen shape index (OFSI)</b>	Obturator foramen length / width	Provides an estimate of the shape of the obturator foramen
<b>Femoral head shape index (FHSI)</b>	Femoral head width / length	Provides an estimate to the roundness of the femoral head
<b>Femoral neck width index (FNWI)</b>	Femoral neck mediolateral width / femoral neck craniocaudal width	Provides a measure of the femoral neck shape
<b>Greater trochanter index (GTI)</b>	Proximal femur width / femur length	Provides an estimate of the distance from the hip joint to the lateral edge of the greater trochanter relative to femoral length

<b>Greater trochanter height index (GTHI)</b>	Greater trochanter height / Mediolateral midshaft width of the femur	
<b>Lesser trochanter length index (LTLI)</b>	Medial extension of lesser trochanter / femur length	Provides an estimate to the size of the lesser trochanter
<b>Lesser trochanter position index (LTPI)</b>	Lesser trochanter distance from proximal femur / distance from distal femur	Provides an indication of the position of the lesser trochanter
<b>Hip Flexor index (HFI)</b>	Distance of lesser trochanter from proximal femur / femur length	An estimate of the distal extent of the lesser trochanter relative to the overall femoral length
<b>Third trochanter length index (TTLI)</b>	Lateral extension of third trochanter / femur length	Provides an estimate to the size of the third trochanter
<b>Third trochanter position index (TTPI)</b>	Third trochanter distance from proximal femur / distance from distal femur	Provides an indication on the position of the third trochanter
<b>Patellar groove width index (PGWI)</b>	Width of patellar groove / distal femoral epiphysis width	Provides an estimate of the proportion of the patellar groove to femoral epiphysis
<b>Patellar groove shape index (PGSI)</b>	Proximodistal length of patellar groove / mediolateral width of patellar groove	Provides an estimate of the overall shape of the patellar groove
<b>Femoral condyle depth index (FCDI)</b>	Craniocaudal length of medial condyle / diaphysis craniocaudal depth	Provides an estimate of the relative moment arm of the extensor muscles that cross the knee.
<b>Femoral condyle shape index (FCSI)</b>	Proximodistal length of medial + lateral condyles / mediolateral width of medial + lateral condyles	Provides an estimate of the overall shape of the femoral condyles
<b>Femoral condyle width index (FCWI)</b>	Medial condyle mediolateral width / lateral condyle mediolateral width	Provides an estimate of the proportion of the lateral and medial femoral condyles to each other
<b>Femoral epicondylar index (FEBI)</b>	Epicondylar breadth of the femur / femur length	Indicates the area available for the origin sites of <i>m. gastrocnemius</i> and <i>m. soleus</i> used in the extension of the knee and plantar flexion of the pes

<b>Femoral robustness index (FRI)</b>	Craniocaudal diaphysis depth / femur length	Provides an estimate of the femurs ability to support body mass and withstand excess vertical forces associated with increased velocity
<b>Gluteal index (GI)</b>	Greater trochanter height / femur length	Provides an estimate of the mechanical advantage of <i>m. gluteus medius</i> and the velocity of femoral extension
<b>Tibial tuberosity shape index (TTSI)</b>	Tibial tuberosity length / length of proximal tibia	Provides an estimate of the overall shape of the tibial tuberosity
<b>Tibial spine index (TSI)</b>	Tibial tuberosity length / tibia length	Provides an estimate for the mechanical advantage of the hamstrings and biceps femoris muscles acting across the knee and hip joints
<b>Tibial proximal end shape index (TPSI)</b>	Tibial proximal end length / width	Provides an estimate of the overall shape of the proximal tibial end shape
<b>Tibial condyle width index (TCWI)</b>	Medial tibial condyle width / lateral tibial condyle width	Provides an estimate of the proportions of the tibial condyles
<b>Tibial robustness index (TRI)</b>	Tibial midshaft width / tibia length	Provides an indication of the strength of the tibia and its ability to resist bending and sheering forces
<b>Crural index (CI)</b>	Tibial length / femur length	Indicates the relative proportions of the proximal and distal elements of the hind limb.
<b>Pes length index (PES)</b>	Metatarsal three length / femur length	Estimates the relative proportions of the proximal and distal elements of the hind limb and size of the hind foot

**Table 4.** Descriptive statistics (mean  $\pm$  standard deviation) of the morpho-functional indices of *Bathyergus suillus*, *Georychus capensis* and *Cryptomys hottentotus natalensis* including both sexes. See abbreviations in Table 3.

***Bathyergus suillus******Georychus capensis******Cryptomys hottentotus natalensis***

Index	Male (n=4)	Female (n=4)	All (n=8)	Male (n=4)	Female (n=4)	All (n=8)	Male (n=4)	Female (n=4)	All (n=8)
ILI	0.609 $\pm$ 0.022	0.623 $\pm$ 0.012	0.618 $\pm$ 0.016	0.627 $\pm$ 0.024	0.616 $\pm$ 0.018	0.621 $\pm$ 0.022	0.614 $\pm$ 0.020	0.594 $\pm$ 0.032	0.603 $\pm$ 0.028
ILSI	0.224 $\pm$ 0.035	0.231 $\pm$ 0.023	0.229 $\pm$ 0.027	0.228 $\pm$ 0.030	0.204 $\pm$ 0.014	0.217 $\pm$ 0.026	0.228 $\pm$ 0.036	0.202 $\pm$ 0.022	0.214 $\pm$ 0.031
ASHI	1.038 $\pm$ 0.040	1.040 $\pm$ 0.052	1.039 $\pm$ 0.046	1.028 $\pm$ 0.109*	1.066 $\pm$ 0.056*	1.046 $\pm$ 0.088	1.090 $\pm$ 0.131*	1.041 $\pm$ 0.175*	1.064 $\pm$ 0.154
ASZI	2.842 $\pm$ 0.192	3.004 $\pm$ 0.210	2.943 $\pm$ 0.213 <sup>a</sup>	2.560 $\pm$ 0.264	2.775 $\pm$ 0.275	2.660 $\pm$ 0.282 <sup>b</sup>	2.783 $\pm$ 0.375	2.489 $\pm$ 0.146	2.627 $\pm$ 0.308 <sup>b</sup>
PLI	0.253 $\pm$ 0.019	0.278 $\pm$ 0.017	0.268 $\pm$ 0.019 <sup>a</sup>	0.221 $\pm$ 0.018	0.194 $\pm$ 0.021	0.207 $\pm$ 0.024 <sup>b</sup>	0.236 $\pm$ 0.058	0.225 $\pm$ 0.026	0.231 $\pm$ 0.043 <sup>c</sup>
ISLI	0.342 $\pm$ 0.044*	0.374 $\pm$ 0.018*	0.361 $\pm$ 0.033	0.350 $\pm$ 0.018	0.361 $\pm$ 0.023	0.355 $\pm$ 0.021	0.392 $\pm$ 0.024*	0.377 $\pm$ 0.036*	0.384 $\pm$ 0.031
ISI	0.783 $\pm$ 0.117*	0.669 $\pm$ 0.046*	0.711 $\pm$ 0.095 <sup>a</sup>	0.630 $\pm$ 0.162	0.603 $\pm$ 0.062	0.616 $\pm$ 0.119 <sup>b</sup>	0.642 $\pm$ 0.093	0.699 $\pm$ 0.095	0.672 $\pm$ 0.095 <sup>a</sup>
OFSI	1.395 $\pm$ 0.055	1.477 $\pm$ 0.104	1.446 $\pm$ 0.096	1.255 $\pm$ 0.227	1.378 $\pm$ 0.078	1.317 $\pm$ 0.175	1.381 $\pm$ 0.053	1.415 $\pm$ 0.194	1.398 $\pm$ 0.136
FHSI	1.044 $\pm$ 0.041	1.013 $\pm$ 0.066	1.024 $\pm$ 0.058	1.040 $\pm$ 0.061	1.014 $\pm$ 0.047	1.028 $\pm$ 0.055	0.980 $\pm$ 0.073	1.021 $\pm$ 0.071	1.001 $\pm$ 0.073
FNWI	1.314 $\pm$ 0.115	1.292 $\pm$ 0.103	1.300 $\pm$ 0.104	1.349 $\pm$ 0.117	1.301 $\pm$ 0.083	1.326 $\pm$ 0.102	1.351 $\pm$ 0.413	1.382 $\pm$ 0.200	1.368 $\pm$ 0.308
GTI	0.284 $\pm$ 0.010	0.275 $\pm$ 0.008	0.278 $\pm$ 0.009 <sup>a</sup>	0.277 $\pm$ 0.025	0.289 $\pm$ 0.022	0.282 $\pm$ 0.024 <sup>b</sup>	0.281 $\pm$ 0.019	0.279 $\pm$ 0.017	0.280 $\pm$ 0.016 <sup>a</sup>
GTHI	1.130 $\pm$ 0.145	0.997 $\pm$ 0.149	1.047 $\pm$ 0.157 <sup>a</sup>	0.930 $\pm$ 0.097	0.948 $\pm$ 0.073	0.939 $\pm$ 0.084 <sup>a</sup>	1.119 $\pm$ 0.149	1.232 $\pm$ 0.256	1.179 $\pm$ 0.214 <sup>b</sup>
LTLI	0.092 $\pm$ 0.011	0.096 $\pm$ 0.010	0.094 $\pm$ 0.010	0.090 $\pm$ 0.010	0.099 $\pm$ 0.006	0.094 $\pm$ 0.012	0.180 $\pm$ 0.259	0.091 $\pm$ 0.013	0.133 $\pm$ 0.178
LTPI	0.227 $\pm$ 0.014*	0.249 $\pm$ 0.013*	0.241 $\pm$ 0.017	0.235 $\pm$ 0.042	0.224 $\pm$ 0.020	0.23 $\pm$ 0.032	0.232 $\pm$ 0.030	0.235 $\pm$ 0.027	0.233 $\pm$ 0.028
HFI	0.176 $\pm$ 0.016*	0.207 $\pm$ 0.013*	0.196 $\pm$ 0.021	0.187 $\pm$ 0.030	0.188 $\pm$ 0.023	0.187 $\pm$ 0.026	0.185 $\pm$ 0.022	0.188 $\pm$ 0.016	0.186 $\pm$ 0.018
TTLI	0.106 $\pm$ 0.040	0.096 $\pm$ 0.008	0.100 $\pm$ 0.025	0.086 $\pm$ 0.012	0.097 $\pm$ 0.018	0.091 $\pm$ 0.016	0.092 $\pm$ 0.021	0.092 $\pm$ 0.015	0.092 $\pm$ 0.017
TTPI	0.457 $\pm$ 0.094*	0.621 $\pm$ 0.065*	0.559 $\pm$ 0.110	0.485 $\pm$ 0.079	0.635 $\pm$ 0.262	0.555 $\pm$ 0.196	0.489 $\pm$ 0.050	0.526 $\pm$ 0.078	0.509 $\pm$ 0.067
PGWI	0.625 $\pm$ 0.029	0.621 $\pm$ 0.030	0.623 $\pm$ 0.029 <sup>a</sup>	0.662 $\pm$ 0.040	0.681 $\pm$ 0.034	0.671 $\pm$ 0.037 <sup>b</sup>	0.650 $\pm$ 0.054*	0.718 $\pm$ 0.049*	0.686 $\pm$ 0.061 <sup>b</sup>
PGSI	0.998 $\pm$ 0.052	0.991 $\pm$ 0.043	0.993 $\pm$ 0.045 <sup>a</sup>	0.920 $\pm$ 0.093	0.796 $\pm$ 0.041	0.862 $\pm$ 0.095 <sup>b</sup>	0.848 $\pm$ 0.106*	0.716 $\pm$ 0.096*	0.778 $\pm$ 0.119 <sup>b</sup>
FCDI	2.242 $\pm$ 0.127	2.050 $\pm$ 0.139	2.122 $\pm$ 0.162	1.974 $\pm$ 0.303	1.906 $\pm$ 0.097	1.942 $\pm$ 0.226	2.204 $\pm$ 0.397	2.142 $\pm$ 0.239	2.171 $\pm$ 0.314

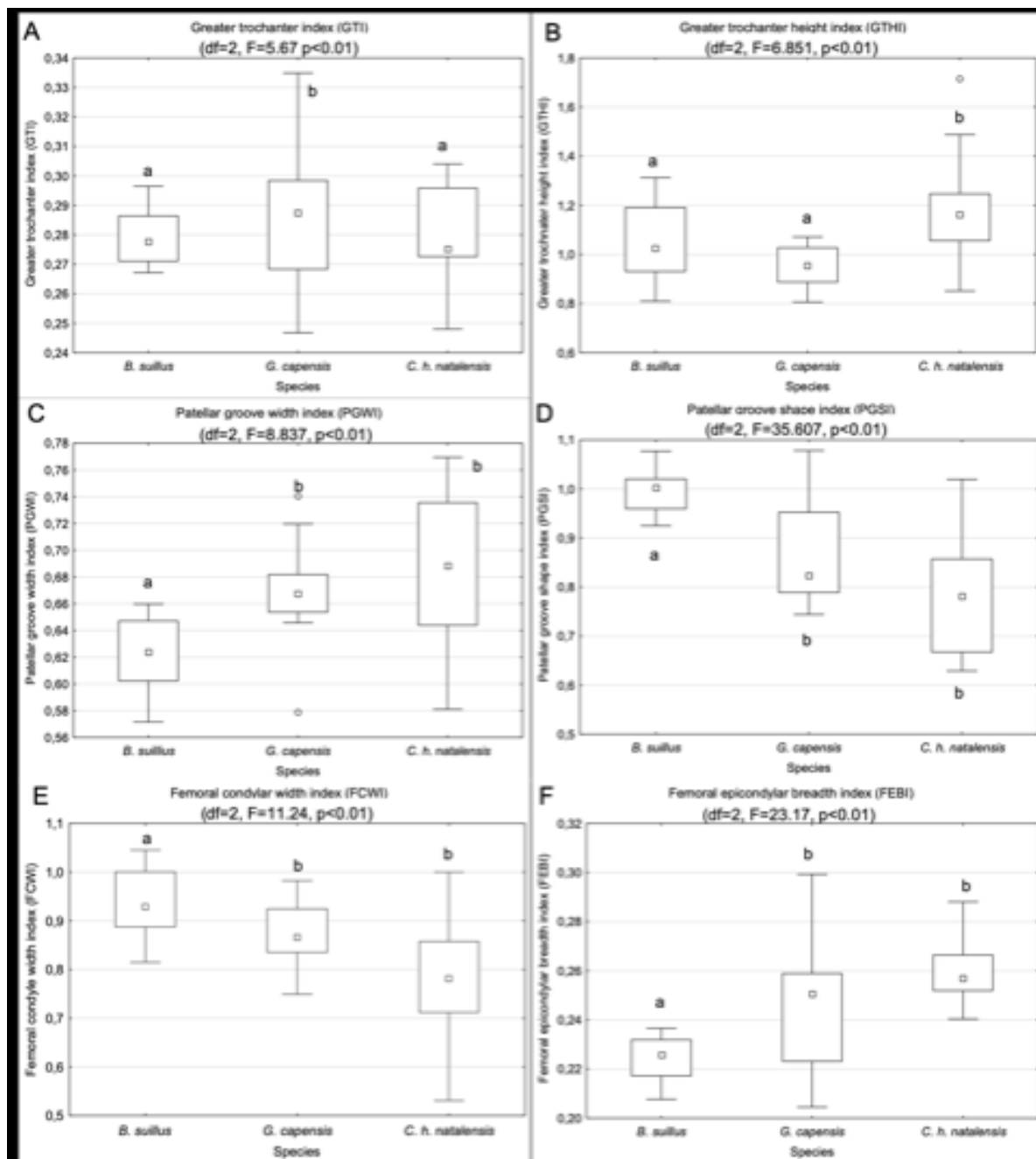
<b>FCSI</b>	1.154 ± 0.111	1.175 ± 0.072	1.167 ± 0.086	1.295 ± 0.236	1.144 ± 0.083	1.225 ± 0.192	1.225 ± 0.164	1.160 ± 0.097	1.191 ± 0.133
<b>FCWI</b>	0.966 ± 0.046	0.922 ± 0.080	0.938 ± 0.071 <sup>a</sup>	0.896 ± 0.068	0.848 ± 0.055	0.873 ± 0.065 <sup>b</sup>	0.792 ± 0.134	0.782 ± 0.109	0.787 ± 0.118 <sup>b</sup>
<b>FEBI</b>	0.229 ± 0.006	0.221 ± 0.009	0.224 ± 0.009 <sup>a</sup>	0.246 ± 0.025	0.243 ± 0.028	0.245 ± 0.025 <sup>b</sup>	0.260 ± 0.017	0.259 ± 0.012	0.256 ± 0.014 <sup>b</sup>
<b>FRI</b>	0.079 ± 0.003*	0.087 ± 0.005*	0.084 ± 0.006	0.087 ± 0.007	0.088 ± 0.009	0.088 ± 0.008	0.081 ± 0.014	0.084 ± 0.006	0.083 ± 0.01
<b>GI</b>	0.130 ± 0.015	0.120 ± 0.013	0.124 ± 0.014	0.122 ± 0.008	0.124 ± 0.017	0.123 ± 0.013	0.121 ± 0.019	0.135 ± 0.016	0.128 ± 0.018
<b>TTSI</b>	0.858 ± 0.085	0.810 ± 0.088	0.828 ± 0.087	0.790 ± 0.053	0.822 ± 0.087	0.805 ± 0.070	0.793 ± 0.059	0.774 ± 0.080	0.784 ± 0.069
<b>TSI</b>	0.503 ± 0.055	0.484 ± 0.047	0.491 ± 0.050 <sup>a</sup>	0.438 ± 0.033	0.447 ± 0.028	0.442 ± 0.030 <sup>b</sup>	0.433 ± 0.040	0.410 ± 0.036	0.422 ± 0.038 <sup>b</sup>
<b>TPSI</b>	0.999 ± 0.076*	1.119 ± 0.083*	1.074 ± 0.099	0.999 ± 0.191	1.125 ± 0.112	1.062 ± 0.164	1.125 ± 0.123	1.103 ± 0.185	1.115 ± 0.150
<b>TCWI</b>	1.315 ± 0.271	1.184 ± 0.077	1.233 ± 0.180	1.357 ± 0.271	1.403 ± 0.355	1.380 ± 0.304	1.305 ± 0.179	1.320 ± 0.180	1.312 ± 0.173
<b>TRI</b>	0.095 ± 0.009	0.094 ± 0.010	0.095 ± 0.009 <sup>a</sup>	0.085 ± 0.005	0.093 ± 0.006	0.089 ± 0.007 <sup>a</sup>	0.080 ± 0.017	0.075 ± 0.011	0.077 ± 0.014 <sup>b</sup>
<b>CI</b>	0.939 ± 0.019	0.932 ± 0.016	0.934 ± 0.017 <sup>a</sup>	1.025 ± 0.046	0.976 ± 0.079	1.002 ± 0.066 <sup>b</sup>	1.093 ± 0.054	1.086 ± 0.054	1.090 ± 0.052 <sup>c</sup>
<b>PES</b>	0.274 ± 0.032*	0.329 ± 0.020*	0.308 ± 0.036 <sup>a</sup>	0.323 ± 0.008	0.282 ± 0.025	0.302 ± 0.028 <sup>a</sup>	0.361 ± 0.029	0.387 ± 0.046	0.375 ± 0.040 <sup>b</sup>

Differing superscript letters (a, b, c) indicate significant differences between species in the and \* indicates a difference between sexes within a species  $p < 0.05$ .

All three species were significantly different with respect to the pubic length index (PLI) (df=2,  $F=12.797$ ,  $p<0.01$ ; Figure 1B), where *B. suillus* had the longest pubis, followed by *C. h. natalensis* while *G. capensis* had the shortest pubis. The ischial length index (ISLI) of *B. suillus* indicated that females had significantly longer ischia than males ( $p=0.019$ ) while the inverse was observed in *C. h. natalensis* ( $p=0.013$ ). *Georychus capensis* had a significantly smaller ischium shape index (ISI) compared to both other species (df=2,  $F=13.672$ ,  $p<0.01$ ; Figure 1C), indicating that *G. capensis* had the least robust ischium of the three species. Additionally, a sex difference was observed in *B. suillus* ( $p<0.01$ ) where the ischium in males was more robust compared to females. While not significantly different between species, the ilium length index (ILI) was higher in *G. capensis* indicating a longer ilium than in both the other two species studied. Furthermore, *G. capensis* males had the highest ILI mean value at 0.627 (Table 4). However, no significant difference was observed between the sexes.

### 3.2 Femoral osteological indices

The greater trochanter index (GTI) was significantly different in *G. capensis* compared to the other two species (df=2,  $F=5.67$ ,  $p<0.01$ ; Figure 2A). The greater trochanter height index (GTHI) of *C. h. natalensis* indicated that the proportion of the greater trochanter to the femoral shaft was significantly larger (df=2,  $F=6.851$ ,  $p<0.01$ ) compared to the two drumming species, (LSD test *B. suillus*  $p=0.045$ ; *G. capensis*  $p<0.01$ ; Figure 2B). A sex difference was observed between the males and females of *B. suillus* regarding the hip flexor index (HFI; LSD  $p<0.01$ ) indicating that the lesser trochanter extended more distally in females compared to males. While not statistically significant between species, the males and females of *B. suillus* differed significantly with respect to the lesser trochanter position (LTPI) and third trochanter position index (TTPI) with p-values  $p=0.042$  and  $p < 0.01$  respectively (Table 4). This indicated that the lesser and third trochanters were positioned more proximally in *B. suillus* females than in males.



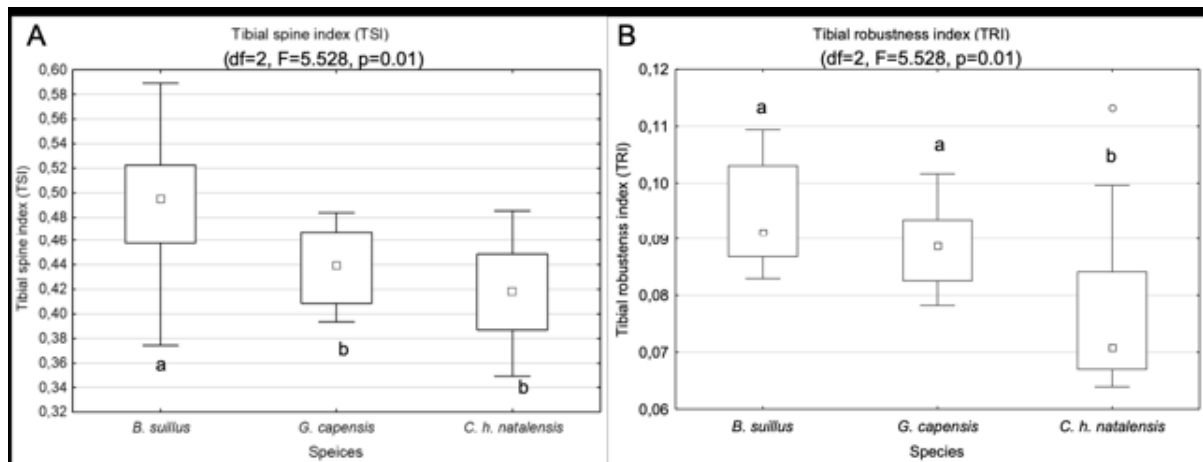
**Figure 2.** Box and whisker plots (with median, interquartile range, non-outlier range, and outliers shown) showing the six significant femoral osteological indices. A. *G. capensis* (a) had a significantly larger greater trochanter index (GTI) compared to both *B. suillus* and *C. h. natalensis* (b). B. The drumming species (*B. suillus* and *G. capensis*; a) had significantly smaller greater trochanter height index (GTHI) values compared to *C. h. natalensis* (b). C. *B. suillus* (a) had a significantly smaller patellar groove width index (PGWI) compared to both *G. capensis* and *C. h. natalensis* (b). D. *B. suillus* (a) had a significantly larger patellar groove shape index (PGSI) compared to both *G. capensis* and *C. h. natalensis* (b). E. *B. suillus* (a) had a significantly larger femoral condyle width index (FCWI) compared to both *G. capensis* and *C. h. natalensis* (b). F. *B. suillus* (a) had a significantly smaller femoral epicondylar breadth index (FEBI) compared to both *G. capensis* and *C. h. natalensis* (b). Differing superscript letters (a, b, c) indicate significant differences between species with  $p < 0.05$ .

The patellar groove width index (PGWI) was significantly larger in *G. capensis* and *C. h. natalensis* compared to *B. suillus* ( $df=2$ ,  $F=8.837$ ,  $p<0.01$ ), indicating that *B. suillus* had the narrowest patellar groove of the three species (Figure 2C). Furthermore, a sex difference was found in *C. h. natalensis* ( $p<0.01$ ) with the females having a wider patellar groove compared to males (Table 4). The patellar groove shape index (PGSI) of *B. suillus* was significantly different to the other two species ( $df=2$ ,  $F=35.6066$ ,  $p<0.01$ ) indicating that *B. suillus* had a long, narrow patellar groove, whereas *G. capensis* and *C. h. natalensis* had broad and short patellar grooves (Figure 2D). Furthermore, a sex difference was observed between the males and females of *C. h. natalensis* ( $p<0.01$ ), where the females had shorter patellar grooves than the males. All three species had relatively larger lateral femoral condyles compared to their medial counterpart. However, *B. suillus* had the largest femoral condyle width index (FCWI) of the three species ( $df=2$ ,  $F=11.12442$ ,  $p<0.01$ ; Figure 2E) with a mean value of 0.938, indicating that the medial and lateral femoral condyle were almost equal in width. Both *G. capensis* and *C. h. natalensis* had significantly larger femoral epicondylar robustness index (FEBI;  $df=2$ ,  $F=23.17$ ,  $p<0.01$ ) values compared to *B. suillus*, indicating that these two species have relatively large femoral epicondyles (Figure 2F). While not significant, the two drumming species had higher femoral robustness index (FRI) values compared to the non-drumming species. In addition, a difference between sexes was observed in *B. suillus* (LSD  $p=0.043$ ), where the females had more robust femora than the males.

### 3.3 Tibia

The tibial spine index (TSI) was significantly larger in *B. suillus* indicating a longer tibial tuberosity compared to the other two species ( $df=2$ ,  $F=5.528$ ,  $p<0.01$ ; Figure 3A). A significant difference was observed between the drumming species and *C. h. natalensis* with regard to the tibial robustness index (TRI;  $df=2$ ,  $F=5.528$ ,  $p<0.01$ ), where *B. suillus* had the most robust tibia and *C. h. natalensis* the least robust tibia (Figure 3C).

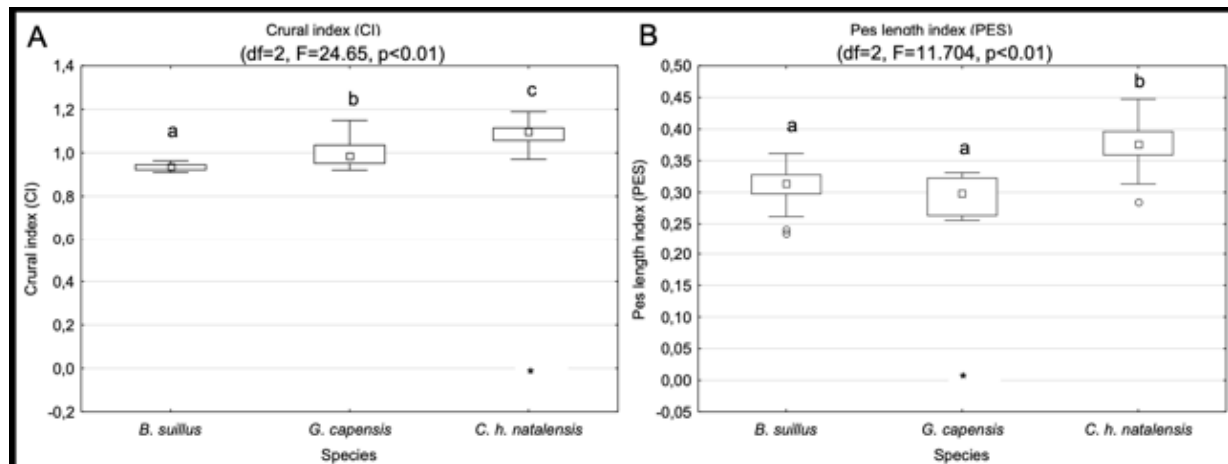




**Figure 3.** Box and whisker plots (with median, interquartile range, non-outlier range, and outliers shown) showing the three significant tibial osteological indices. A. *B. suillus* (a) had a significantly higher tibial spine index (TSI) compared to both *G. capensis* and *C. h. natalensis* (b). B. The drumming species (*B. suillus* and *G. capensis*; a) had significantly higher tibial robustness index (TRI) values compared to *C. h. natalensis* (b). Differing superscript letters (a, b, c) indicate significant differences between species with  $p < 0.05$ .

### 3.4 Other osteological indices

The crural index (CI) was the highest in *C. h. natalensis* followed by *G. capensis* and finally *B. suillus* (df=2, F=24.64567,  $p < 0.01$ ) indicating that in *B. suillus* the femur was relatively longer than the tibia while the inverse was seen in *C. h. natalensis* (Figure 4A). The pes length index (PES) was significantly smaller in the drumming species (*B. suillus* and *G. capensis*) compared to *C. h. natalensis* (df=2, F=11.704,  $p < 0.01$ ) indicating that *C. h. natalensis* had a relatively large pes compared to the drumming species (Figure 4B). Furthermore, a sex difference was observed in *B. suillus* ( $p < 0.01$ ) where the females had a relatively larger pes compared to the males (Table 4).



**Figure 4.** Box and whisker plots (with median, interquartile range, non-outlier range, and outliers) showing the two significant other osteological indices. A. All three species had significantly different crural index (CI) values. B. The drumming species (*B. suillus* and *G. capensis*; a) had significantly smaller pes length index (PES) values compared to *C. h. natalensis* (b). Differing superscript letters (a, b, c) indicate significant differences between species with  $p < 0.05$ .

## DISCUSSION

Many studies have used osteological indices to analyze the long bones of rodent species for adaptations to locomotory behavior (Sargis, 2002; Elissamburu & Vizcaino, 2004; Samuels & Van Valkenburgh, 2008; Salton & Sargis, 2009; Echeverria, *et al*, 2014; Montoya-Sanhueza *et al*, 2019). These indices provide insight into various parameters of osteology including indications of function. The present hind limb morphological study therefore aimed to use many more morpho-functional osteological indices than reported in any previous studies to identify possible adaptations for hind foot drumming.

Rodent studies that include osteological indices on the pelvis are sparse. One study by Coutinho, de Olivera & Pessôa (2013) reported on the osteology of various South American rodents, including semi-fossorial species, using only linear measurements instead of morpho-functional indices. Alveraz, Ercoli & Prevosti (2013) used shape analysis to study the pelvis and hind limb in various small mammals and additionally reported linear measurements of these bones but not indices.

The proportional indices of ilium length, ischium length and pubic length of the pelvis may reflect the range of motion of the muscles that originate and insert at these localities, therefore affecting the moment arm of the muscles. In turn, the moment arms

influence the speed and power abilities of the individual muscles in mammals (Smith & Savage, 1965). The gluteal muscle group is adapted for rapid movements while the ischio-pubic muscle group (*mm. semitendinosus, semimembranosus, gracilis* and *abductor magnus*) are adapted for a more powerful, propulsive motion while causing relatively slow extension of the femur (Smith & Savage, 1965; Sargis 2002). Due to these muscle characteristics, the ilium is large in species that require rapid movement of the hind limb, resulting in a relatively small ischium. The inverse is reported for species that need powerful hind limb propulsion such as semiaquatic species (Smith & Savage 1965). While not significantly different, the ilium length index (ILI) of *G. capensis* was higher than both other species, specifically the males (mean ILI of 0.627). The longer ilium in this species indicates more developed and elongated gluteal muscles which reflect a greater moment arm of *m. gluteus medius*, allowing for more rapid extension of the femur during drumming. Furthermore, *G. capensis* had the smallest and least robust ischium of the three species as indicated by the ischial length and shape indices (ISLI and ISI). This suggests that the moment arms of the ischio-pubic muscles are shortened, causing less powerful movements of these muscles thereby allowing for enhanced speed of contraction during rapid drumming. Short pubic length is associated with a decreased moment arm of the adductor muscle group which constrains hip flexion and extension (Sargis, 2002). Therefore, the relatively short pubic length in *G. capensis* would be an advantage with rapid hip flexion and extension during drumming. Pubic length is closely correlated to body size in mammals (Alvarez *et al*, 2013). It is likely that the comparatively large body size of *B. suillus* has more influence on the length of the pubis than a functional adaptation for drumming.

All three species of the present study had large acetabula but *B. suillus* had a significantly larger acetabulum compared to the other two species. While no specific data are available correlating acetabular size and body size in rodents, a positive correlation has been observed in primates (Fleagle & Anapol, 1992). The large acetabular size in *B. suillus* may therefore reflect its relatively large body size compared to the other two species studied here (Table 1). Argot (2002) postulated that a large acetabulum allows for greater hip mobility in marsupials. Salton & Sargis (2009) in their study on tenrecs (Tenrecoidea) hypothesized that a large acetabulum allows for a more abducted position of the femur while digging as well as rotational movement

for maneuvering within a burrow. As hindfoot drumming in quadrupeds requires rapid extension and flexion of the hip (Randall, 2010) it is likely that extensive hip mobility is needed in drumming species. Hip mobility is affected by the height of the greater trochanter as seen in arboreal porcupines (Candela & Picasso, 2008). The significantly larger greater trochanter height index (GTHI) seen in *C. h. natalensis* compared to the drumming species indicates that the more proximally projected greater trochanter in *C. h. natalensis* could decrease hip mobility and limit abduction of the femur (Sargis, 2002; Candela & Picasso, 2008). Furthermore, a short greater trochanter results in a smaller in-lever which increases the velocity ratio of the hind limb (Hildebrand, 1985b). Therefore, in the case of the drumming species of the present study, it is likely that the relatively shorter proportions of the greater trochanter of *B. suillus* and *G. capensis* could reflect increased hip mobility which is needed for the high speed of foot motion required during drumming.

The hip flexor index (HFI), gluteal index (GI) and greater trochanter index (GTI) are closely correlated to the moment arms of the muscles that attach to the lesser and greater trochanter (Polly, 2007; Wilson & Geiger, 2015). These large values seen in the present study correlate with the increased mobility needed by the major extensor muscles for navigating burrows. The GTI of *G. capensis* was significantly increased compared to the other two species, indicating that the moment arm of the *m. gluteus medius*, which attaches to the greater trochanter, is further increased compared to the other two species. This may be an adaptation for the particularly rapid speed of flexion and extension of the hip joint achieved by *G. capensis* during hind foot drumming. Additionally, the third trochanter was more proximally located in females than males in all three species, however, only significantly different in *B. suillus*. The great speed at which males of *G. capensis* and *B. suillus* drum may be possible due to the distally located third trochanter. The latter may be related to the powerful mechanics of the *m. gluteus superficialis* (Salton & Sargis, 2009; Sahd *et al.*, 2019) which would allow for fast hip extension.

All three species had large patellar groove width index (PGWI) values which coincides with what has been observed in various fossorial species such as *Paraechinus micropus* (Indian hedgehog; Verma, 1963) and two *Oryzocites* species (Rice tenrec; Salton & Sargis, 2009). These wide, shallow patellar grooves are indicative of highly

mobile knee joints (White, 1993) and most likely facilitate lateral abduction and rotation of the tibia and pes during digging when the body is braced against the walls of the burrow system (Hildebrand, 1985a; Salton & Sargis, 2009). Furthermore, the patellar groove shape index (PSHI) reflects the increased width, and short and broad shape of the femoral trochlea as seen in *G. capensis* and *C. h. natalensis* compared to a long narrow patellar groove seen in *B. suillus*. The soft sandy soil in which *B. suillus* burrows (Bennett & Faulkes, 2000) as well as their size and digging method (scratch digging compared to chisel-tooth digging in the other two species), may influence the width of their patellar groove. It is unlikely that the width and shape of the patellar groove influences drumming, as broad short patellar grooves were observed in both a drumming (*G. capensis*) and non-drumming species (*C. h. natalensis*) in the present study.

Compared to non-fossorial rodents, all three species studied here have large femoral epiphysis breadth index (FEBI) and tibial spine index (TSI) values (Elissamburu & Vizcaino, 2004). It is postulated that these indices in other mole-rat species reflect enlarged muscles of the hind limb, specifically *mm. gluteus medius*, *gastrocnemius* and the hamstrings to resist backwards movement during digging (Samuels & Van Valkenburgh, 2008). The robustness of the bones (femoral robustness index [FRI], in our case tibial robustness index [TRI]), has been shown to be an adaptation to resist torsional and compressive forces encountered during digging in various fossorial species (Savage & Smith 1965; Biknevičius, 1993; Stein, 1993; Samuels & Van Valkenburgh, 2008). In the present study, the enlarged epicondyles in *G. capensis* and *C. h. natalensis* could indicate a greater reliance on *m. gastrocnemius* to prevent backwards movement during chisel-tooth digging compared to the scratch digging *B. suillus*. However, the large TSI of *B. suillus* indicates a large insertion area for the hamstrings (*m. semitendinosus*, *m. semimembranosus*) implying an increased mechanical advantage (Samuels & Van Valkenburgh, 2008) to resist the torsional forces during scratch digging. Additionally, the high TRI values seen in the two drumming species (*B. suillus* and *G. capensis*) could be due to the force exerted onto the tibia by the large, single *m. gracilis* and hamstring muscles during drumming (Sahd *et al.*, 2019).

High crural index (CI) values have been correlated to powerful hindlimb extension during digging in tenrec species (Salton & Sargis, 2009) and is reflected in all three species of the present study. However, the CI in *C. h. natalensis* was greater than in both drumming species, indicating an elongated tibia (Samuels & Van Valkenburgh, 2008) which was longer than the femur. Furthermore, the two drumming species differed from each other where *B. suillus* had a relatively short tibia compared to the femur, and the tibia of *G. capensis* was almost equal in length to the femur. As the tibia decreased with increased body size (Elissamburu & Vizcaino, 2004), it is likely that these differences are due to size of the species (Table 1), rather than a possible adaptation for drumming.

Fossorial rodents typically have small feet (Nevo, 1995; Stein, 2002; Samuels & Van Valkenburgh, 2008). The drumming species in the present study had relatively smaller hind feet compared to the non-drumming *C. h natalensis*. The small size of the feet could aid in the rapid motion of drumming by decreasing the amount of weight required to be lifted during extension and flexion of the hind limb. Interestingly, the females of *B. suillus* had larger feet than the males which could potentially influence drumming speed, as females have been shown to drum slower than males (Bennett & Faulkes, 2000).

## **CONCLUSION**

The differences reflected in the hind limb osteological indices when the two drumming mole-rat species are compared to the non-drumming species, indicate adaptations such as a short femoral greater trochanter for increased hip mobility, more robust tibias for muscle attachment and small hind feet to reduce limb weight.

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The authors have no conflict of interest to declare

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## AUTHOR CONTRIBUTIONS

Lauren Sahd performed the analysis and drafted the manuscript. Nigel Bennett provided the samples and edited the manuscript. Sanet Kotzé was the principle investigator, designed the project and edited the manuscript.

## DATA SHARING STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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