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The appendicular skeleton of the *Eidolon helvum* (African fruit bat): Gross anatomical investigations

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ABSTRACT

The bats are the only known flying mammals. The skeleton is an essential aspect of anatomy and the shape and characteristics of each bone is peculiar to each animal species. Despite the widespread distribution of the African fruit bat (*Eidolon helvum*), there is no documented data on the morphometrics and description of the skeleton, apart from the axial skeleton documented by this team. This study therefore aims at highlighting the gross description of the individual bones of the appendicular skeleton – fore and hind limbs – of the *Eidolon helvum* captured from the wild. The bats (5 males, 10 females) were captured from the southwestern part of Nigeria used for this study. They were humanely sacrificed, de-fleshed and subjected to cold maceration. The appearance of the individual bones was unique. Of particular interest were the scapula, *ossa coxarum* and the metacarpal bones. Similar to neotropical bats, the scapula had a strong similarity in shape and appearance to the human counterpart, while differing greatly from other mammals and avians. The *ossa coxarum* was the only bone that showed a distinct sexual dimorphism. The shape of the obturator foramen was ovoid in males but more triangular in females. Also, there was non-fusion of the pubic symphysis in the females, unlike that observed in males. The metacarpal was not observable in all subjects, as the carpal bones were seen to articulate directly with the digits distally, and the ulna proximally. Linear measurement results obtained showed that the males had generally higher values, with the wingspan (609.96±64.53 mm) showing a statistically significant difference between the genders (P<0.05), males being 663.45±14.48 mm, and the females 580.14±62.23 mm. Results obtained from this study provide baseline, data which may find application in basic and comparative anatomical studies, forensic, archaeological and anthropological studies, and wildlife clinical procedures.

Keywords: *Eidolon helvum*, fore- and hind-limb skeleton, morphometry, osteology

INTRODUCTION

Bats remain the only known mammals which can fly (Balthazary *et al.*, 2007; Igado *et al.*, 2015). The *Eidolon helvum*, also known as the straw-coloured fruit bat and the African fruit bat, belongs to the Order Chiroptera, Family Pteropodidae, Genus *Eidolon*, and Species *E helvum*. Of the West African fruit bats, it is the largest (DeFrees and Wilson, 1988). As a nocturnal animal, it roosts during the day and seeks food at night (Hunter, 2007). Bats are of great economic and public health importance.

They have been identified as natural hosts for many emerging zoonotic viruses having high fatality rates. These viruses include the Marburg virus, paramyxoviruses, Ebola virus and lyssa viruses (Gibson *et al.*, 2021). They cause serious damage to plants when they feed on the fruits, and they have also been reported to be responsible for the transmission of several viral diseases, like rabies (Crawford *et al.*, 2002; Igado *et al.*, 2012).

Reportedly having over 1,400 species, with a high variation in morphology and ecology, bats offer a unique opportunity for studying morphological and ecological changes. They possess special features for adaptation, to enhance survival in their environments such as flight, echolocation, olfaction and hibernation (Currie *et al.*, 2015; Brokaw and Smotherman, 2020).

The appendicular skeleton comprises the bones of the fore and hind limbs. It has been extensively described in some mammalian and avian species (Panyutina *et al.*, 2015; Singh, 2017), including four families of neotropical bats (Noctilionidae, Phyllostomidae, Vespertilionidae, and Molossidae) (Sánchez and Carrizo, 2021) but this cannot be said for the *Eidolon helvum*. The bones of the forelimb are an important part of the bat wing, forming a critical component of the alar mass, serving to support soft tissue and also prevent deformation (Sánchez and Carrizo, 2021). Relative to terrestrial mammals, the bat's forearm bones are long and curved, with the radius larger than the ulna and the digits elongated and serving as a support frame for the membranous wings. The hindlimb skeleton has the fibula reduced or absent, while the femur and tibia are slimmer and longer than those of similarly sized terrestrial mammals. The femur and tibia rotate 90 – 180° from the normal mammalian pattern. These specialisations adapt the bat to flight. Capable walking has been reported in some bats, although the majority shuffle awkwardly along the ground (Riskin *et al.*, 2005)

This study aims to describe the morphology and osteometrics of the appendicular skeleton of this bat, provide baseline data for forensic and comparative studies, and assess sexual dimorphism if present, while also providing information which could be useful in understanding the osteological mechanisms of movement in the different regions of the bat body.

This article is one in the series on the osteology of the *Eidolon helvum*, with previous articles being on the morphometry of the axial skeleton (skull, ribs, sternum and vertebrae) (Igado and Ade-Julius, 2018; Igado and Joannis, 2022).

MATERIALS AND METHOD

Ethical approval for this work was obtained from the Ethical Committee, Faculty of Veterinary Medicine, ethical code no 12/13/03. Experimental animals used for this study were 15 adult bats consisting of 10 females and 5 males. Age was determined based on weight and dentition (eruption and dental wear), according to previous reports (DeFrees and Wilson, 1988; Richter and Cumming, 2006). The bats were captured at roosting and foraging sites with the use of mist nets and were transported to the laboratory in metal cages. All procedures for handling the animals complied with the Guidelines for the Care and Use of Experimental Animals (National Institute of Health – NIH, USA).

All procedures for euthanasia and cold water maceration were as previously described (Igado and Ade-Julius, 2018). The wingspan (in millimetres) was obtained before the commencement of maceration. Pictures were taken with a digital camera (Sony® Cyber-shot, DSC-HX400V, 50x optical zoom). All linear measurements were obtained using a digital vernier calliper (Neiko®, sensitivity of 0.01mm, Germany). Except otherwise indicated, measurements were recorded in millimetres. For paired bones, measurements for both the right and left sides were reported. All terminologies regarding the bones and their features were based on Nomina Anatomica Veterinaria (2017) and some other anatomy texts (Getty, 1975; Abrahams *et al.*, 1998; Rohen *et al.*, 1998; Netter, 2006; Singh, 2017).

Definition of measured parameters and their landmarks

1. **Wing span** – the distance between the most lateral tips of the 2 wings, measured in inches with the aid of a centimetre rule. This was obtained before the commencement of maceration.
2. **Length of clavicle** – measured from the sternal to the acromial end
3. **Length of humerus** – from the head of the humerus to the most distal aspect of the distal epiphysis.
4. **Length of radius** – from the radial head to its tip, along the length of its articulation with the ulna.
5. **Length of ulna bone** – measured from the point of articulation with the distal head of the humerus, till its articulation with the carpal bones.
6. **Length of the pelvic bone** – measured along its longitudinal axis, from the crest of the ilium to the tip of the pubic/ischium.
7. **Length of femur** – measured from the head of the femur to its distal epiphysis, where it articulates with the proximal end of the tibia.
8. **Length of tibia** – measured from the point of articulation with the femur, to the point of articulation with the proximal end of the tarsal bones.
9. **Length of each digit of the fore and hind limbs** – the lengths of individual digits, from the proximal epiphysis of the proximal phalanx to the tip of the claws.

Statistical Analysis

Statistical analysis was calculated using the Student 't' test (Graphpad Prism statistical software, Version 5, La Jolla, CA, USA). The level of significance was $p<0.05$.

RESULTS

Wing span

Measured in millimetres, the average wingspan was 609.96±64.53 for all the animals, 663.45±14.48 in males and 580.14±62.23 in the females, with statistically significant difference occurring between the genders ($P<0.05$).

Thoracic Limb

Clavicle

The clavicle was slightly sickle or C-shaped, bilaterally flattened around its body, with the acromial and sternal ends terminating into dorso-ventrally flattened articular surfaces. The anterior (cranial surface) had ridges, unlike the posterior surface which was smoother (Fig. 1). The lengths of the clavicles were 28.87±3.53 mm (right) and 28.58±3.50 mm (left). The males recorded higher values for both the right and left clavicular lengths (31.59±1.03 mm and 30.95±1.65 mm respectively) relative to the females (30.95±1.65 mm and 27.40±3.63 mm respectively), although no statistically significant difference was observed ($p > 0.05$).

Scapula

The scapular had a characteristic triangular shape (Fig 1A & B). It possessed costal (medial surface) and lateral surfaces, cranial, caudal and superior borders (the cranial and caudal borders meet ventrally to form an apex), dorsal (proximal/superior) and ventral (distal/inferior) angles. The lateral surface bore the spine which divided it into the supraspinous and infraspinous fossae, and the acromion, which projected dorsally, the height being the same as the coracoid process. The infraspinous fossa was larger and cranially placed, while the supraspinous fossa was smaller and caudally placed. The tip of the acromion was bilaterally flattened. The coracoid process, sickle-shaped, emanated from the dorsal/proximal aspect of the glenoid cavity and directed cranio-medially to it. A supra-glenoid tubercle was distinct (Fig 1A – C). In addition, there was the presence of an infra-glenoid tubercle. The cranial border showed a V-shaped depression in the proximal aspect, immediately ventral to the glenoid fossa. This depression bore a foramen in the upper one-third (Fig. 1C). The costal surface was divided into two fossae (cranial and caudal) by a prominent subscapular ridge or spine, dividing this surface into two distinct subscapular fossae (Fig. 2B).

Humerus

The humerus has a curved appearance (slightly "S"), especially from the medial and lateral sides. The shaft was thicker in the proximal aspect than the distal aspect. The proximal shaft was mediolaterally flattened, while the distal aspect was craniocaudal (anteroposteriorly) flattened. The proximal end (epiphysis) bore the head (caudally placed) and three tubercles (medially, laterally and cranially placed – with the medial tubercle being the most prominent and the cranial one the least prominent). The distal end bore the medial and lateral epicondyles, the trochlear and the coronoid fossa. The olecranon fossa was however conspicuously absent. The caudal surface of the shaft, on the proximal third, had a distinct and pronounced ridge, while the cranial surface was relatively smooth. Slight ridges were also observed on the medial and lateral aspects of the shaft, still in the proximal third (Figs. 3A-D).

The lengths of the humeri (in mm) were 51.10 ± 6.16 (right) and 51.35 ± 5.30 (left). The males recorded values of 55.33 ± 1.76 (right) and 54.04 ± 1.71 (left) which were higher than the values obtained in the females – 48.69 ± 6.56 (right) and 50.16 ± 5.99 (left). No statistically significant difference was recorded between genders.

Ulna and Radius

The ulna was considerably larger than the radius, a very thin bone. The two were closely attached at the proximal end and part of the shaft, with the radius being about three-quarters of the length of the ulna. In life, the two bones are attached by ligaments, but thorough maceration results in a complete separation (Figs. 4A-F).

Ulna: The cranial surface of the ulna was rounded, while the caudal surface was flat in appearance. The shaft was relatively straight but, curved slightly caudally in the proximal aspect. The proximal end articulating with the trochlear of the humerus was flattened, with a central depression (trochlear notch). A prominent olecranon was absent, but what could be taken as the anconeal process was present. Two tubercules (medial and lateral) were also observed, with the lateral tubercle being more pronounced. The caudal part bore an articular surface, for articulation with the head of the radius. A short ridge was located below the articular surface for the radius. The distal end bore a deep notch to accommodate the carpal bones. The radius was attached to the caudal surface of the ulna (Figs 4A-C, F).

The average length of the ulna was 79.69 ± 10.61 mm (right) and 79.21 ± 9.96 mm (left). The values obtained for the males were 84.90 ± 6.06 mm (right) and 82.68 ± 9.39 mm (left), while the females recorded values of 76.71 ± 11.86 mm (right) and 77.67 ± 10.35 mm (left), lower than that obtained in males, but with no statistically significant difference.

Radius: This was observed as a very thin and fragile bone with a wide proximal aspect that can be described as a cranio-caudally flattened head. It bore a neck, between the head and the thin shaft (Figs 4D-F).

Morphometric values obtained for the radii were 51.70 ± 8.10 mm (right) and 52.41 ± 9.03 mm (left). The values for the males were 54.26 ± 6.04 mm (right) and 51.47 ± 9.97 mm (left), higher than what was obtained in females – 50.23 ± 9.18 mm (right) and 52.83 ± 9.18 mm (left).

Carpus

This joint was observed to be in two rows – proximal and distal. The distal row (articulating with the digits) consisted of three tiny bones, while the proximal row (articulating with the ulna) was a single large ‘proximo-distally’ compressed and quadrilateral-shaped bone (Fig. 5).

Metacarpal

This was not observable in the *E helvum*. Immediately distal to the carpal bones were the digits.

Digits

Each forelimb (wing) had five digits, numbered I to V, with I being the most medial and the shortest, and the middle digit (III) was the longest. All the digits, except I, had 3 phalanges (proximal, middle and distal), with claws at the end. The first and shortest digits had 2 phalanges, with a claw at the end. The proximal and distal articular surfaces (or epiphyses) of the phalanges were typically wider than the shafts. These bones were generally thin, with the proximal phalanx being the thickest and the distal phalanx being the thinnest (Fig. 5).

Linear measurement values for the digits are in Table 1.

Pelvic Limb

Os coxae (ossa coxarum)

This is the pelvic bone and the only bone that showed distinct gender dimorphism. The ossa coxarum was completely fused with the sacrum (Fig. 6A – D), to form the pelvic girdle. The sacrum had been previously described by the authors (Igado and Ade-Julius, 2018).

The os coxae consisted of the ilium, ischium and the pubis.

The ilium: the two ilia had the typical appearance of most mammalian ilium, with the crest and wing cranially located, and the body (shaft) caudal to it. The ilium was the most cranially placed of the bones of the os coxae. The ilium met at the acetabulum with the ischium (caudally) and the pubis (ventrally).

The ischium: this bone extends caudally and then ventrally, from the acetabulum. It articulates ventrally with the pubis, forming distinctly differing shapes in both genders (Fig. 6).

The pubis: the pubic bone joins to the ilium ventrally at the acetabulum, it "arched" cranially, forming a notch and a tubercle, at what can be described as the iliopubic eminence. This further extends ventrally and caudally to articulate with the ischium. In the males, the 2 pubic bones become fused ventrally, resulting in an ovoid shape with the ischium when viewed from the caudal aspect (Fig. 6A & B). In the female, the pubic bones "diverge" laterally and do not come together to form a symphysis, resulting in a crescent shape (half-moon) when viewed caudally (Fig. 6C & D).

The acetabulum was typical, with an acetabular notch medially placed, towards the obturator foramen. The acetabular notch was more pronounced in the females, relative to the males (Fig. 6B & D). The obturator foramen was bounded by the ischium dorso-caudally, and by the pubis cranio-ventrally. This foramen was typically large and also showed variations in the shape based on gender. In the males, it had a distinctly ovoid shape, while in the females, it was more triangular (Fig. 6B & D).

Morphometric values (mm) for the length of the pelvic bone were 23.64±3.57 (right) and 23.37±3.26 (left), while values for males were 26.89±1.88 (right) and 26.13±1.71 (left), and females 21.84±2.95 (right) and 21.84±2.91 (left). Male values were observed to be statistically significantly higher than those of females ($p>0.05$).

Femur

The hindlimb was considerably shorter than the forelimb.

The femur could be described as having 2 surfaces (caudal and cranial), with the caudal surface being slightly curved/rounded and bearing the head, which protruded quite higher than the medial and lateral trochanters. The rounded head was more medially placed, and the medial trochanter was slightly higher than the lateral trochanter. *Fovea capitis* was observable on the cranial aspect of the head. The distal part displayed the medial and lateral epicondyles, and a smooth surface that could have been taken to be the patellar surface, although a patella was not observed. The cranial surface was flattened, the proximal aspect showed a trochanteric fossa, and the distal aspect had lateral and medial condyles (Fig. 7).

Morphometric values (mm): length – 20.53±2.44 (right) and 20.78±2.59 (left); males – 21.69±0.79 (right), 22.25±0.78 (left); females – 19.95±2.81 (right), 20.13±2.87

(left). No statistically significant differences were observed among the genders.

Tibia and Fibula

The tibia is quite longer than the femur. The proximal aspect of the tibia is wider than the distal. The body is slightly curved, with a tubercle in the proximal third of the cranial part (Fig. 8).

The fibula was seen as a very thin and fragile bone (Fig. 9C), shorter than the tibia, and articulating with it at the distal end.

Tibia length (mm): 32.05±4.03 (right) and 31.95±4.01 (left); males – 34.24±1.61 (right), 34.54±1.73 (left); females – 30.96±4.51 (right), 30.80±4.26 (left).

Tarsus

These were extremely tiny, and only 2 could be identified. This joint appeared in a single row comprising a larger bone and a smaller calcaneus (Fig. 9A & B).

Metatarsal

These bones were observable immediately distal to the tibia and tarsal bones (Fig. 9A), and also proximal to the digits. They were 5 in number. The measurement was taken as a single measurement, from the tarsus to the proximal aspect of the first phalanx.

Digits

Like the forelimb, each hindlimb had five digits, numbered I to V. The most medial and most lateral (I and V respectively) were the shortest, while the remaining 3 had similar lengths. All the digits had 3 phalanges (proximal, middle and distal), with claws at the end. The proximal and distal articular surfaces (or epiphyses) of the phalanges were typically wider than the shafts. These bones were generally thin, and the phalanges appeared to have similar thickness (Fig. 9A)

Linear measurement values for the digits are in Table 1.

Table 1: Linear measurements of the forelimb digits of the *E. helvum* (in millimetres)

		Male (n = 5)		Female (n = 10)		Total (n = 15)	
		Right	Left	Right	Left	Right	Left
Digit I	1st phalanx	11.0 ± 0.00	11.0 ± 0.00	10.0 ± 0.00	10.0 ± 0.00	10.5 ± 0.58	10.5 ± 0.58
	2nd phalanx	17.5 ± 0.71	17.5 ± 0.71	15.0 ± 0.00	15.5 ± 0.71	16.25 ± 1.50	16.50 ± 1.25
Digit II	1st phalanx	42.5 ± 0.71	42.5 ± 0.71	40.0 ± 0.00	40.0 ± 1.41	41.25 ± 1.50	41.25 ± 1.71
	2nd phalanx	10.0 ± 0.00	10.0 ± 0.00	10.0 ± 1.41	9.50 ± 0.71	10.0 ± 0.82	9.75 ± 0.50
	3rd phalanx	6.50 ± 0.71	6.50 ± 0.71	6.50 ± 0.71	6.50 ± 0.71	6.5 ± 0.58	6.0 ± 0.82
Digit III	1st phalanx	62.0 ± 1.41	62.0 ± 1.41	57.0 ± 1.41	56.5 ± 0.71	59.5 ± 3.11	59.25 ± 3.30
	2nd phalanx	38.0 ± 0.00	38.0 ± 0.00	37.0 ± 1.41	37.0 ± 1.41	37.5 ± 1.00	37.5 ± 1.00
	3rd phalanx	54.0 ± 0.00	54.0 ± 0.00	53.0 ± 0.00	53.50 ± 0.71	53.50 ± 0.58	53.75 ± 0.50
Digit IV	1st phalanx	58.0 ± 1.41	57.50 ± 0.71	53.50 ± 2.12	53.0 ± 2.83	55.75 ± 2.99	55.25 ± 3.10
	2nd phalanx	29.00 ± 0.00	29.00 ± 0.00	27.50 ± 0.71	26.50 ± 0.71	28.25 ± 0.96	27.75 ± 1.50
	3rd phalanx	30.0 ± 0.00	30.0 ± 0.00	30.0 ± 0.00	30.5 ± 0.71	30.0 ± 0.00	30.25 ± 0.50
Digit V	1st phalanx	57.0 ± 1.41	57.0 ± 1.41	54.0 ± 1.41	54.0 ± 1.41	55.5 ± 2.08	55.5 ± 2.08
	2nd phalanx	28.0 ± 1.41	28.0 ± 1.41	26.0 ± 1.41	26.5 ± 2.12	27.0 ± 1.63	27.25 ± 1.71
	3rd phalanx	27.5 ± 0.71	27.5 ± 0.71	27.0 ± 1.41	27.0 ± 1.41	27.25 ± 0.96	27.25 ± 0.96

Table 2: Linear measurements of the hindlimb digits of the *E. helvum* (in millimetres)

	Male (n = 5)		Female (n = 10)		Total (n = 15)	
	Right	Left	Right	Left	Right	Left
Digit I	13.5 ± 0.71	13.5 ± 0.71	13.5 ± 0.71	13.5 ± 0.71	13.5 ± 0.58	13.5 ± 0.58
Digit II	17.0 ± 0.00	17.0 ± 0.00	16.0 ± 0.00	16.0 ± 0.00	16.5 ± 0.58	16.5 ± 0.58
Digit III	16.5 ± 0.71	16.5 ± 0.71	15.0 ± 0.00	15.0 ± 0.00	15.75 ± 0.96	15.75 ± 0.96
Digit IV	15.5 ± 0.71	15.5 ± 0.71	16.0 ± 0.00	16.0 ± 0.00	15.75 ± 0.50	15.75 ± 0.50
Digit V	14.0 ± 0.00	14.0 ± 0.00	13.0 ± 0.00	13.0 ± 0.00	13.5 ± 0.58	13.5 ± 0.58

means ± SD of 5 rats per group

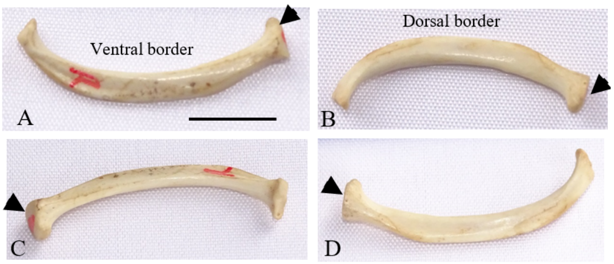

Fig. 1: Right clavicle of the *E. helvum*. A – cranial surface, B – caudo-ventral surface, C – cranio-ventral, D – caudo-dorsal. Arrows indicate the acromial end, while the opposite end is the sternal end. Scale bar – 1 cm.

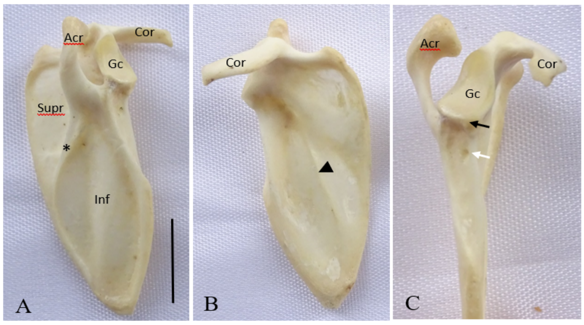

Fig. 2: Right scapula of *E. helvum*. A – lateral surface, B – medial/costal surface, C – proximal aspect of the cranial border. Gc – glenoid cavity; Acr – acromion; Cor – coracoid process; Supr – supraspinous fossa; Infra – infraspinous fossa; * - scapular spine; black arrowhead – subscapular ridge; black arrow – subglenoid tubercle; white arrow – subglenoid foramen.
Scale bar – 1 cm (A & B) and 0.8 cm (C).

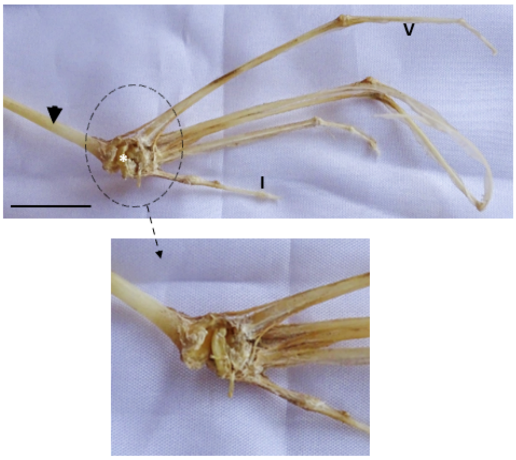

Fig. 5: Right manus of the *E. helvum*, palmar surface. Lower picture shows magnification of region in black circle in the upper one. I – first digit, V – fifth digit, * – carpal bone, black arrowhead – ulna. Scale bar – 2 cm.

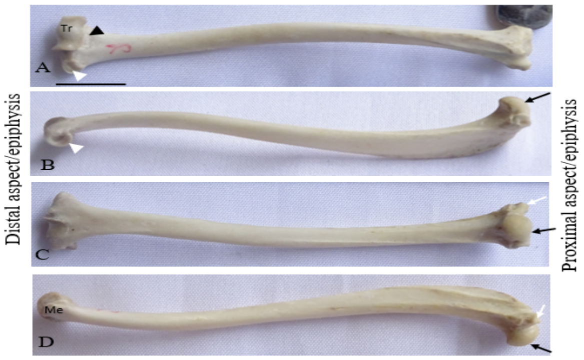

Fig. 3: Right humerus of *E. helvum*. A – cranial view, B – lateral view, C – caudal view, D – medial view. Black arrow indicates head of humerus, white arrow – greater tubercle, black arrowhead – coronoid fossa, white arrowhead – lateral epicondyle, Me – medial epicondyle, Tr – trochlear. Scale bar – 1 cm for all views.

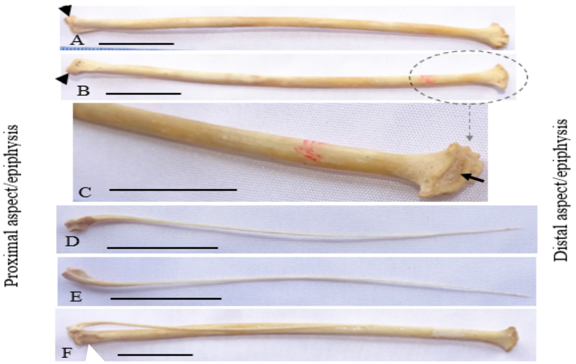

Fig. 4: Right ulna (A) and radius (D) of the *E. helvum*. A – medial surface of the ulna, B – caudolateral surface of the ulna bone, C – magnification of the distal aspect of 'B' (the distal epiphysis), showing the notch for articulation of the carpal bones (black arrow), D – medial surface of radius, E – lateral surface of radius, F – left radius and ulna. Black arrowhead – articular surface for head of radius, white arrow – trochlear notch. Scale bar – 2 cm.

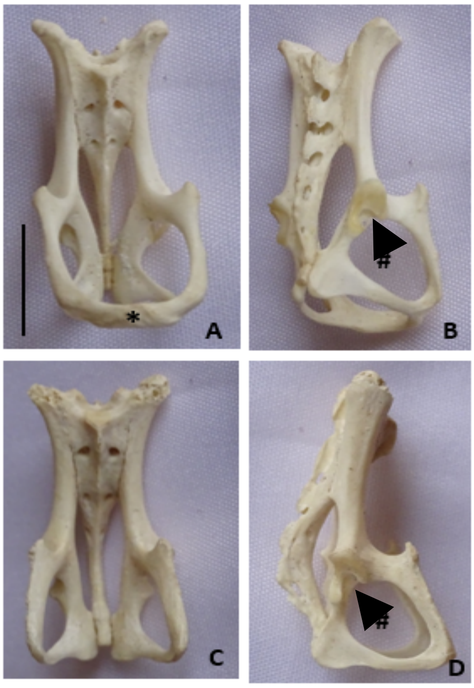

Fig. 6: Os coxae of the male (A & B) and female (C & D) *E. helvum*, showing the ventral (A & C) and lateral (B & D) views. Note the separate pubic bones in the females, relative to the fused ones in the male (*), and also the difference in shape of the obturator foramen (#). The acetabular notch (arrowhead) is visible in both sexes. Scale bar – 1 cm, same across all figures.

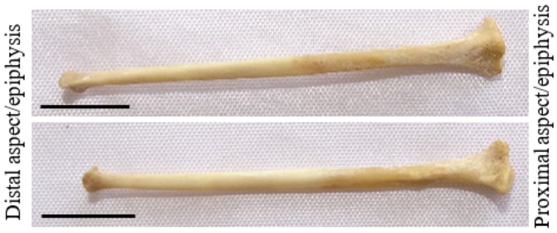

Fig. 7: Right femur of the female *E. helvum*, showing the caudal (upper picture) and cranial (lower picture) views. The head of the femur is depicted by an arrowhead. Scale bar – 1 cm, same for both figures.

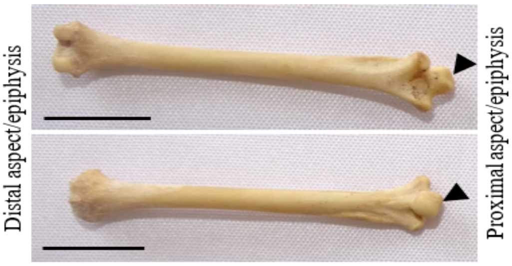

Fig. 8: Right tibia of the female *E. helvum*, showing the cranial (upper picture) and caudal (lower picture) views. Scale bar – 1 cm, same for both figures.

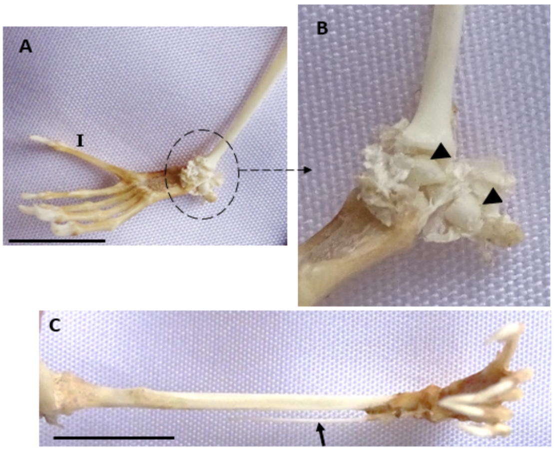

Fig. 9: Right hind digits (palmar surface) of the female *E. helvum*. In ‘A’, digit I is depicted with I, while the circled region is magnified in ‘B’, to show the two observable tarsal bones (arrowheads). The fibula (arrow) is shown in ‘C’. Scale bar – 1 cm.

DISCUSSION

Careful electronic search using Google and Pubmed search engines, at the time of commencement of this study and at the time of manuscript submission, did not show previous documentation on morphometrics of the limbs of the *Eidolon helvum.* This is probably the first report of such in this species. This study was a continuation of the previous studies on the gross osteology of the *Eidolon helvum* (Igado and Ade-Julius, 2018; Igado and Joannis, 2022).

Morphometrics

Morphometric values could not be compared to other similarly sized bats due to unavailability. The morphometric values which, were higher in the males could be a function of the bigger body size and weight observed in the fresh specimens (Igado *et al.*, 2012). The asymmetry observed between the values for the left and right specimens is consistent with previous reports of asymmetry on measurements of the left and right sides (Getty, 1975; Blackwood *et al.*, 2010; Igado *et al.*, 2012)

Forelimb

Wingspan: similar to results obtained (Balthazary *et al.*, 2007), the males had statistically significantly wider wingspans relative to the females. Results obtained in this study were lower than that observed in *E helvum* by Balthazary et al. (Balthazary *et al.*, 2007).

Clavicle: The clavicle is a horizontally placed tubular bone, connecting the forelimb to the axial skeleton. In avian, the two clavicles are seen as slender rod-like bones, ventrally fused into a flattened plate called the hypocleidium (Getty, 1975; Singh, 2017). Relative to that of the colugo, a gliding and leaping mammal, although not flying (Panyutina *et al.*, 2015), the clavicle of the *E. helvum* was more curved and appeared to have more ridges, making it more similar to humans in this regard.

The clavicle, although present in avian, is not always present in all animals, as it is reduced to a fibrous intersection in the brachiocephalicus. In the dog, it is seen as a nubbin of bone, while in the cat as a slender rodlet. In equines and ruminants, it is absent or rudimentary. Because the clavicle is rudimentary/vestigial, it can be misinterpreted in radiographs (Singh, 2017).

In humans, the clavicles are ‘f’ shaped and articulate medially with the manubrium to form the sternoclavicular joint, laterally with the acromion of the scapula to form the acromioclavicular joint (Kumar *et al.*, 1989).

In comparison with other animals, the clavicle of the *E helvum* was most similar to that of humans in being bilaterally flattened but had a more sickle shape unlike the 'f' or slightly ‘s’ shape observed in humans (Abrahams *et al.*, 1998; Rohen *et al.*, 1998; Netter, 2006).

Scapula: The scapula is a flat, roughly triangular-shaped bone in mammals. It is the basis of the shoulder region (Singh, 2017). In avian, the scapula is a flattened blade-like bone, unlike the triangular shape seen in mammals generally (Getty, 1975; Singh, 2017). The scapula shape is also observed in neotropical bats (Sánchez and Carrizo, 2021). This observed shape in the *E helvum* and the neotropical bats is strikingly similar to that of humans, with the arrangement of the acromion and coracoid. Scapular diagrams by Sánchez and Carrizo (2021), were pencil drawings of the lateral aspect and did not show the presence or location of any foramina. The limited comparisons (e.g. positions of the spine, glenoid fossa and acromion) that could be made from the diagrams nevertheless showed similarities between the 2 groups of bats. It is however worth mentioning, that despite the similarity in shape to the human scapula, differences observed include: i) a relatively more shortened distance between the superior angle and the supraglenoid tubercle, ii) the curvature from the superior angle to the spine was far straighter in the bat, giving the caudal border a far “straighter” appearance. This gave the scapula roughly the appearance of an isosceles triangle, with the superior border being the base. An infraglenoid tubercle was observed, similar to that seen in humans, but could not be ascertained from pictorial diagrams from other bats. The presence of a foramen (Fig. 2C) in the sub-glenoid space was however not present in humans and other animals assessed. This foramen was consistently present in all subjects examined, both male and female. The foramen serves as a passage for blood vessels which supply the shoulder region. Because this is the first report, the authors venture the name ***Sub-glenoid foramen of Igado in the Eidolon helvum***.

The scapular has two surfaces – the medial (coastal) and lateral surfaces. The lateral surface has a prominent ridge in all domestic animals and humans, but the coastal surface is without any ridge (Getty, 1975; Abrahams *et al.*, 1998; Rohen *et al.*, 1998; Netter, 2006; Singh, 2017). The costal surface of the scapula in this study showed a very distinct ridge/spine (Fig. 2B), unlike any report in other animals.

This is to the best of our knowledge, the first report of this subscapular spine. Therefore, the authors venture the name: *Subscapular spine of Igado in the Eidolon helvum*.

Humerus: This was one of the longest bones in the *E. helvum*, forming the skeleton of the arm. Similar to pictorial reports in other animals – humans, domestic and livestock animals and even the colugo (Popesko, 1977; Popesko *et al.*, 1990; Abrahams *et al.*, 1998; Rohen *et al.*, 1998; Netter, 2006; Panyutina *et al.*, 2015; Singh, 2017), the humerus was the stockiest bone, thicker than the other long bones. The shape was similar to that of the colugo, being slightly curved, with a prominent and long tubercle (*crista tuberculi minoris*) (Panyutina *et al.*, 2015) on the caudal surface of the proximal one-third. For quadrupeds, the humerus is a weight-bearing bone, which probably accounts for its thickness and strength. However, bats being birds of flight may require a stocky humerus to support some of the flight muscles, since bats are known to travel over long distances (Richter and Cumming, 2006). The ridges observed on the humerus are also probably meant for the attachment of the muscles. The caudally placed head was similar to that observed in humans.

Ulna and Radius: The olecranon process of the ulna was not as prominent as observed in other animal species. A trochlear notch was however present for the articulation of the distal part of the humerus. Differences in the length of the radius relative to the ulna, and also the extent of fusion have been documented in many animal species – humans (both separate and roughly the same length), dogs (slightly shorter radius, attached by interosseous ligaments), swine (slightly shorter radius, attached throughout whole length by interosseous ligaments), ruminants (shorter radius, fused except at 2 points), equine (larger radius, fused to ulna), chicken (2 separate bones, large interosseous space) (Getty, 1975; Singh, 2017). In this study, the radius was a very fragile bone of about two-thirds the length of the ulna and attached by interosseous ligaments which were not visible after maceration.

Carpus: The arrangement of this joint in two rows, is similar to previous reports in other mammals. The number of bones in each row however differed from reports observed in humans, swine, dogs, ruminants and even the colugo (Getty, 1975; Rohen *et al.*, 1998; Netter, 2006; Panyutina *et al.*, 2015; Singh, 2017).

Metacarpal: This forms the palm in humans. In animals, these bones are generally flattened in the dorso-palmar direction (Singh, 2017). However, this part of the forelimb was not observable in the *E. helvum*, unlike reports in other mammals.

Digits of the forelimb: The 5 digits and 3 phalanges per digit are similar to that observed in some animals, and also in humans, except for the shortest digit (I) which had 2 phalanges. This first digit was the shortest and most medially placed, being similar to the thumb, which is normally used for grasping in humans. The considerably longer lengths of the digits on the forelimb relative to that of the hindlimb are probably due to the function as an organ of flight, supported by the webbing of the digits.

Pelvic limb

Os coxae (ossa coxarum): This was the only bone that showed sexual dimorphism. The os coxae is also called the hip bone. It articulates distally with the femur, and proximally with the sacrum of the vertebral column (Singh, 2017). The non-closure of the pubic symphysis is similar to that observed in some rodents(Tavares and Pessôa, 2022), and previously reported in the *E helvum* (Nwoha, 2000). The sex differences observed in the shape of the *E helvum* obturator foramen are quite similar to those observed in humans

(Abrahams *et al.*, 1998; Rohen *et al.*, 1998; Netter, 2006).

Femur: The femur is a strong bone and the longest of the long bones as observed in mammals (Getty, 1975; Abrahams *et al.*, 1998; Rohen *et al.*, 1998; Netter, 2006; Singh, 2017). This however is not the same as observed in this study. Although the femur was quite strong, it was roughly half to a third in length of the humerus, radius and ulna, in length. It was observed that the bones of the hindlimb were shorter than those of the forelimb. This could be an adaptive feature, as the limbs are mainly used to support when roosting while the forelimbs are employed when flying. This will also account for the very well-developed muscles of the pectoral region and arms. Although great care was exercised to preserve all the bones, it is worth mentioning that the absence of a patella, though not likely, may be due to the maceration process. This absence was observed in all specimens examined.

Tibia and fibula: The tibia was observed to be longer than the femur, a normally unusual occurrence in mammals, but not an uncommon feature in corresponding bones in birds, as seen by pictorial depictions (Getty, 1975; Singh, 2017). Further studies will highlight the similarities in osteology of the *E helvum* to flying birds.

Tarsus: This is also known as the ankle joint. It articulates proximally with the tibia, and distally with the metatarsal. A varying number of bones making up this joint has been reported in different species of animals

Digits: Similar to humans and other animals, digits were observed, with 3 phalanges per digit. The digits are used for grasping and also for balancing. These functions are very readily observed in the bats when roosting.

CONCLUSIONS

Osteological studies in wildlife remain an important aspect of wildlife care, due to the increasing interest and focus on wildlife. The skeleton serves to protect vital organs and also serves as a landmark for locating different structures. This report highlights the peculiarities of the skeleton of the *Eidolon helvum*, like the absence of the metacarpal bones, and the sexual dimorphism observed in the pelvic bones. Results obtained from this study will find application in basic anatomy, forensic science, anthropology and archaeology, and surgical manoeuvres.

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Conflict of Interest

The authors declare that there is no conflict of interest.

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