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Musculoskeletal structure of the shoulder and arm in large flying fox (*Pteropus vampyrus*)

DANANG DWI CAHYADI, NURHIDAYAT♥, CHAIRUN NISA', SUPRATIKNO, SAVITRI NOVELINA, HERU SETIJANTO, SRIHADI AGUNGPRIYONO

Division of Anatomy Histology and Embryology, School of Veterinary Medicine and Biomedical Sciences, Institut Pertanian Bogor. Jl. Agatis, Kampus IPB Dramaga, Bogor 16680, West Java, Indonesia. Tel./fax.: +62-251-8629462, ♥email: nhdayat@apps.ipb.ac.id

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Abstract. *Cahyadi DD, Nurhidayat, Nisa' C, Supratikno, Novelina S, Setijanto H, Agungpriyono S. 2022. Musculoskeletal structure of the shoulder and arm in large flying fox (*Pteropus vampyrus*). Biodiversitas 23: 5902-5913.* The flight activity of bats is the most energy-consuming activity compared to other locomotion activities. The anatomical characteristic of its musculoskeletal system is believed to play important role in their flight ability. The present study aimed to describe the musculoskeletal morphology of the shoulder, arms, and wing of the large flying fox (*Pteropus vampyrus*). In this study, the parameters used are observing the specific body parts of the shoulder and arm skeletons and muscles, comparing skeletons and muscles of the other species of bats and related literature. The arm and wing skeleton of the large flying fox were relatively simple, lengthened, and flexible at the distal end of the distalmost phalanx, demonstrating the flexibility of a flying fox's arm and wing during flight. The muscles involved in flying movement that moved the wings, either in adduction or in abduction. The muscles that play a role in the wing adduction phase of the large flying fox are *musculi* (*mm.*) *pectorales, musculus* (*m.*) *serratus ventralis thoracis, m. clavodeltoideus*, and *m. biceps brachii caput coracoideus*. Conversely, the wing abduction phase is played by several main muscles, such as *m. clavotrapezius, m. acromiotrapezius, m. latissimus dorsi, m. teres major, m. acromiodeltoideus, m. spinodeltoideus, m. triceps brachii caput laterale,* and *m. triceps brachii caput longum.* Briefly, the musculoskeletal characteristics of the shoulder and arms of the large flying fox are suggested as morphological adaptation to allow free shoulder area movement, reduce the body mass, and resist the large torsional stress in the wing.

Keywords: Kalong, morphology, musculoskeletal, *Pteropus vampyrus,* shoulder, wing

INTRODUCTION

Flying animals have distinctive characteristics in their anatomy, physiology, and behavior. Only certain animals have active flight ability; they are some species of insects, flying birds, and bats. Bat (order Chiroptera) is the only flying mammal and it has been known that this animal could become a reservoir of various types of viruses that are the source of infectious diseases. Previous studies reported some bat-associated viruses such as Hendra virus (Edson et al. 2015), Nipah virus (Sendow et al. 2013; Islam et al. 2016), rabies virus (de Thoisy et al. 2016; Kunkel et al. 2022), and Australian bat lyssavirus (Field 2018). Our research group also reported the infection of Pteropine orthoreovirus in the flying fox (Takemae et al. 2018). The flight ability has also made this animal play an important role in the seed dispersal and pollination of plant species (Walldorf and Mehlhorn 2014; Sheherazade et al. 2019; Aziz et al. 2021). The order Chiroptera has two suborders in the latest classification, Yinpterochiroptera and Yangochiroptera (Lei and Dong 2016). Morphological differences can be found among flying fox species, both within the same or different orders although they generally look the same (Norberg 1972).

One of the bat species from the family Pteropodidae (suborder Yinpterochiroptera) that is commonly found in many areas in Southeast Asian regions, is the large flying fox (*Pteropus vampyrus*). These bats are widely distributed in the Malay Peninsula, Philipines, and some islands in Indonesia such as Sumatera, Bangka, Mentawai, Java, Timor, Kalimantan, and Natuna Islands (Wilson and Mittermeier 2019). The International Union for Conservation of Nature (IUCN) notes that the trend of the population of the large flying fox is declining and that it is on the list of endangered species (Bates et al. 2008).

Bat as a flying mammal has different musculoskeletal systems compared to that of bird species. One of the characteristics of bird wings is the presence of feathers arranged in a way that forms wings, while bat wings are composed of four elongated digital bones that strengthen the wing membrane or *patagium*, a special dermal structure developed in the shoulder, lateral of the body, interfemoral, and interdigital parts (Kovalyova 2014; Walldorf and Mehlhorn 2014). It is known that this animal can fly for a long distance as reported in some previous studies (Oleksy et al. 2015; Hengjan et al. 2018; Oleksy et al. 2019). Such ability is believed to be supported by both morphological and physiological factors. Flying with high-speed flapping flight characteristic requires the highest energy cost, compared to other locomotor activities, such as running and swimming (Bale et al. 2014; Alerstam and Bäckman 2018). It is necessary to understand both morphological and physiological aspects of the large flying fox that are thought to support its flight ability. Our research group previously revealed the relatively higher number of total erythrocytes, hemoglobin concentration, and hematocrit value of the Indonesian short-nosed fruit bat (*Cynopterus titthaecheilus*) and the large flying foxes (*P. vampyrus*) compared to that of terrestrial mammals, demonstrating the physiological characteristics required for the flying activity (Rahma et al. 2017; Cahyadi et al. 2018). However, information about the musculoskeletal structure of the large flying fox is still limited. Several bat musculoskeletal studies have been conducted on the Egyptian fruit bat, *Rousettus aegyptiacus*, Jamaican fruit bat, *Artibeus jamaicensis* and the Indian flying fox, *Pteropus giganteus* (Shil et al. 2013). Therefore, the present study was carried out to obtain information that could support other research related to its behavior as a flying mammal. This study aimed to analyze the musculoskeletal anatomy of the shoulders and arms that support the flight ability of the large flying fox. The results are expected to provide new information related to the morphology of the large flying fox, especially regarding the anatomical structure of its flight muscles.

MATERIALS AND METHODS

Animals

This study used two adult male large flying foxes to analyze the muscles and skeletons, mainly in the shoulder, arms, and wing regions. Animals used in the present study were taken from Leuweung Sancang conservation area, Garut, West Java, Indonesia. The large flying fox specimens were obtained from the samples used in the research project hosted by the Faculty of Veterinary Medicine, Institut Pertanian Bogor entitled Science and Technology Research Partnership for Sustainable Development (SATREPS) Project on Ecological Studies on Flying Foxes and Their Involvement in Rabies-related and Other Viral Infectious Diseases. Flying foxes were caught with a permit from the Directorate General of Natural Resources and Ecosystem Conservation, Ministry of Environment and Forestry of the Republic of Indonesia (Decree No. 211/KSDAE/SET/KSA.2/7/2016). Ethical approval for this study was obtained from Animal Care and Use Committee, Institute for Research and Community Services, Institut Pertanian Bogor (Approval No. 59-2017 IPB). A chemical immobilization procedure was carried out using a combination of intramuscular ketamine 10% and xylazine 2% with a dose of each was 10 and 2 mg/kg of the body weight (Heard 2014).

Musculoskeletal specimens' preparation and observation

Preparation of the shoulder, arms, and digital skeleton of the large flying fox started by removing any muscles and connective tissues from those bones using a scalpel. The bones free from any muscles were then air-dried. The observation was performed on the shoulder girdle bones (*scapula* and *clavicula*), upper arm bones (*humerus*), forearm bones (*radius* and *ulna*), and wing bones (*ossa carpi, ossa metacarpalia, ossa digitorum manus*). The shoulder girdle, upper arm, and forearm muscle groups of the different specimens were dissected carefully and identified. Both skeletal and muscular findings were compared to the results published in other bats and mammal species in general. Furthermore, the nomenclature of the bones and muscles referred to a study conducted by Norberg (1972) and *Nomina Anatomica Veterinaria* (ICVGAN 2017). Images of the bones and muscle specimens were captured using a digital camera and then clear illustrations were created. All the observation results were analyzed descriptively and presented in the form of figures.

RESULTS AND DISCUSSION

Skeletal structure

Thoracic girdle (cingulum membri thoracici)

The thoracic or shoulder girdle in the large flying fox is formed by the *scapula* and *clavicula*. The *scapula* is located in the dorsal area of the body, has a triangular shape, craniocaudad elongation, and has a *spina scapulae* that is curving craniolaterad. This bone has three edges namely *margo cranialis*, *margo lateralis*, as well as *margo vertebralis*. *Margo vertebralis* and *margo lateralis* form an angle in the caudal part of *scapula*, while *margo vertebralis* and *margo cranialis* create a curved edge (Figure 1A-D).

In the large flying fox, *fossa infraspinata* has about two times wider in size compared to *fossa supraspinata* and is separated by *spina scapulae* (Figure 1A) which crosses the *scapula* craniolaterally and ends in the caudal of *cavitas glenoidalis*. This cavity has joint surfaces that are relatively elongated to the craniocaudal axis (Figures 1C and 1D). *Spina scapulae* in this animal is relatively not well-developed, but it has a curved and well-developed process, *acromion*. This process has joint surfaces, *facies articularis,* connected with *extremitas acromialis* of *clavicula*. Besides, there is a very well-developed *processus coracoideus*, curving ventrolaterally. *Fossa subscapularis* is located in *facies costalis*, a surface facing *costae* (Figure 1B). *Clavicula* has a simple curved shape, convex in *margo cranialis* and concave in *margo caudalis* (Figures 1E and 1F). This bone had a length that could reach 4.2 cm. The distal end of *clavicula* (*extremitas acromialis*) is connected with the *acromion* of the *scapula*, while the proximal end (*extremitas sternalis*) is connected with the *sternum*.

Upper and forearm bones (skeleton brachii et antebrachii)

The upper arm bone, *humerus*, in the large flying fox is cylindrical and long in size, reaching 14.5 cm. This bone shaft is double curved, convex toward cranial in the proximal and concave in the distal. This bone has a narrow craniocaudad in its distal part (Figures 2A, 2B and 2C). Well-developed *crista pectoralis* can be observed in the proximolateral aspect. *Caput humeri* is located at the proximal end of the bone, in the form of a large-rounded prominence with a wide articular surface. This hemispherical surface is connected with the *cavitas glenoidalis* of the *scapula*.

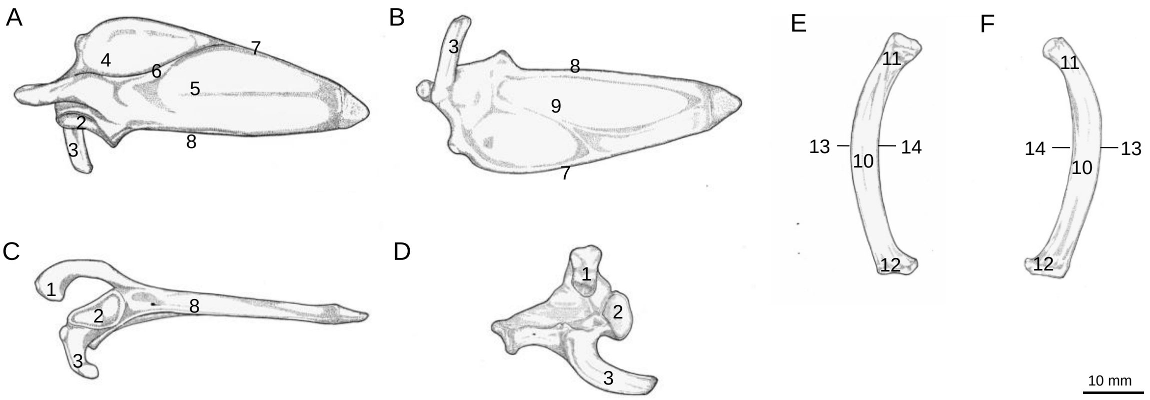

Figure 1. Left *scapula* and *clavicula* of the large flying fox. A. dorsal; B. ventral; C. lateral; D. cranial view of the *scapula*; E. lateral; F. medial view of the *clavicula.* 1. *acromion*; 2. *cavitas glenoidalis*; 3. *processus coracoideus*; 4. *fossa supraspinata*; 5. *fossa infraspinata*; 6. *spina scapulae*; 7. *margo vertebralis;* 8. *margo lateralis*; 9. *fossa subscapularis*; 10. *corpus clavicula*; 11. *extremitas acromialis*; 12. *extremitas sternalis*; 13. *margo cranialis*; 14. *margo caudalis*

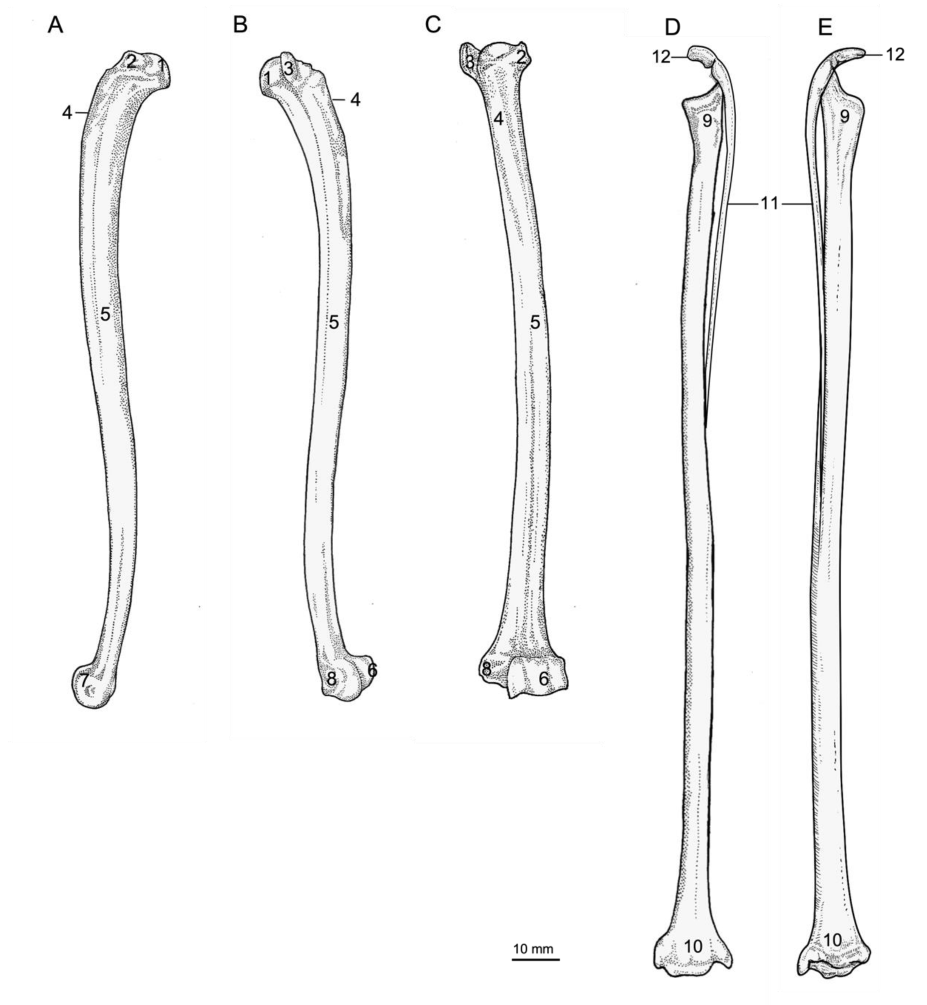

Figure 2. Left *humerus* and *radius-ulna* of the large flying fox. A. dorsal; B. ventral; C. cranial view of the *humerus*; D. dorsal; and E. ventral view of the *radius-ulna.* 1. *caput humeri*; 2. *tuberculum majus*; 3. *tuberculum minus*; 4. *crista pectoralis;* 5. *corpus humeri*; 6. *condylus humeri;* 7. *epicondylus lateralis;* 8. *epicondylus medialis;* 9. *extremitas proximalis;* 10. *extremitas distalis;* 11. *ulna;* 12. *os sesamoideum*

There are two smaller tubercles in the proximal epiphysis, namely *tuberculum majus* on the dorsal and *tuberculum minus* on the ventral. *Sulcus musculi brachialis* of this bone is not as distinct as that in quadrupedal mammals. At the distal end of the *humerus,* at the lateral portion, there is *condylus humeri* which has an articular surface (*trochlea humeri*) with *radius* and *ulna* forming the elbow. In addition, the *epicondylus medialis* in this animal was very prominent.

The forearm bone consists of *radius* and *ulna* (Figures 2D and 2E). The *radius* is the longest bone of the large flying fox skeleton, with a length reaching 19.7 cm. This bone has a larger size compared to the *ulna* and becomes the major bone in the *antebrachium.* On the ventral, in the proximal of the *radius*, there is a shallow groove that serves as a place for the muscle tendon of *m. biceps brachii* to interlock. The *ulna* is a very thin bone, about half of the length of the proximal in the caudal aspect of the *radius*. In addition, in the proximal of the *ulna*, there is a small sesamoid bone fixed by ligaments.

Wing bone (skeleton manus)

Wing bone consists of *ossa carpi*, *ossa metacarpalia*, and *ossa digitorum manus*. *Ossa carpi* in the large flying fox comprises eight small and irregular-shaped bones (Figure 3). *Ossa carpi* in this animal consists of *os lunare* (the largest bone directly connected with *radius*), *os scaphoid, os cuneiform*, *os trapezium*, *os trapezoid*, *os magnum*, *os unciform,* and *os pisiform*. Large flying fox has five *ossa metacarpalia* with the longest one was 14.7 cm in *os metacarpale V* (Figure 4). *Ossa digitorum manus* are relatively long, with the length of the third digit reached 26.5 cm. Each digit has two *phalanges*, except the second digit which has three *phalanges*. The last *phalanx* in the first and second digits are covered by claws. The end of *phalanx II* in digits *III, IV,* and *V* are thin and flexible.

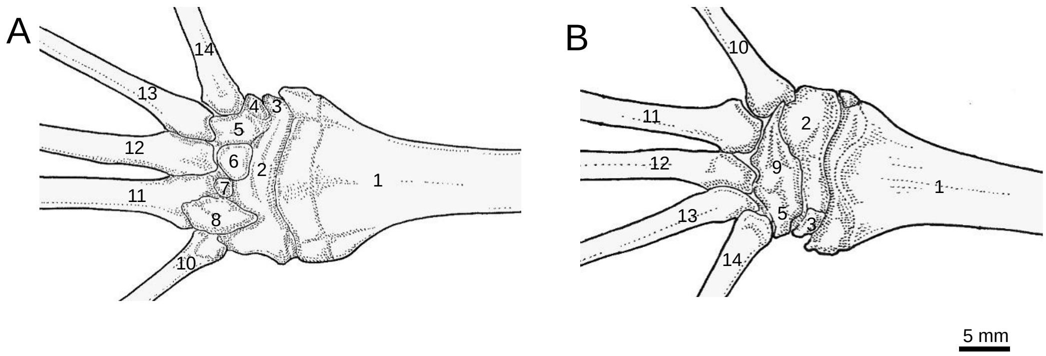

Figure 3. Right carpal joint of the large flying fox. A. dorsal and B. ventral view of the carpal joint. 1. *radius;* 2. *os lunare*; 3. *os cuneiform;* 4. *os pisiform;* 5. *os unciform;* 6. *os scaphoid;* 7. *os trapezoid;* 8. *os trapezium;* 9. *os magnum;* and 10-14. *ossa metacarpalia I-V*

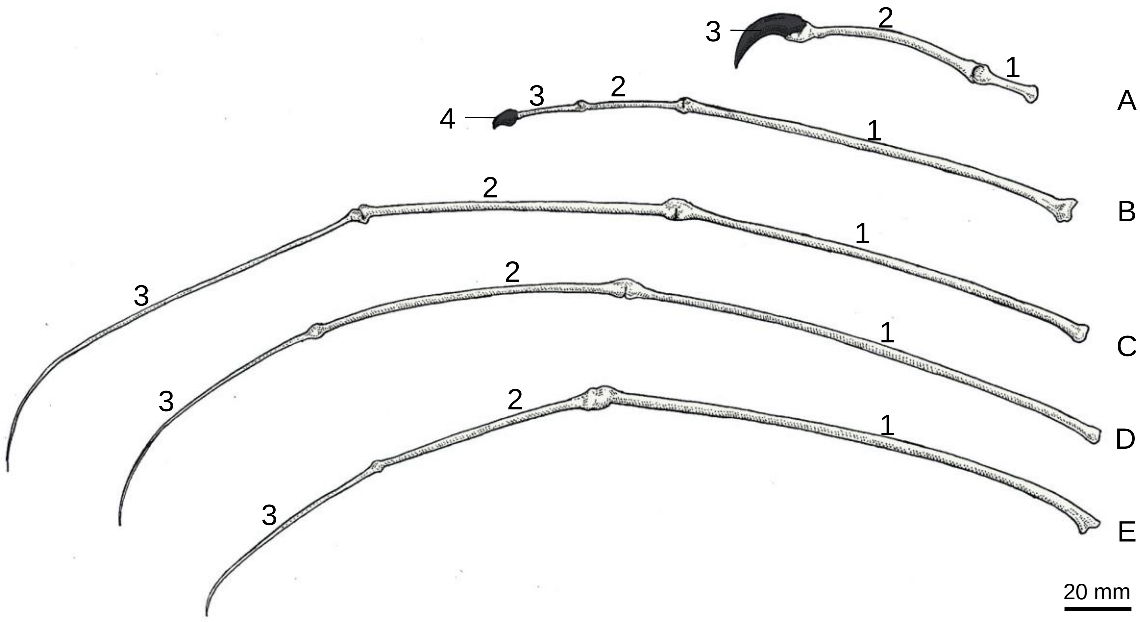

Figure 4. Left metacarpal and digital bones of the large flying fox. A. digit I; B. digit II; C. digit III; D. digit IV; E. digit V. 1. *ossa metacarpalia;* 2. *phalanx I*; 3. *phalanx II;* 4. *phalanx III*

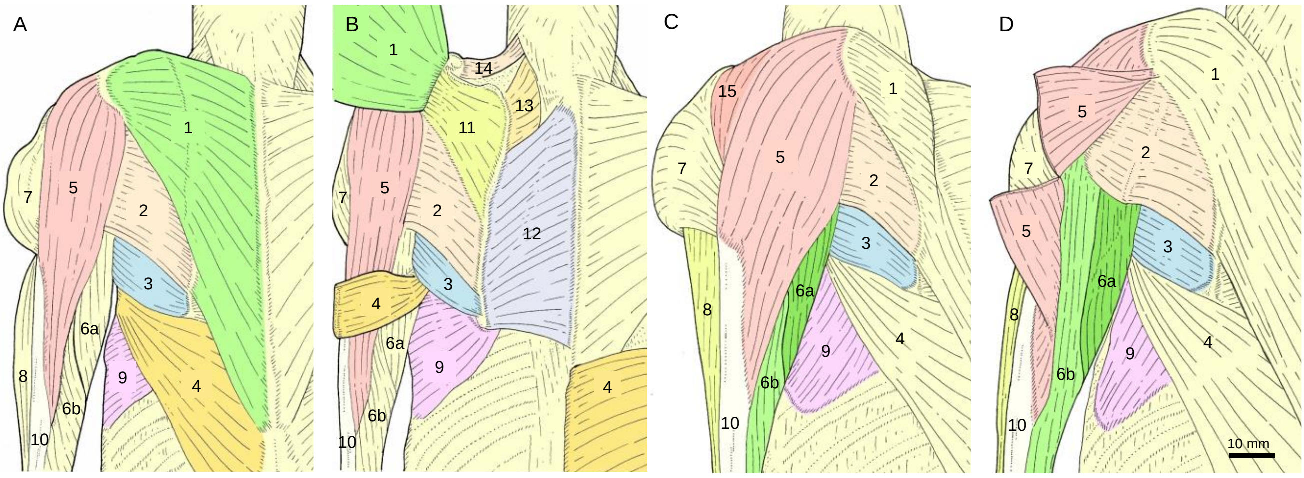

Figure 5. Back, shoulder girdle, and lateral upper arm muscles of the large flying fox. A. dorsal view; B. dorsal view after removal the *m. trapezius* and *m. latissimus dorsi*; C. laterodorsal view; D. laterodorsal view after removal the *m. acromiodeltoideus*. 1. *m. trapezius;* 2. *m. spinodeltoideus*; 3. *m. teres major;* 4. *m. latissimus dorsi;* 5. *m. acromiodeltoideus; 6. m. triceps brachii* (a. *caput longum;* b. *caput laterale*)*;* 7. *m. pectoralis pars caudalis*; 8. *m. biceps brachii*; 9. *m. serratus ventralis pars caudalis*; 10. *humerus*; 11. *m. supraspinatus*; 12. *m. rhomboideus;* 13. *m. levator scapulae*; 14. *m. omocervicalis;* 15. *m. clavodeltoideus*

Muscular structure

Back muscles (musculi dorsi) connected to the shoulders

Certain back muscles have insertions in the shoulder region, particularly in the *scapula* and *humerus*. *Musculus* (*m.*) *trapezius*, *m. latissimus dorsi*, and *m. rhomboideus* are some back muscles connected with the shoulder region (Figure 5). ***Musculus trapezius*** of the large flying fox is a triangular-shaped superficial muscle, located on the dorsal side of the body (Figure 5A). This muscle consists of two parts named according to its location, *m. clavotrapezius* and *m. acromiotrapezius*. *Musculus clavotrapezius* originates in the ligament that lies dorsally from the *vertebrae cervicales VI* to the *vertebrae thoracicae II* and is connected to the ligament that connects the *scapula* and *clavicula*. In addition, this muscle is attached to the cranial part of the distal third of the *clavicula* and the cranial surface of the origin of the *m. acromiodeltoideus* and *m. clavodeltoideus*. Another part of the *m. trapezius* in the large flying fox is *m. acromiotrapezius*, which arises from the midline of the vertebrae in the *vertebrae thoracicae III-XII*. The insertion of this muscle is on the cranial surface and the medial of *processus acromialis*. This muscle also attaches to the transverse ligament of the *scapula*, and caudally to the *margo vertebralis* of the *scapula*. We found that both parts of the muscle are not clearly separated in the large flying fox.

Musculus latissimus dorsi is a long muscle that has a wide region of insertion, starting from the *processus spinosus* of the *vertebrae thoracicae X* to the *vertebrae lumbales V*. This muscle runs from the dorsal of the body to the cranial and inserts in the proximal part of the *tuberculum minus*, on the ventral side of the *humerus* (Figure 5A).

Musculus rhomboideus is made fully observable after removing the *m. trapezius* (Figure 5B). This muscle lies from the dorsal ligaments from the *vertebrae cervicales VII* to the *vertebrae thoracicae III* and in the *processus spinosus* of the *vertebrae thoracicae IV-IX*. This muscle has a strong insertion in the caudal two-thirds of the *margo vertebralis* to the caudal end of the *scapula*.

Pectoral muscles (musculi thoracis)

We observed the very well-developed pectoral muscles in the large flying fox. An extremely wide and thick muscle, ***m. pectoralis pars caudalis*** is located in the superficial region (Figure 6). The origin of this muscle is in the manubrium and body of the sternum, as well as in the ligament that connects the two projections of the *carinae* and the *crista ventralis* of the sternum. This muscle inserts on the ventral and craniodorsal surfaces of the *crista pectoralis* of the *humerus*. *Musculus pectoralis pars cranialis* and the *m. subclavius* could be seen after removing the caudal part of *m. pectoralis*.

Musculus pectoralis pars cranialis arises from the ventrolateral surface of the *clavicula* and inserts on the cranial side of the *crista pectoralis* of the *humerus*, at the proximal part. ***Musculus subclavius*** lies from the lateroventral surface of the *os costale II* and attaches to the *margo caudalis* of the *clavicula*. Another pectoral muscle, ***m. pectoralis abdominalis***, a band-like muscle was observed, runs from the abdominal fascia, and inserts on the ventral side of the *crista pectoralis* of the *humerus.*

Muscles of the shoulder region

The superficial layers of shoulder muscle are *m. acromiodeltoideus* and *m.spinodeltoideus* (Figures 5 and 6). ***Musculus acromiodeltoideus*** is a thick and long muscle, that runs from the lateral surface of the *acromion* of the *scapula* and the cranial third of the transverse ligament of the *scapula*. This muscle inserts on the dorsal surface of the *crista pectoralis* of the *humerus*, on the caudodorsal surface of the *corpus humeri*, and has an aponeurosis that attaches to the fascia of *m. triceps brachii caput laterale*.

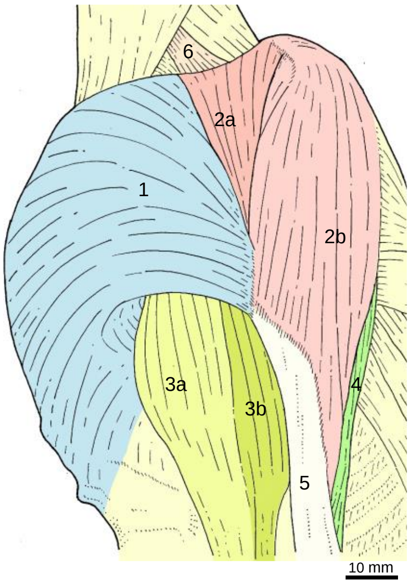

Figure 6. Superficial layer of the pectoral and upper arm muscles of the large flying fox in lateral view. 1. *m. pectoralis pars caudalis;* 2a. *m. clavodeltoideus;* 2b. *m. acromiodeltoideus*; 3. *m. biceps brachii* (a. *caput glenoidalis;* b. *caput coracoideus*); 4. *m. triceps brachii;* 5. *humerus;* 6. *m. omocervicalis*

The profundal muscles layer of the shoulder region, including *m. supraspinatus*, *m. infraspinatus*, *m. teres major*, *m. omocervicalis*, and *m. levator scapulae* could be observed by reflecting the back muscles and *m. acromiodeltoideus* (Figures 5B and 5D). Another muscle seen in the cranial part of the shoulder is *m. clavodeltoideus* (Figures 5C and 6).

Musculus spinodeltoideus runs from the lateral surface of the caudal half of the *spina scapulae*, the transverse ligament of the *scapula*, and the dorsolateral surface of the caudal part of *margo vertebralis* of the *spina scapulae*. This muscle inserts on the caudal surface of the *humerus*. It was about 5 mm distal to the *tuberculum majus*. Deep into this muscle are the ***m. teres minor***, which originates at the *margo lateralis* of the cranial portion of the *scapula*, runs laterally and joins the lateral surface of the *tuberculum majus* of the *humerus* to its distal portion.

Musculus teres major is located at the caudal to the *m. spinodeltoideus*. This muscle arises from the caudal half of the *margo lateralis* of the *scapula* and inserts in the *tuberculum minus*, distal to the insertion of *m. latissimus dorsi*.

Musculus levator scapulae, a part of the neck muscles, lies from the transverse process of the *vertebrae cervicales IV* in the form of aponeurosis and from *vertebrae cervicales V-VII*. The insertion of this muscle is at the *margo vertebralis* of the *scapula*, cranial to the tip of the *spina scapulae* (Figure 5B).

Musculus omocervicalis runs from the transverse process of the *vertebrae cervicales III-V* and inserts to the dorsal surface of the distal of *clavicula*, in the form of connective tissue fibers. ***Musculus clavodeltoideus***, a part of the deltoid muscle group, originates in the distal two-thirds of the *clavicula* and the tip of the *acromion* of the *scapula*. This muscle inserts on the proximal and dorsal surfaces of the *crista pectoralis* of the *humerus*.

Musculus serratus ventralis thoracis muscle is located medial to the shoulder and consists of two parts: *m. serratus ventralis thoracis pars cranialis* and *m. serratus ventralis thoracis pars caudalis*. The cranial part of the muscle originates on the lateral surface of the *os costale I-II* and inserts along the cranial portion of the *margo vertebralis* of the *scapula*. The caudal part of the muscle is a broad, fan-shaped muscle with a ventral edge shaped like a saw-tooth. This muscle arose from the lateral part of the *os costale I-VII* and inserts along the caudal part of the *margo lateralis* and the ventral portion of the *margo lateralis* in the form of a muscle attachment. ***Musculus subscapularis*** is located on the ventral side of the *scapula*, originates on the ventral surface of the *scapula,* and inserts on the *tuberculum minus* of *humerus*.

Upper arm muscles

We observed some superficial muscles group of the large flying fox's upper arm, they are *m. biceps brachii*, *m. brachialis*, *m. triceps brachii*, and *m. coracobrachialis*. ***Musculus biceps brachii*** of the large flying fox is a thick and long muscle. This muscle is divided into two based on its origin, namely the *m. biceps brachii caput coracoideus* (*caput brevis*) and *caput glenoidalis* (*caput longum*) as shown in Figure 6. *Caput coracoideus* originates from the distal region or at the tip of the *processus coracoideus* of the *scapula*, while *caput glenoidalis* originates proximal to the *processus coracoideus* near the *tuberculum supraglenoidale* of the *scapula*. Both heads of these muscles insert into the distal part of the articulation surface of the *radius*, at the proximal end of the bone. ***Musculus brachialis*** of this animal is a relatively small muscle, arising from the cranioventral surface of the distal third of the *humerus* (Figure 7B). This muscle inserts on the cranioventral surface of the proximal end of the *ulna*.

Musculus triceps brachii of the large flying fox is a thick and long muscle. This muscle has three heads according to their location: *caput laterale*, *caput longum*, and *caput mediale* (Figures 5 and 7). *Caput longum* and *caput laterale* of the muscle could be found profundal to *m. acromiodeltoideus*. *Caput laterale* of this muscle originates on the caudal surface of the proximal portion of *humerus*. *Caput longum* originates at the *margo lateralis* of the *scapula* and runs caudally to the *cavitas glenoidalis*. *Musculus triceps brachii caput mediale* of this animal arises from the caudoventral surface of the *humerus*, distal to the origin of *m. coracobrachialis*. The insertion tendons of the three heads also attaches to the sesamoid bone before joining at the proximal end of the *olecranon*. ***Musculus coracobrachialis*** originated at the end of the *processus coracoid* of the *scapula* and inserts on the caudoventral surface of the *humerus*, about the distal half of the origin of *m. triceps brachii caput laterale*. This muscle is located in the profundal of *m. biceps brachii caput coracoideus*.

Muscles of the forearm and fingers

Musculus brachioradialis of the large flying fox extends from the *humerus* to the *radius*. This muscle originates on the dorsal surface of the distal end of the *humerus*. The site of origin was about 15 mm from the *condylus lateralis*. The insertion of this muscle is on the cranial surface of the *radius*, about the proximal quarter of the bone. This muscle of the large flying fox was considerably thick and has a wide distance or gap to the elbow.

The superficial muscles located on the dorsal part of the forearm are *m. extensor carpi radialis longus*, *m. extensor carpi radialis brevis*, *m. supinator*, *m. extensor digitorum communis*, *m. extensor pollicis brevis*, and *m. extensor carpi ulnaris* (Figure 7A). ***Musculus extensor carpi radialis longus*** originates in the *epicondylus lateralis* of the *humerus*. This muscle inserts on the craniodorsal surface of the base of the *os metacarpale II*. ***Musculus extensor carpi radialis brevis*** is located at the caudal of the *m. extensor carpi radialis longus*, arising from the cranial side of the *epicondylus lateralis* of the *humerus*. The tendon origins of this muscle unite and infiltrate profundally from the tendon origin of *m. extensor carpi radialis longus*. The insertion tendon of the muscle divides into several parts which attach on the dorsal surface of the bases of the *os metacarpale III-V*. ***Musculus extensor digitorum communis*** is a thick muscle, originating in the *epicondylus lateralis* of the *humerus*. The tendon of this muscle is supported by the sesamoid bone on the lateral side of the epicondyle. This muscle originates from a fairly wide surface of the ligament that covers the joint region between the *humerus*, *radius*, and *ulna*. This muscle inserts on the cranial surface of the base of *phalanx II* of the third digit, the dorsal surface of *phalanx II* of the fourth digit, and on the dorsal surface of the *phalanx II* of the fifth digit after attaching at the dorsal of metacarpo-phalangeal joint of the same digit. ***Musculus extensor pollicis brevis*** originates on the dorsal edge of the *ulna* at the proximal extremity and inserts on the dorsolateral surface of metacarpophalangeal joint and the dorsal surface of the *phalanx II* of the first digit. This insertion tendon also joins the tendon of *m. adductor pollicis* in the *phalanx I*. ***Musculus extensor carpi ulnaris*** is the most caudal muscle of the dorsal side of the forearm. This muscle originates on the caudal surface of the *ulna*, proximal to it. This muscle inserts on the dorsomedial surface of the *os metacarpale V*, about one-fifth of the proximal part of the bone.

Musculus extensor carpi radialis longus et brevis, *m. extensor digitorum communis*, and *m. extensor pollicis brevis* were reflected to expose the profundal layer of the dorsal side of the forearm muscles, namely *m. supinator*, *m. abductor pollicis longus*, and *m. extensor indicis muscle*. ***Musculus supinator*** originates on the dorsal surface of the sesamoid bone, which lies dorsal to the *radius*, in the *epicondylus lateralis* of the *humerus*. In addition, its tendon of origin is attached to the ligaments in the joint region between the *humerus*, *radius*, and *ulna*. This muscle inserts on the cranial surface of the proximal os of the *radius*, and on the surface of the *m. extensor digitorum communis*. ***Musculus abductor pollicis longus*** originates on the proximal caudodorsal surface of the *radius*, on the ligamentous surface in the region between the *radius* and *ulna*, and on the dorsal surface of the proximal edge of the *ulna*. This muscle inserts on the medial side of the carpal region. ***Musculus extensor indicis*** originates on the dorsal surface of the *ulna*, distal to the border of the origin tendon of *m. abductor pollicis longus*. This muscle inserts on the dorsal surface of the *os metacarpale I*, at the joint of the metacarpo-phalangeal joint of the second digit, and joins on the dorsal surface of the base of the *phalanx II* of the same digit.

We observed that superficial muscles located on the ventral side of the forearm are *m. pronator teres*, *m. flexor carpi radialis*, *m. palmaris longus*, and *m. flexor carpi ulnaris* (Figure 7B). ***Musculus pronator teres*** is located caudal to *m. brachioradialis*. This muscle arises from the *epicondylus medialis* of the *humerus* and inserts on the cranioventral surface of the *radius*, along with the proximal third of the bone. ***Musculus flexor carpi radialis*** is located just caudally from the *m. pronator teres*. This muscle originates in the *epicondylus medialis* of the *humerus*, and also in the proximal part of the *m. pronator teres* and the caudal of *m. palmaris longus*. This muscle passes through the ventral part of the carpal joint and inserts at the base of the *os metacarpale II*. ***Musculus palmaris longus*** originates in the *epicondylus medialis* of the *humerus* and the proximal part of the *m. flexor carpi radialis*. This muscle has insertions in several parts, namely on the ventral surface of the metacarpo-phalangeal joint of the first digit, on the cranial surface of the proximal part of *os metacarpale II*, and on the ventral side of the metacarpo-phalangeal joint of the second digit, and on the ventral side of the *os metacarpale V*.

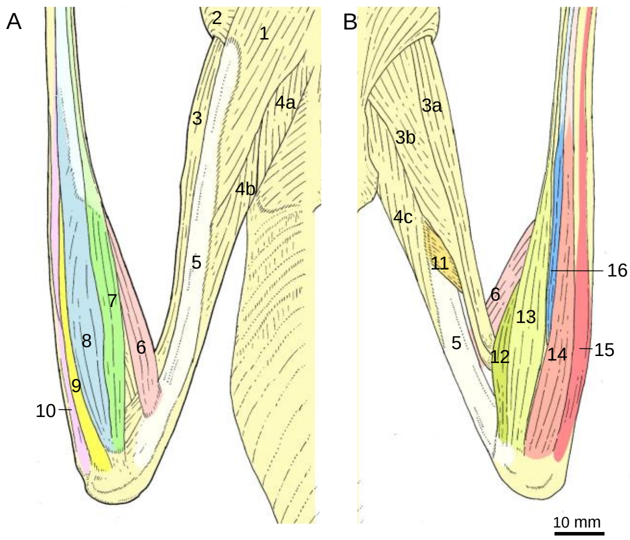

Figure 7. Forearm muscles of the large flying fox. A. dorsal; B. ventral view. 1. *m. acromiodeltoideus;* 2. *m. pectoralis caudalis*; 3. *m. biceps brachii* (a. *caput glenoidalis;* b. *caput coracoideus*); 4. *m. triceps brachii* (a. *caput longum;* b. *caput laterale;* c. *caput mediale*); 5. *humerus;* 6. *m. brachioradialis*; 7. *m. extensor carpi radialis longus et brevis;* 8. *m. extensor digitorum communis*; 9. *m. extensor pollicis brevis*; 10. *m. extensor carpi ulnaris*; 11. *m. brachialis;* 12. *m pronator teres;* 13. *m. flexor carpi radialis;* 14. *m. palmaris longus;* 15. *m. flexor carpi ulnaris;* 16. *m. flexor digitorum profundus*

Musculus flexor carpi ulnaris originates from the *epicondylus medialis* of the *humerus* and on the ventral surface of the proximal part of the *ulna*. This muscle inserts on the lateral side of the carpal joint, particularly on the lateral surface of the *os pisiform*. In the profundal layer, ***m. flexor digitorum profundus*** could be observed after removing *m. flexor carpi radialis* and *m. palmaris longus*. This muscle originates from the *epicondylus medialis* of the *humerus* and the proximal part of the *m. pronator teres*. On the ventral side of the carpal joint, the insertion tendon of this muscle divides into three. The first tendon inserts on the ventral side of the base of the *phalanx II* of the first digit, the second inserts on the ventral side of the *phalanx III* of the second digit, and the third tendon inserts on the ventral side of the *phalanx II* of the third digit. In addition to those muscles mentioned above, there were some tiny digital flexor muscles that originated in the area of carpal and digits such as *m. abductor pollicis brevis*, *m. flexor pollicis brevis*, *m. adductor pollicis*, *m. abductor digiti quinti*, *m. opponens digiti quinti*, and *m. interossei* which are not discussed in the present study.

Discussion

Thoracic girdle, arms, and wing bones

A very well-developed *acromion* in the large flying fox indicates three well-developed parts of *m. deltoideus* and functionally play an important role in locomotion. A very well-developed *acromion* found in apes enhances the mechanical strength for deltoid muscle and is thought to be related to the arm suspensory and their climbing locomotion (Matsuo et al. 2019). The shape of the *scapula* was suggested to be related to the rotation ability of the *scapula* and the function of *m. serratus ventralis* which is attached in the cranial part of the *margo vertebralis* of the *scapula*. Scapular retraction must be greater in this flying animal, according to the previous report that the retraction of the *scapula* is greater in arboreal animals that have climbing ability compared to that in terrestrial animals (Argot 2001). The transverse scapular ligament plays a role to extend the attachment surface of the shoulder muscles (Norberg 1972).

Differences in the shoulder conformation between large flying foxes and quadrupedal mammals are seen in the position of the *scapula* structure. The *scapula* of the large flying fox is in the dorsal area and has a craniocaudal elongation, while that in quadrupedal mammals is in the lateral part of the body. Similar to that of humans (*Homo sapiens*) and chimpanzees (*Pan troglodytes*), the *scapula* that is located in the dorsal position enhances the mobility of the scapulohumeral joint to facilitate complex locomotions such as vertical climbing and brachiation (Gómez et al. 2020), and wing flapping in the large flying fox. The location of this bone in the dorsal area is an adaptation that enables the rotational motion of the *caput humeri* and supports the adduction and abduction movement of the arm and wings. In addition, the motion of the *scapula* in large flying fox is limited on the frontal plane (Panyutina et al. 2013).

Flapping activity of the wings in animals with active flight ability such as large flying fox requires firm support of the wings. The sternoclavicular joint serves as the basis for the rotational motion of the *clavicula*. However, the surface of the sternoclavicular joint is relatively flat, so the fixation of this joint is reinforced by *ligamentum sternoclaviculare laterale et mediale*. When flapping the wings upward (abduction phase), the acromial extremity of the *clavicula* will be pushed to the medial along with the *scapula,* on the other hand, when flapping the wings downward (adduction phase), the *clavicula* moves to the lateral as described by Panyutina et al. (2013). The joint between the *clavicula* and *scapula* is reinforced by two ligaments, namely *ligamentum acromioclavicularis* that connects *acromion* with the *clavicula*, and *ligamentum coracoclavicularis* which connects the *processus coracoideus* with the *clavicula*. According to Panyutina et al. (2013), the presence of such ligaments limits the ability of acromioclavicular joint motion.

Caput humeri is connected to the *cavitas glenoidalis* of the *scapula* which also has a wide joint surface and craniocaudal elongation. This structure allows flexibility of extension-flexion and abduction-adduction motion of the scapulohumeral joint, as well as rotation of the *humerus* on the *cavitas glenoidalis.* Maximum extension of the shoulder joint is required to extend the wings, while abduction and adduction motions are to flap the wings during flight. Panyutina et al. (2013) suggest that the movement of the *humerus* in the shoulder joint of the large flying fox is quite extensive, with abduction-adduction on the transverse plane, retraction-protraction on the frontal plane, and rotation of the longitudinal axis of the *humerus*. However, the presence of protruding *tuberculum majus* of the *humerus* in the proximal extremity limits the abduction movement of the *humerus* to the *scapula* (Norberg 1972). The simple structure of the *humerus* in the large flying fox was similar to that in *P. giganteus* which has a shape that is like that in humans, in terms of the structure of *sulcus m. brachialis* that is not very distinct (Shil et al. 2013). In addition, the laterally displaced *trochlea humeri* (articular surface) of the *condylus humeri* of the large flying fox shares similar characteristics with Phyllostomidae which is a narrow space forager (Sánchez and Carrizo 2021).

The forearm bone in this animal, *radius*, is a strong bone and becomes the main element that supports the wing membrane. The forelimb of the bat has relatively elongated bones compared to non-flying mammals to enlarge the wingspan (Hedenström and Johansson 2015). On the ventral side of the proximal of *radius*, there is a groove that serves as a place for the tendon of *m. biceps brachii* to attach. In general, the typical appearance of the long bone of the upper and forearm, *humerus*, and *radius*, were relatively simple and demonstrated thin-walled bone forming the hollow structure. This characteristic reduces the bone mass as suggested to be required in a flying mammal and correlates with the resistance to the large torsional stresses of the wing (Swartz et al. 1992).

The articular connection between *ossa carpi* and *ossa metacarpalia* causes the movement in this area to be limited. The carpal joint has pronation when extending the wings laterally. *Ossa metacarpalia* will experience flexion movement when flexing the wings (Norberg 1972). The flying fox can do flexion movement in carpo-metacarpal joints up to 180°, enabling this animal to flex its wings when resting (Panyutina et al. 2015). The claws observed in the last *phalanx* in the first and second digit is similar to the one reported in *R. aegyptiacus* (Norberg 1972). Moreover, the characteristic of the *ossa metacarpalia* and *ossa digitorum manus* bones that are long in size could extend the surface of the wingspan. This affects the aerodynamic pressure on the wing membrane, which the animal needs to balance and maneuver during flight (McMasters 2004). The thin and flexible structure of the digital bones prevents the occurrence of trauma (fracture) due to air pressure during flight. Swartz and Middleton (2008) describe that the flexible distal of the digital bone results in a wing structure that is dynamic to the changes in the air flow. These distal bones are tailored to resist forces within the plane of the wing membrane. However, these bones are thought to mainly keep the wing membrane stretched during flight rather than adaptability to the aerodynamic forces as mentioned by Hedenström and Johansson (2015). In addition to the flexible structure of the digital bones, elastin fibers distributed in the wing membrane allow the wing to stretch and receive air pressure. These elastin fibers are anatomically arranged parallel to the proximodistal direction of the axis of the wingspan, in the interdigital membrane, in the area between *os metacarpale IV* and *V*, and between *radius-ulna* and *os metacarpale V* (Cheney et al. 2017).

Back, pectoral, shoulders, and arms muscles

Musculus trapezius in the large flying fox has a different origin compared to that in *R. aegyptiacus* (Norberg 1972) but has the same insertion. In *R. aegyptiacus, m. trapezius* has two insertions and is divided into two parts: *m. acromiotrapezius* and *m. clavotrapezius* (Norberg 1972). The two parts of the muscle in the large flying fox cannot be clearly demarcated, but the insertion part is clearly separated. In contrast, *Artibeus jamaicensis* was reported to have three parts: *m. acromiotrapezius*, *m. clavotrapezius*, and *m. spinotrapezius*, with a different origin from that of the large flying fox. In addition, no clear boundaries were found between the fibers of *m. clavotrapezius* and *m. acromiotrapezius* (Hermanson and Altenbach 1985). *Musculi* (*mm.*) *acromiotrapezius* and *clavotrapezius* are named according to the term used by previous researchers (Norberg 1972; Hermanson and Altenbach 1985). However, these muscles are part of *m. trapezius* as listed in the *Nomina Anatomica Veterinaria* (ICVGAN 2017). This muscle group plays a role in supporting the function of the dorsal movement of the wing. *Musculus clavotrapezius* pulls the *clavicula* and *scapula* medially, while *m. acromiotrapezius* pulls the *scapula* caudomedially and rotates the *scapula* (Norberg 1972). In addition, this muscle keeps the *scapula* stable during the contraction of the adductor muscles of the arm in the early phase of the ventral movement of the wing (Hermanson and Altenbach 1985). Another back muscle, *m. latissimus dorsi* in terrestrial mammals acts as a propulsion muscle of the body, while in the large flying fox it performs flexor movements and rotation of the *humerus* (Norberg 1972). The flexor movements and rotation of the *humerus* are associated with the dorsal flap (abduction) of the wing and the repositioning of the wing during the ventral (adduction) phase of wing flapping (Hermanson and Altenbach 1985). *Musculus rhomboideus* of the large flying fox has a wider origin than that of *R. aegyptiacus*. This muscle serves to pull the caudomedial portion of the *scapula* towards the craniomedial (Norberg 1972).

Musculus deltoideus in the order Chiroptera consists of three parts: *pars clavicularis*, *pars acromialis*, and *pars scapularis*. The muscle parts are sequentially known as *m. clavodeltoideus*, *m. acromiodeltoideus*, and *m. spinodeltoideus*, which is part of the deltoid muscle as previously described (Hermanson and Altenbach 1985). *Musculus clavodeltoideus* functions as an adductor of the arm or wing, with high activity in the adduction phase, while *m. acromiodeltoideus* and *m. spinodeltoideus* act as an abductor of the arm or wing (Norberg 1972). Both of these muscles have high activity at the end of the adduction phase and early abduction phase of the wing, as a stabilizer of the shoulder joint against excessive adductor movement of the pectoral muscles (Hermanson and Altenbach 1985). *Musculus acromiodeltoideus* or the *m. deltoideus pars acromialis* is the main abductor muscle for the arm, supported by the *m. supraspinatus* (Argot 2001). In some primates, elevating and stabilizing functions of the deltoid muscles is important for arboreal locomotion (Gómez et al. 2022) and it is suggested that the deltoid muscles in the large flying fox share similar functional characteristic to support active flying activity. *Musculus infraspinatus* that fills the *fossa infraspinata*, has the opposite function to *m. supraspinatus*, since it acts as a flexor of the *humerus*, although synergistically it makes the wing abduction movements (Norberg 1972). The relatively larger *m. supraspinatus* and *m. infraspinatus* are correlated to the size of the scapular fossa where the muscles are lied, which is important for stabilizing the shoulder and improving the scapulohumeral joint mobility.

Musculus teres minor as a short muscle functions synergistically with *m. acromiodeltoideus* and *m. spinodeltoideus* as a flexor of the *humerus* (Norberg 1972). *Musculus clavodeltoideus* has a homologous correlation with *m. brachiocephalicus pars clavicularis* (*m. cleidobrachialis*) in domestic animals. *Musculus levator scapulae*, which belongs to the neck muscle (*mm. colli*), is named after humans, and is homologous to *m. serratus ventralis cervicis* in domestic animals (ICVGAN 2017).

The pectoral muscles of the large flying fox, the *m. pectoralis pars caudalis*, is the widest and thickest muscle of all other muscles. This muscle exerts a powerful caudoventromedial pull on the *humerus*. The shape and size of this muscle is determined by the function of the adduction movement of the wings that requires strong muscles to go against air pressure. *Musculus pectoralis* plays a role in the adduction phase of the wing (Hermanson and Altenbach 1985). The origin of the *m. pectoralis abdominalis* is different from that of *R. aegyptiacus*, which has its origin on the *os costale X*. This muscle functions in rotational and flexor movements of the *humerus* (Norberg 1972).

Musculus pectorales major, *m. serratus ventralis thoracis* (*m. serratus anterior*), *m. clavodeltoideus*, and *m. biceps brachii caput coracoideus* (*caput brevis*) are some main muscles that are responsible for the adduction phase of the wing. Meanwhile, *m. clavotrapezius, m. acromiotrapezius, m. latissimus dorsi*, *m. teres major*, *m. acromiodeltoideus, m. spinodeltoideus, m. triceps brachii caput longum et laterale* are the main muscles involved in the abduction phase of the wing (Hermanson and Altenbach 1985). The two heads of *m. biceps brachii* perform flexor movements and arm rotation and have synergic functions with *m. brachialis* (Norberg 1972).

Musculus triceps brachii functions as an extensor of the forearm (elbow joint) (Norberg 1972). Hermanson and Altenbach (1985) described that *m. triceps brachii caput longum et laterale* are responsible for wing abduction. *Musculus coracobrachialis* is located deep to *m. biceps brachii caput coracoideus* and serves as a flexor and adductor of the *humerus* (Norberg 1972). In birds, *m. biceps brachii* serves to stabilize the elbow joint and to flex it during the adduction phase. On the other hand, the bird's triceps group muscles, *m. humerotriceps* and *m. scapulotriceps* serve as extensor of the elbow joint during the abduction-adduction phase transition and adduction phase, respectively (Robertson and Biewener 2012).

Large flying fox has the same *m. brachioradialis* as in carnivores (Junior et al. 2015; Sánchez et al. 2019) as well as in primates, which serves as a flexor and supinator of the *radius* (elbow) (Garcia et al. 2015; Boettcher et al. 2019). This muscle is not commonly found in Microchiroptera, but it is found in *Hipposideros armiger* (family of Rhinolophidae, and suborder of Yinpterochiroptera) (Norberg 1972), which is included in the members of the suborder of Microchiroptera according to the previous classification.

The ventral part of the forearm generally consists of the arm, carpal, and digital flexor muscle groups. *Musculus pronator teres* plays a role as a flexor of the *radius*. The *m. flexor carpi radialis* makes the wing arch laterally by pulling the *os metacarpale II* ventrally. *Musculus palmaris longus* acts as a flexor of the first, second, and fifth digits, thereby creating a curved wing. *Musculus flexor digitorum profundus* acts as a flexor of the first, second, and third digits and in some way, functions as a flexor to all digits (Norberg 1972). Thus, we suggested that the absence of *m. flexor digitorum superficialis* in the flying fox is correlated to the evolutionary development that is possibly required for the flying mammal. The forelimb musculature of the flying fox had to be strengthened to allow powerful wing abduction and adduction. In addition, compared to other mammals, bat musculature has rearranged and simplified, allowing two muscles to be fused or some muscles to be absent (Thewissen and Babcock 1992). Moreover, the reducing of the number of joints accompanied by the loss of certain digital flexor muscle is thought to be the adaptation for energetic saving during the wing flapping (Bahlman et al. 2016).

The muscles located on the dorsal side of the forearm are generally extensor muscle groups for the carpal and digital regions. The *m. extensor carpi radialis* of the large flying fox consists of two parts: *m. extensor carpi radialis longus et brevis*, which is the same as that in cats (ICVGAN 2017). The *m. extensor carpi radialis longus* functions as a digital extensor. Although the insertion of this muscle attaches to the second metacarpal bone, it indirectly pulls the other digits. The *m. extensor carpi radialis brevis* functions as an extensor of the third, fourth, and fifth metacarpal bones, and thus in general it serves as a digital extensor. *Musculus extensor digitorum communis* is responsible for the extensor movement of the *ossa metacarpalia* of the third to fifth digits. *Musculus extensor pollicis brevis* functions as the extensor of the first digit. The *m. extensor carpi ulnaris* pulls the fifth digit dorsally and medially. The contraction of *m. abductor pollicis longus* medially pulls the *os scaphoid* and indirectly strengthens the *os metacarpale V* to withstand air pressure during the adduction phase of the wing. The *m. extensor indicis* functions as an extensor of *os metacarpale I* of the second digit (Norberg 1972).

Wing movements of the abduction and adduction in the large flying fox are played by the back and pectoral muscles, respectively. Compared to bats, avian pectoralis and supracoracoideus muscles have the main function in wing movement of both abduction and adduction phases (Cao and Jin 2020). However, these thickest muscles in birds, are responsible for the downstroke that provide the major movement power in the flapping flight (Tobalske 2016). This pectoralis muscle has high activity in the adduction phase of the arms and wings at the start of the flight process (Robertson and Biewener 2012).

In conclusion, the large flying fox has a relatively simple musculoskeletal structure, which is mainly aimed at reducing body mass and resisting the large torsional stresses in the wing membranes. Based on the morphological findings, the large flying fox's flight ability was supported by a structure of the shoulders and wing skeletons that allow free shoulder area movement as well as relatively elongated arm and digital bones characteristics to extend the wingspan. The pectoral and back muscles of the large flying fox are also very well-developed to perform abduction movement and arm enhancement of the flapping activity of the wings.

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