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From skin folds to flight: elastic and collagen fibers architecture in the wing of the large flying fox (*Pteropus vampyrus*)

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ABSTRACT: Flight in bats is the primary mode of locomotion as they are the only flying mammals. The morphological characteristics of the wing membrane have been suggested to play an important role in its flight ability. The present study analysed the functional morphology of the wing membrane of the large flying fox (*Pteropus vampyrus*), focusing on the organisation of elastic and collagen fibres. In this study, we used two wild-caught adult flying foxes from West Java, Indonesia. The wing membrane tissue sections were stained using haematoxylin-eosin, Masson's trichrome, and Verhoeff-Van Gieson staining. The bat wing membrane comprises double-layered skin covered by a thin epidermal layer. The wing membrane is comprised of collagen fibres and well-organised elastin bundles inserted between the two skin layers. Collagen fibres strengthen the wing membrane by holding air pressure, whereas elastic fibres provide flexibility to the wings. This can describe the strength and flexibility of the wing membranes of large flying foxes during flight.

Keywords:
chiroptera, flight, morphology, patagium, wing

■ INTRODUCTION

Flight is the primary mode of locomotion used by bat species, only flying mammals, and other powered flight-capable birds and insects (Maina 2000, Cao & Jin 2020). In addition to its protective and regulatory roles, the bat wing membrane (patagium) is also a major locomotor organ (Swartz *et al*. 1996). The large flying fox (*Pteropus vampyrus*) belongs to the Pteropodidae suborder Yinpterochiroptera (Telling *et al*. 2005), which is a species found in Southeast Asia, including Indonesia. They are known to be reservoirs of numerous disease viruses and are thought to play an important role in disease transmission owing to their long-distance flight ability (Breed *et al*. 2010).

These morphophysiological attributes likely enhance bat flight capability. As flight is the most energy-demanding locomotive activity (Maina 2000, Shen *et al*. 2010), the collagen and elastic fibre structure in the wing membrane of a large flying fox is believed to support flight. Despite the importance of bat wings for their unique locomotion, histological studies of bat wing structures, especially in tropical Indonesia, are limited. Therefore, this study examined the functional morphology of the wing membrane of a large flying fox, focusing on the organisation of elastic and collagen fibres beneath the membrane.

■ MATERIALS AND METHODS

This study used two large wild-caught adult (male and female) flying foxes from West Java, Indonesia. Species confirmation of both individuals was performed through morphological identification. All experimental procedures were approved by the Animal Care and Use Committee of the School of Veterinary Medicine and Biomedical Sciences, IPB University (no. 57-2017 IPB). Bats were captured using net traps, with official permission from the Directorate General of Natural Resources and Ecosystem Conservation, Ministry of Environment and Forestry (No. 211/KSDAE/SET/KSA.2/7/2016). Chemical immobilisation of bats was performed using a combination of ketamine (10%) and xylazine (2%) at doses of 10 and 2 mg/kg body weight (i.m.), respectively (Heard et al. 1996). Intracardiac perfusion was

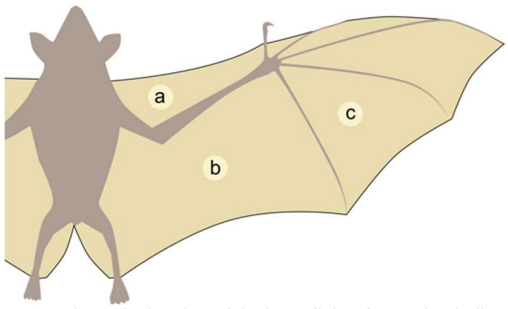

Figure 1. Schematic drawing of the large flying fox's wing indicating the area of tissue collection, a) propatagium, b) dactylopatagium, and c) plagiopatagium

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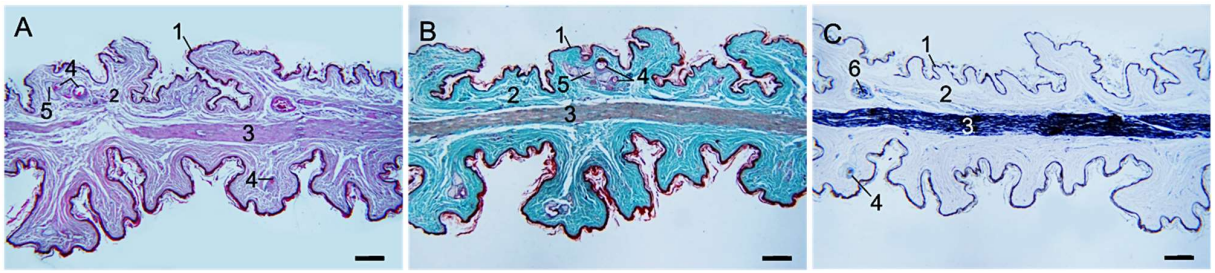

Figure 2. Representative histological images of the patagium with (A) hematoxylin-eosin, (B) Masson trichrome, and (C) Verhoeff-Van Gieson. 1. epidermis, 2. collagen fibers, 3. elastic fibers, 4. hair follicles, 5. sebaceous gland, 6. blood vessels. Scale bar = 200 µm

performed to remove blood and fix the entire body tissue. Tissue samples for histology were excised from the following locations: the propatagium, dactylopatagium, and plagiopatagium (Figure 1). Tissues were preserved in 4% paraformaldehyde and subjected to standard histological procedures, followed by staining with haematoxylin-eosin, Masson trichrome, and Verhoeff-Van Gieson. These stains were used to observe general tissue structure, collagen composition, and elastin bundles. Histological images of the 5 µm sections were captured using a Nikon Eclipse E600 microscope. Data from this study were descriptively analysed.

■ RESULTS AND DISCUSSION

The wing membrane of the large flying fox consists of double-layered skin with a relatively thin epidermis. Deep into the epidermal layer, a thick collagen fibre layer was observed in the dermis. A relatively thick elastin bundle was situated in the profundal to collagen fibre layers on both the dorsal and ventral sides (Figure 2). The skin layers on both sides of the wing membranes of the large flying fox form folds similar to those found in the wing membranes of gliding animals (Russell *et al*. 2001; Russell & Dijkstra 2001). The skin fold of the wing is a unique structure that provides a wider cross-sectional area when the wing is stretched and simultaneously facilitates the folding mechanism of the wing.

The connective tissues in the wing membrane were arranged in parallel between the elastic and collagen fibres. Elastin contributes to the ability to stretch the skin twofold (Swartz et al. 1996). This allowed the wing membrane to stretch when resisting air pressure to prevent damage to the membrane. The elastic fibres were arranged parallel to the proximodistal direction along the wing span. They are located in dactylopatagium and plagiopatagium (Cheney *et al*. 2017). In this study, elastic fibres were also found in the propatagium.

Unlike animals that can glide short distances, the large flying fox has a thick collagen fibre layer in its wing membrane, which provides the strength to withstand relatively high air pressure during flight involving wing flapping activities. Although collagen fibres have limited stretchability, they offer resistance to the stretching of elastic and muscle fibres in the wing membrane (Swartz *et al*. 1996, Bennett 2000). In addition to collagen and elastic fibres, several intramembranous muscles are present in certain areas, originating from the dorsal scapula, axillae, plagiopatagium, elbow, and distal femur (Cheney *et al*. 2017). These musculatures also support the wing movement.

■ CONCLUSION

The prominent features of elastic and collagen fibers architecture describe the strength and flexibility of the large flying fox's wing membrane during flight.

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