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Short Communication

Homology of the chiropteran “dactylopatagium” brevis

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ABSTRACT

Bats possess a series of patagial tracts that together act as an aerofoil for powered flight. Here we discuss the homology of a small portion of the patagium, the brevis section, traditionally assigned as a part of the handwing (dactilopatagium). Using dissected specimens and literature references we show that the muscle occipitopollicalis, a morphological marker of the propatagium, extends into the brevis section in a variety of bats. This led us to conclude that the brevis section is in fact a part of the propatagium, which is also supported by developmental evidence.

Aerial transportation characterizes several mammalian lineages. Two rodent clades (Sciuridae: Petauristinae, and Anomaluridae), the colugos (Dermoptera), and three marsupial clades (Acrobatidae, Petauridae, and Pseudocheiridae) contain species of gliders (Jackson, 1999), together with Volaticotheria, an independent Mesozoic lineage of gliding mammals (Meng et al., 2006). In addition, bats (Chiroptera) are the only mammals capable of powered flight. In all cases (gliders and flyers), the aerofoils consist of double (dorsal and ventral) membranes of skin of variable extension, all together known as patagia (e.g., Norberg, 1972). The patagia are responsible for generating the aerodynamic force that can be decomposed into lift and trust (Norberg and Rayner, 1987). Each patagial tract appears to be anatomically, developmentally, and evolutionary distinct (e.g., Tokita et al., 2012). Besides the plagiopatagium, of constant presence in all gliders and flyers, these tracts vary across aerial mammals in presence and degree of differentiation (Jackson, 1999). Bats in particular possess propatagium (leading edge of wing), plagiopatagium (sides of body), uropatagium (tail membrane), and dactylopatagium (handwing; Fig. 1A; see Norberg, 1972). Gliders generally lack the handwing and sometimes the pro- or the uropatagium (Jackson, 1999). Colugos do exhibit a short manual dactyloptagium (i.e., without lengthened digits as in bats) and additionally, a short pedal dactylopatagium (i.e., webbed feet; Simmons, 1994) of limited expansion (only extended to the first phalanx) also in a few megachiropteran bats (see Bergmans, 1997; Giannini and Simmons, 2003, 2005).

Each patagial tract features a specific set of structures, particularly wing muscles that tighten the flight membrane (Fig. 1A). The chiropteran handwing, which is the most complex tract, lacks distinctive associate muscles (Norberg, 1972). So given the unique occurrence of these muscles, or their lack thereof, together with their signature developmental pattern (see Tokita et al., 2012), they represent morphological markers of each patagium. The elongate digits of bats support the dactylopatagium and divide its distinct sections (Fig. 1A); here we focus on the anteriormost portion of the handwing, section brevis, extended between manual digits I and II (Fig. 1A).

In a paper on functional osteology and myology in the megabat Rousettus aegyptiacus (Pteropodidae), Norberg (1972: Fig. 20) depicted the ventral aspect of a manually dissected left wrist of this species, in which m. occipitopollicalis, the flying-membrane muscle of the propatagium, reaches the thumb and passes it distally. Norberg (1972:10) stated that this “muscle extends along the anterior edge of the propatagium and dactylopatagium brevis”, and her description of the distal portion of this muscle reads: “Some

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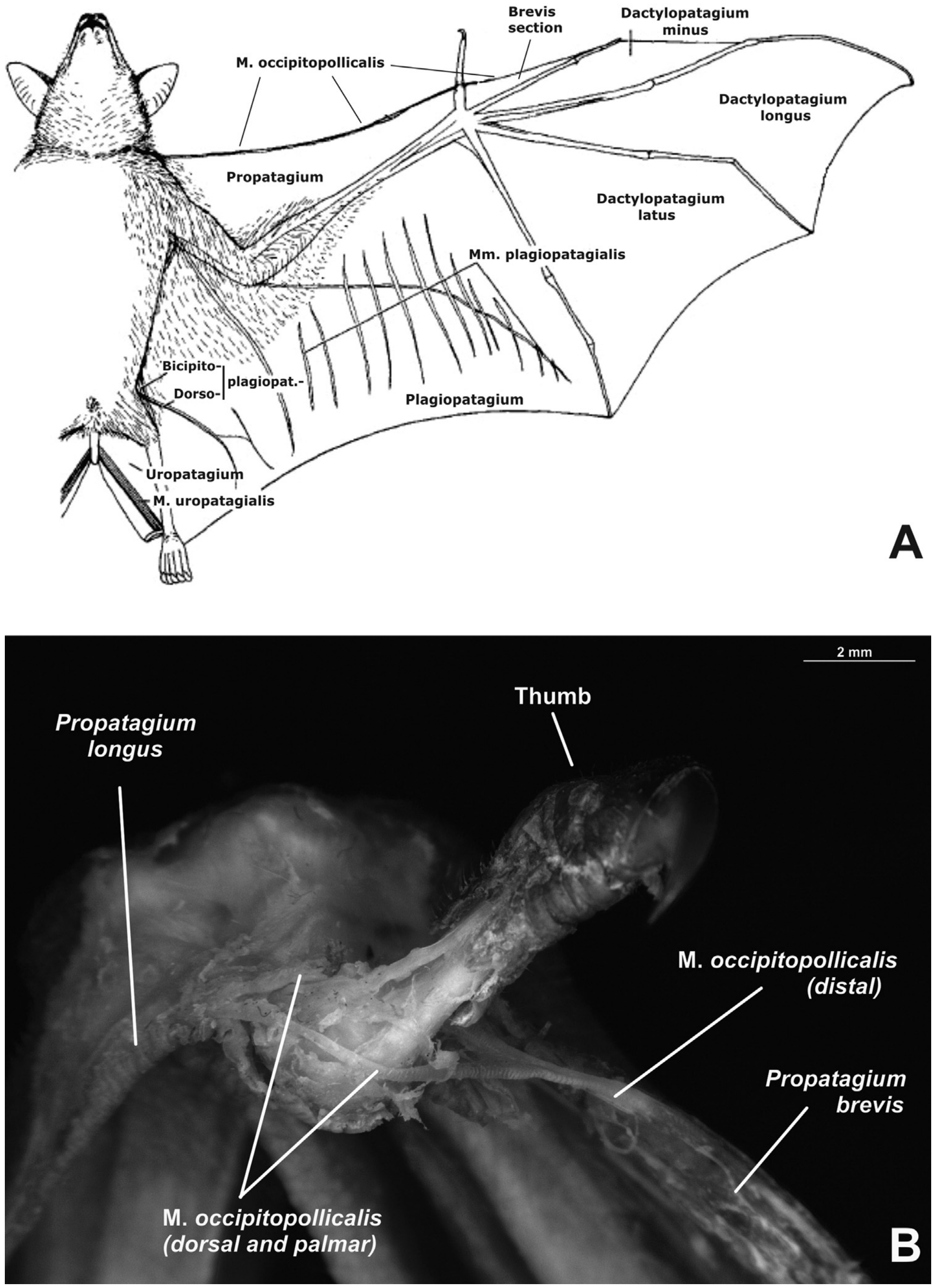

Fig. 1. Schematic representation of the bat aerofoil (A; modified from Norberg, 1972) showing the patagial tracts and associated muscles [abbreviations: M. – Mm.: muscle(s)]; and (B) a photograph of a manually dissected left wrist of Artibeus planirostris CML 8578 indicating the course of the tendinous m. occipitopollicalis around digit I (thumb) and its distal integration to the brevis section of the handwing.

of [the fibers] pass ventrally to the thumb and along the edge of dactylopatagium brevis together with new parallel-lying strands from the thumb tissue and some strands insert on the thumb at the level of the distal part of the first metacarpal". As a pteropodid species, R. aegyptiacus belongs in one of the two major bat groups, the Yinpterochiroptera (sensu Teeling et al., 2005). Here we report dissections of species that belong in the other major bat group, the Yangochiroptera, that show the same pattern of insertion of muscle occipitopollicalis and permitted to propose an alternative homology of the brevis section of the chiropteran handwing.

In order to expose the muscle occipitopollicalis in its insertion region, we removed the double skin (flight membrane) around the thumb with surgical tools in 70% ethanol preserved specimens of selected yangochiropteran bats (Molossidae: Eumops perotis from the Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina, MACN 13455; Eumops glaucinus MACN 14233; Vespertilionidae: Lasiurus ega MACN 8.57, Lasiurus cinereus MACN 13111, Lasiurus blossevillii MACN 38.194; Phyllostomidae: Artibeus planirostris CML 8578 and Instituto de Bio y Geociencias del Noroeste Argentino, Salta, Argentina, IBIGEO-M 0216, 0217, Sturnira lilium IBIGEO-M 0218, and Desmodus rotundus IBIGEO-M 0215). Fig. 1B shows the dissected left wrist of Artibeus planirostris (Phyllostomidae; Colección Mamíferos Lillo, Tucumán, Argentina, CML 8578, adult female) in palmar view. The pattern described in Norberg (1972) for Rousettus is essentially mirrored in this bat. The m. occipitopollicalis originates at the lateral side of the occiput as a wide muscle whose fibers converge in a thin tendon that extends along the leading edge of the propatagium; this tendon continues distally until reaching the thumb, where the fibers bifurcate sending one tendon in palmar and another in dorsal direction, both of which bypass the thumb just distal to the metacarpal-phalangeal joint; the two tendons reunite in a single one, and the latter continues parallel to the index finger along the leading edge of the brevis section toward its insertion in the membrane near the tip of this digit (Fig. 1B). The leading edge of the propatagium also envelops the cephalic vein (not shown) in close association with m. occipitopollicalis (see Thewissen and Babcock, 1992). The same holds true for the other bat species dissected. In D. rotundus, the propatagial complex is entirely composed of muscle fibers, without any tendinous portion, a condition reported also for other bats (e.g., Pteropus; Thewissen and Babcock, 1992).

We propose that wing muscles are reliable markers of different patagial tracts and that the trajectory of m. occipitopollicalis along the leading edge of the bat wing may have a bearing on the homology of the anterior handwing. The implication is that the brevis section, traversed by the m. occipitopollicalis along its leading edge, belongs in the propatagium rather than in the dactylopatagium. The fact that species from the two major bat clades (Yinpterochiroptera and Yangochiroptera) exhibit the same condition indicates a widespread occurrence in bats and strongly suggests that this is the chiropteran ancestral character state. Next we examine the developmental support of this homology.

Development of the chiropteran handwing is exceptionally well documented (e.g., Cretekos et al., 2005; Hockman et al., 2008, 2009; Sears, 2008; Tokita et al., 2012). The handwing membrane itself represents the embryonic interdigital membrane of the handplate retained (and highly modified) in the adult (Weatherbee et al., 2006). It is subtended by the greatly elongate metacarpal and phalangeal bones of digits II to V (Kunz and Pierson, 1994). Digital elongation is attained by a significant alteration of the chondrocyte cycle in these bones, chiefly by the up-regulated expression of the bone morphogenetic protein 4 (BMP4; e.g., Farnum et al., 2008; Sears et al., 2006). The thumb, however, remains short (Cretekos et al., 2005; Hockman et al., 2009; Giannini et al., 2006) and so morphologically close to a plesiomorphic mammalian state that also retains the function of a clawed, grasping digit (Giannini, 2012). The interdigital membranes are retained by means of a complex genetic interaction that includes the major players of the developing hand and additional recruits, including sonic hedgehog (SHH), fibroblast growth factor 8 (FGF8), BMP2, and gremlin (GRE; e.g., Hockman et al., 2008; Sears, 2008). BMP2 promotes programmed cell death (apoptosis) but its action is prevented by its antagonists, GRE and FGF8, such that the interdigital tissue survives and becomes the handwing membrane (Weatherbee et al., 2006). The wing membrane around the thumb is not affected in the same way because GRE and FGF8 are strongly AP-patterned and only poorly traced in this small area (Hockman et al., 2008; Wang et al., 2014), so their effect on preventing apoptosis via BMP inhibition is deduced to be minimal and most of the corresponding embryonic tissue is lost. Thus, the membrane next to the thumb, i.e. the brevis section, seems to have a separate origin. The pattern of expression of other genes in the wing membrane (the T-Box Transcription Factor gene TBX3, the homeobox HOXD), the perichondrium of elongate digits (Hoxd), and the tip of digits (the family with sequence similarity 5, member C gene FAM5C) also exhibit contrasting expression patterns between membrane areas around elongate digits II to V versus the thumb area (Wang et al., 2014).

Developmental data that support the uniqueness of the thumb area, as opposed to the dactylopatagium proper (extended between the elongate digits), and the presence of m. occipitopollicalis in the thumb area and distally, strongly suggest that the brevis section is in fact an extension of the propatagium. Tokita et al. (2012) have shown that the propatagium develops from a primordium that recruits facial muscles into it as it grows distally. This muscle is the occipitopollicalis which has been shown by Norberg (1972) and this study to extend into the anterior handwing. As a consequence, we identify the brevis section, formerly considered a part of the dactylopatagium, as a part of the propatagium, thereby proposing the latter to be composed of propatagium longus and propatagium brevis. Furthermore, this means that the wing leading-edge function (e.g., Muijres et al., 2008) rests on a single anatomical unit, the propatagium, which was found to be present in bats as early as the Eocene epoch (e.g., in Archaeonycteris, 49 my old; see Thewissen and Babcock, 1992: Fig. 1). Although a minor component of the flight apparatus, we believe that the brevis section, and its revised homology that allowed us to transfer it from the dactylopatagium to the propatagial tract, adds significantly to an appreciation of the developmental, evolutionary and functional complexity of the bat wing, and more broadly, of adaptation to new functions (aerial transport) in highly derived mammals.

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