



Pterosaurs evolved a muscular wing–body junction providing multifaceted flight performance benefits: Advanced aerodynamic smoothing, sophisticated wing root control, and wing force generation

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Pterosaurs were the first vertebrate flyers and lived for over 160 million years. However, aspects of their flight anatomy and flight performance remain unclear. Using laser-stimulated fluorescence, we observed direct soft tissue evidence of a wing root fairing in a pterosaur, a feature that smooths out the wing–body junction, reducing associated drag, as in modern aircraft and flying animals. Unlike bats and birds, the pterosaur wing root fairing was unique in being primarily made of muscle rather than fur or feathers. As a muscular feature, pterosaurs appear to have used their fairing to access further flight performance benefits through sophisticated control of their wing root and contributions to wing elevation and/or anterior wing motion during the flight stroke. This study underscores the value of using new instrumentation to fill knowledge gaps in pterosaur flight anatomy and evolution.

pterosaur | fossil soft tissue | wing root fairing | aerodynamics | flight performance

Here, using laser-stimulated fluorescence (LSF), we observe direct soft tissue evidence of a wing root fairing (sometimes called wing fillets) in a pterosaur and discuss its functional and ecological implications. Pterosaurs were the first vertebrate group to achieve powered flight and were successful in the aerial realm for over 160 million years (1). Pterosaurs operated uniquely with a membrane wing held in tension by a hyperelongated fourth finger (1). Bats are the only surviving vertebrate powered flyers that use a membranous wing, but this is supported by a hyperelongated hand. Birds use a feathered wing to fly. As powered, flapping flyers, pterosaurs, bats, and birds all use(d) lift to provide both weight support and thrust. Powered flight in all animals comes at the cost of essentially “pushing” against drag (or more precisely, injecting enough momentum to the air to overcome drag). For manufactured aircraft, engineers work to minimize drag effects by creating streamlined aerodynamic profiles, including the addition of aerodynamic “fairings” to smooth shapes and joints on the aircraft, including the wing root, wing tips, and the landing gear. Fairings are typically curved sections and are used to direct airflow smoothly over the structure, which reduces profile drag and (in some cases) helps prevent stall by delaying flow separation (2). There are various effects caused by the size and shapes of fairings but these are beyond the scope of this paper. Fairings are not always added, because of economic reasons. Wing root fairings are commonly added between the aircraft fuselage and the wing, especially in low wing configurations where a fairing shows greater benefit (3), but not all shapes change airflow in a desirable way (4).

Rather than relying heavily on soft tissue structures, birds primarily use varying extents of feathering to construct the wing–body junction shape, in addition to smoothing out the

rest of their body outline (5, 6). Birds possess a membrane-integument hybrid wing comprising feathers, patagia, and muscles (7). Over half of the feather area proximal to the elbow is rooted in membrane (proptagium) (7). The feathers along the wing root are not flat against the membrane, but rather, they form a convex shape on both the upper and lower surfaces that refines the camber (7) and also (along with the contour feathers of the shoulder) forms a wing root fairing (8). Bats have a fairing around their neck that is predominantly made of fur. This fur smooths airflow around their wing–body junction. Fairings have been identified in pterosaurs within the wing digits and the pneumatic skeleton (9), but not in their soft tissues.

Specimen Bayerische Staatssammlung für Paläontologie (BSP) 1937 I 18 is a pterodactyloid pterosaur from the Late Jurassic Solnhofen Limestones of southern Germany (10, 11) repositied in the BSP in Munich. It is a fully articulated skeleton with extensive soft tissue remains apparent under white light (11). The wings are preserved in dorsal view and the head is preserved in right lateral view. The anatomy of the specimen was studied under LSF (12). Suspected soft tissues were visible on this specimen under white light. However, Solnhofen specimens are known to have flow lines around the skeleton due to taphonomic processes, which could be misinterpreted as soft tissues. The use of LSF provides a geochemical signature of the area and showed that the areas in question fluoresced pink, similar to other specimens with known soft tissue preservation (13). The use of LSF also revealed other areas of soft tissue preservation within the skeleton. A 405-nm blue laser diode was projected from a line lens and scanned over the specimen in a dark room using standard laser safety protocol. Long exposure photographs over 30 s were taken with a Nikon digital single-lens reflex camera fitted with a 425-nm laser blocking filter. These photographs were postprocessed in Adobe Photoshop CS6 for equalization, saturation, and color balance.

Under LSF, the soft tissues and bones fluoresced in pink and cream colors, respectively (Fig. 1). The right brachioptagium, along with sections of the proptagium and uropatagium are observed. The proptagium of BSP 1937 I 18 is represented by a faintly striated section on the right wing. The leading edge runs from the proximal end of the humerus to the pteroid

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The authors declare no competing interest.

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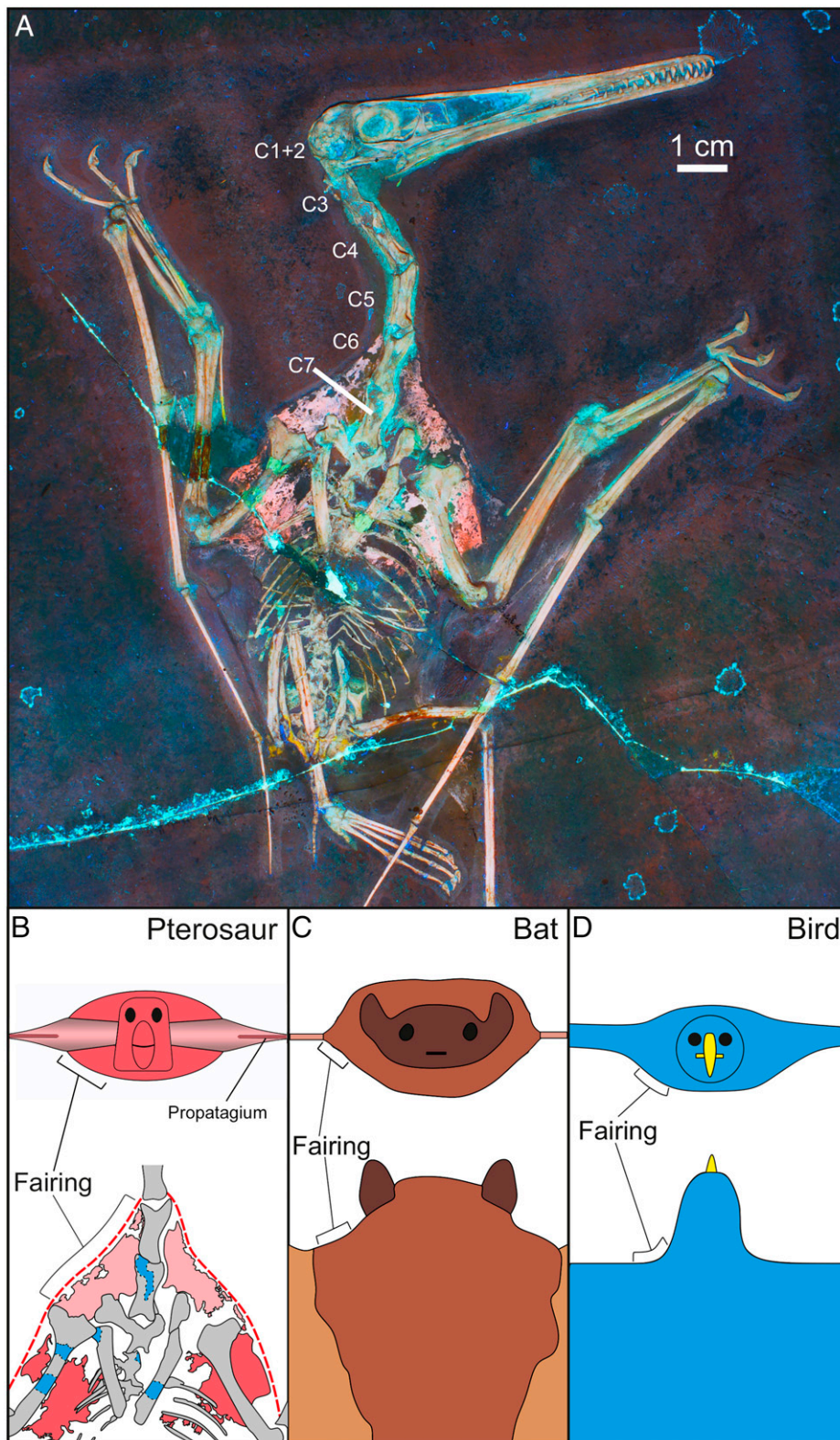


Fig. 1. Pterodactyloid pterosaur BSP 1937 I 18 reveals soft tissues around the base of the neck, the shoulders, and the upper arm. BSP 1937 I 18 was recovered from the Late Jurassic Solnhofen Limestones of Southern Germany. (A) Observed soft tissues around the base of the neck, the shoulder, and the forewing (brachium). (B) Conceptual drawing of the wing root fairing (light pink) in life in anterior view as well as its two-dimensional preservation in the fossil. (C) Bats have a fur-dominated wing root fairing (anterior and dorsal view). (D) Birds have a feather-dominated wing root fairing (anterior and dorsal view).

bone. This membrane has a lighter pink fluorescence color than other soft tissues. There are extensive soft tissues preserved around the base of the neck, shoulders, and forewing (brachium). This shallow propatagium arrangement is also evident in the Vienna specimen of *Pterodactylus antiquus* (figure 19.12 in ref. 1). Actinofibrils within the right dactylopatagium are evident through marked striations present across the length of the wing (14). These striations are also present to a lesser extent on the left-wing surface. Toward the proximal end of the right-wing finger, the membranous material preserved fluoresces pink. This is also the case for a preserved section of the right uropatagium, near the knee joint. This membrane sweeps broadly from a third of the way up the tibia toward the hip.

BSP 1937 I 18 provides direct evidence of a biological wing root fairing in a pterosaur. This drag-reducing feature provides a wide outline for the animal to smooth airflow across the wings and is composed of extensive soft tissue between the cranial end of the sixth cervical vertebrae (counting the atlas and axis separately) and proximal end of the humerus (Fig. 1 A and B). This soft tissue structure contrasts with previous reconstructions that lack this feature (figure 12 in ref. 15). We interpret the imaged soft tissue making up the fairing as being primarily composed of skeletal muscle because the forewing (brachium) muscle also shows pink fluorescence. The fairing streamlined the contours of the wing root created by the brachium musculature bulging outside the planar contour of the wing membrane.

The visualized musculature appears to have integrated into the propatagial membrane (Fig. 1 A and B). These skeletal muscles likely ran throughout the wing membrane, as has been shown for other specimens (16, 17). At full span, Palmer and Dyke (18) proposed that limb articulation was sufficient to keep the membrane tensioned during soaring. In other flight modes, such as during the flight stroke or increased soaring speed, the wing would not be at full span. The skeletal muscles could have contributed to continuous, active camber and flutter control throughout the wing stroke or reduced span. These muscle-mediated control benefits would be further enhanced if they were performed locally/differentially across the wing, e.g., to create reflex camber as discussed by Palmer and Dyke (18).

Birds and bats also use muscles within the wing membrane for camber and flutter control. Such additional membrane control is also important at high speeds in flapping flight, as some living membrane flyers, such as bats, achieve speeds over 25 m/s (19). We therefore propose that pterosaurs made even more extensive use of muscle-mediated regional wing surface control on account of their single-spar membrane wing morphology.

Unfortunately, the wing root fairing muscle is only preserved in two-dimensions in BSP 1937 I 18 and does not show direct evidence of camber, unlike in similarly preserved early birds like *Anchiornis*, which show shading gradients suggesting camber (12). The fairing muscle is expected to be no thicker than the muscle's anchor points on the neck and on the proximal end of the humerus. The fairing musculature looks to have been made up of some kind of extrinsic back complex (perhaps a trapezial–deltoid complex), and it may have contributed to wing elevation and/or anterior wing motion during the flight stroke, suggesting an additional force generation function.

The wing root fairing visible in BSP 1937 I 18 is similar to adaptations for drag reduction seen in bats and birds, but their configurations are individually distinctive. Fur around the necks of many bats smooths out the transition from the wing to the body. In birds, the feather covering smooths out the bulbous body outline and long neck into a fusiform shape (5). We observed that the fairing in BSP 1937 I 18 is formed of soft tissue body contours. Such a fairing muscle supports the aerodynamic requirements of the mobile insectivore ecology proposed for this pterodactyloid pterosaur (20). This would have benefitted from the fairing muscle's role in aerodynamic smoothing, camber and flutter control as well as wing force generation. Our study underscores the power of new instrumentation in improving our understanding of pterosaur flight anatomy and evolution.

Data Availability. All study data are included in the main text.

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1. M. P. Witton, *Pterosaurs: Natural History, Evolution, Anatomy* (Princeton University Press, Princeton, 2013).
2. E. Jacobs, K. Ward, *Interference of Wing and Fuselage From Tests of 209 Combinations in the N.A.C.A. Variable-Density Test Tunnel*. Langley Field (National Advisory Committee for Aeronautics, 1935).
3. A. Anscombe, D. J. Raney, *Low-Speed Tunnel Investigation of the Effect of the Body on C_m and Aerodynamic Centre of Unswept Wing-Body Combinations* (Aeronautical Research Council Current Papers, 1950), p. 16.
4. M. Maughmer, D. Hallmann, R. Ruzkowski, G. Chappel, I. Waitz, Experimental investigations of wing-fuselage integration geometries. *AIAA J. Aircraft*. (8):705–711 (1989).
5. D. G. Homberger, K. N. de Silva, Functional microanatomy of the feather-bearing integument: Implications for the evolution of birds and avian flight. *Am. Zool.* 40, 553–574 (2000).
6. D. B. O. Savile, Adaptive evolution in the avian wing. *Evolution* 11, 212–224 (1957).
7. R. E. Brown, J. J. Baumel, R. D. Klemm, Anatomy of the propatagium: The great horned owl (*Bubo virginianus*). *J. Morphol.* 219, 205–224 (1994).
8. M. Habib, T. Whitlatch, *Flying Monsters: Illustrating Flying Vertebrates Real and Imagined* (Design Studio Press, Los Angeles, 2021).
9. C. Palmer, Flight in slow motion: Aerodynamics of the pterosaur wing. *Proc. Biol. Sci.* 278, 1881–1885 (2011).
10. F. Broili, *Beobachtungen an Pterodactylus* (Bayerischen Akademie der Wissenschaften, München, 1938).
11. S. U. Vidovic, D. M. Martill, *Pterodactylus scolopaciceps* Meyer, 1860 (Pterosauria, Pterodactyloidea) from the Upper Jurassic of Bavaria, Germany: The problem of cryptic pterosaur taxa in early ontogeny. *PLoS One* 9, e110646 (2014).
12. X. Wang et al., Basal paravian functional anatomy illuminated by high-detail body outline. *Nat. Commun.* 8, 14576 (2017).
13. C. Foth, C. Haug, J. T. Haug, H. Tischlinger, O. W. M. Rauhut, "Two of a feather: A comparison of the preserved integument in the juvenile theropod dinosaurs *Sciurumimus* and *Juravenator* from the Kimmeridgian Torleite Formation of Southern Germany" in *The Evolution of Feathers* C. Foth, O. Rauhut, Eds. (Springer, Cham, 2020). pp. 79–101.
14. S. C. Bennett, Pterosaur flight: The role of actinofibrils in wing function. *Hist. Biol.* 14, 255–284 (2000).
15. S. Chatterjee, R. Templin, Eds., *Posture, Locomotion, and Paleoecology of Pterosaurs* (Geological Society of America, Boulder, CO, 2004).
16. A. W. A. Kellner et al., The soft tissue of *Jeholopterus* (Pterosauria, Anurognathidae, Batrachognathinae) and the structure of the pterosaur wing membrane. *Proc. Biol. Sci.* 277, 321–329 (2010).
17. S. C. Bennett, New interpretation of the wings of the pterosaur *Rhamphorhynchus muensteri* based on the Zittel and Marsh specimens. *J. Paleontol.* 89, 845–869 (2016).
18. C. Palmer, G. Dyke, Constraints on the wing morphology of pterosaurs. *Proc. Biol. Sci.* 279, 1218–1224 (2012).
19. G. F. McCracken et al., Airplane tracking documents the fastest flight speeds recorded for bats. *R. Soc. Open Sci.* 3, 160398 (2016).
20. J. Bestwick, D. M. Unwin, R. J. Butler, M. A. Purnell, Dietary diversity and evolution of the earliest flying vertebrates revealed by dental microwear texture analysis. *Nat. Commun.* 11, 5293 (2020).