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# New interpretation of the wings of the pterosaur *Rhamphorhynchus muensteri* based on the Zittel and Marsh specimens

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**Abstract.**—The Zittel wing of *Rhamphorhynchus muensteri* is reinterpreted as preserving negative impressions of closely spaced broad flat actinofibrils that were replaced by calcite but were prepared away by the specimen's finder. The Marsh specimen preserves positive impressions of the dorsal and ventral surfaces of the wing, which show that the skin was smooth with fine wrinkles and that actinofibrils were not on the wing surface. Based on comparisons of those specimens, the dactylopatagium consisted of dorsal and ventral skins of epidermis and dermis surrounding a common hypodermis core, and keratinous actinofibrils developed in place within the dorsal epidermis adjacent to a layer of linear collagen fibers in the dorsal dermis. The actinofibrils and linear collagen fibers together formed the main functional structure of the dactylopatagium. That structure made the dactylopatagium somewhat stiff and essentially inextensible so that it folded up along discrete fold lines that probably were genetically determined. A pneumatic retrophalangeal wedge behind the antebrachium through at least wing phalanx 3 streamlined the transition between the thick wing spar and thin patagium.

## Introduction

The wings of pterosaurs have intrigued researchers for more than 100 years, and one of the first found and most important specimens preserving evidence as to the structure of the pterosaur wing is the so-called Zittel wing of *Rhamphorhynchus muensteri* (Goldfuss, 1831). It is an isolated left wing skeleton exposed in ventral view, fully articulated with the elbow and wingfinger flexed, that preserves a seemingly undamaged wing membrane or patagium. Zittel (1882) described the specimen and noted a radiating pattern of fine, almost straight, raised longitudinal strips that nearly paralleled the wing phalanges in the lateral part of the patagium and became more anteroposteriorly angled in the medial part. He compared the wing to that of bats and suggested that the strips functioned like the network of elastic fibers in bat wings. That same year, Marsh (1882) described another *Rhamphorhynchus* specimen that preserved soft tissues of the patagia, but mentioned only folds and fine striae that he interpreted as wrinkles. Subsequent authors ignored Marsh's specimen and followed Zittel in interpreting the raised longitudinal strips of the Zittel wing as structural fibers of some type, termed them actinofibrils in recognition of their radiating pattern, and interpreted actinofibrils as internal, elastic, and forming a reinforcing system within the patagium (e.g., Wellnhofer, 1975) or as external, keratinous, and transferring lift forces to the wing spar (e.g., Padian and Rayner, 1993).

I examined the Zittel wing in 1988 and 1993 and accepted Padian and Rayner's (1993) interpretation of the structure and position of actinofibrils. However, based on that interpretation of structure I argued against previous interpretations of actinofibril function and for an interpretation that actinofibrils prevented narrowing of the patagium under tension and redirected spanwise tension to the proximal wing phalanges, reducing loads on the distal wing phalanges (Bennett, 1995, 2000). My interpretation of actinofibril function went largely unchallenged, but in 2008 I decided to reexamine the available evidence as to the structure of pterosaur patagia and photographed the Zittel wing for high-resolution mapping of the distribution of actinofibrils and other structures. Subsequently, while processing the photographs and maps I became convinced that the raised longitudinal strips of the Zittel wing are not the actual structural elements that imparted special properties to the patagium (i.e., actinofibrils) preserved in place or positive impressions of such structures, but rather represent the spaces between negative impressions of the actual structural elements; so for 130 years we have misunderstood the Zittel wing's message. This paper presents redescriptions of the Zittel wing and Marsh specimen, and a reinterpretation of the structure and relations of actinofibrils and the structure of the wings of *Rhamphorhynchus* based on those specimens. Note that the present paper is not a continuation of my previous paper on actinofibril function (Bennett, 2000); whereas that paper was a reinterpretation of function based on others' interpretations of structure, the present paper is a reinterpretation of structure based on new examinations of important specimens. However at the end of this paper, I briefly review the interpretation of actinofibril function from my 2000 paper in light of the new interpretation of structure and present corrections necessitated by the new understanding of structure.

*Institutional abbreviations*.—BSP, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, People's Republic of China; JME SOS, Jura-Museum (Solnhofen Sammlung), Eichstätt, Germany; MB.R., Humboldt Museum, Berlin, Germany; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.;

NHMW, Naturhistorisches Museum Wien, Vienna, Austria; SNSD-MMG, Senckenberg Naturhistorische Sammlungen Dresden, Museum für Mineralogie und Geologie, Germany; and YPM, Peabody Museum of Natural History, Yale University, New Haven, U.S.A.

## Literature review

One of the most important specimens preserving evidence as to the structure of the pterosaur wing is the Zittel wing of *Rhamphorhynchus muensteri* (BSP 1880 II 8; Fig. 1.1) from the Upper Jurassic Solnhofen Limestone at Wintershof, an isolated left wing skeleton with a seemingly undamaged impression of the patagium exposed in ventral view, which based on the catalog number was probably acquired by the museum in 1880. Zittel (1882) soon described the specimen, beginning with the following:

> “This glorious fossil was found on the Winterberg near Eichstädt and purchased through the agency of the kind Herrn Geistlichen Rathes [Raymund] Schlecht for the local State Museum. The solid, 2 cm. thick slab contains the left flight-organ in completely undisturbed condition, the wing membrane is not torn or broken, but is imprinted in impeccable sharpness from its extreme tip to the attachment to the trunk. It differs sharply from the surrounding rock mass by somewhat lighter coloring and even more from the yellow-colored bones. Although its margin, as seen clearly even now, was very clearly demarcated, the finder was not satisfied with the breaking off of the rock, which covered the wing membrane initially, but also scraped and smoothed the surroundings thereof, apparently with the intention thereby to bring out the patagium even sharper.” (Zittel, 1882, p. 52; translated from the original German)

Zittel went on to note 8–10 prominent longitudinal folds and a pattern of fine, almost straight, raised longitudinal strips (*Längsstreifen*, also referred to as *erhabenen Streifen*) that nearly paralleled the wing phalanges in the lateral part of the patagium and became progressively more anteroposteriorly angled in the medial parts. He noted that some of the strips were larger than surrounding ones and compared them to ossified tendons. The wing was compared to that of gliding lizards (*Draco* spp.) and bats, and though it was noted that the *Rhamphorhynchus* wing differed significantly from both, it was suggested that the raised longitudinal strips were functionally comparable to the elastic fibers in bat wings.

Six months earlier, Marsh (1882) had described another specimen of *Rhamphorhynchus muensteri* (YPM 1778; Fig. 2) with excellent preservation of parts of both wing membranes and the tail vane, which had been found in the Solnhofen Limestone at Eichstätt in 1873. Marsh purchased the specimen while at work on the American *Pteranodon* materials, but delayed publishing until finished with *Pteranodon*. The patagia of the specimen were only briefly described as being partially folded and having a smooth surface with delicate striae that were interpreted as wrinkles, and the membrane was interpreted as similar to that of bats.

Subsequently, additional wing specimens of *Rhamphorhynchus muensteri* from the Solnhofen Limestone at Eichstätt and Schernfeld were described. Wanderer (1908) described the Dresden specimen (SNSD-MMG BaJ 2210), which preserves an impression of the right wing in ventral view, and stated that it agreed with Zittel’s description in all details, though the impression distal to the first interphalangeal joint of the wingfinger was covered by a thin layer of matrix that could not be prepared away. Ammon (1909) briefly described a specimen (BSP AS I 772; MB.R. 69/2191b) that preserves impressions of both wings with the distal part of the patagium of one wing detached from wing phalanx 4. Döderlein (1929a) described a specimen (BSP 1907 I 37) that preserves traces of the patagium and the tail vane, and noted fine parallel raised strips, closely spaced at 25–35 per 10 mm. Following Zittel (1882), Döderlein interpreted the strips as elastic fibers. Meanwhile, Short (1914) interpreted the pterosaur patagium as bat-like, elastic, and extensible, a view that was later shared by Bramwell and Whitfield (1974).

Wellnhofer (1975) presented a review of the structure of the wings of *Rhamphorhynchus* based on the ~20 specimens then known to preserve traces of soft tissues, and observed that the fact that naturally articulated forelimbs commonly occur as isolated specimens or as part of otherwise disarticulated specimens indicates that the patagium was much more resistant to decay than most soft tissues and so must have been coarse, leathery, and tough. Wellnhofer referred to the parts of the patagium as the propatagium anterior to the arm and forearm and controlled by the pteroid bone, the chiropatagium posterior to the arm, forearm, and wingfinger and attaching to the side of the body but not the hindlimb, and the uropatagium posterior to the hindlimb and attaching to pedal digit V. He provided the first measurements of the raised longitudinal strips of the Zittel wing (referring to it as BSP AS I 771 because the original number was misplaced in World War II and had not yet been recovered; O. Rauhut, personal communication, 2012), stating that their width was ~0.05 mm and that they were spaced very evenly in the taut patagium at 0.2 mm apart so that they were 18–20 fibers per 5 mm. Wellnhofer followed Zittel in interpreting the raised longitudinal strips as elastic fibers that reinforced the patagium without limiting its elasticity, and although he did not comment on the distribution of the fibers, his life reconstruction of *Rhamphorhynchus* suggests that he thought they were present throughout the chiropatagium.

Schaller (1985) presented a theoretical review of wing evolution and introduced many new terms including tenopatagium, which he defined as a formlabile tensile flight-membrane, and actinopatagium, which he defined as a formstabile self-cambering ray-structured flight-membrane. He interpreted the wings of the rhamphorhynchoid *Sordes* as representing the archetypal pterosaur pattern with a propatagium anterior to the arm and forearm, a tenopatagial plagiopatagium posterior to the arm and forearm and attaching to the side of the body and hindlimb, an actinopatagial dactylopatagium posterior to the wingfinger and lateral to the plagiopatagium, and a uropatagium posterior to the hindlimb and attaching to pedal digit V. Schaller argued that in derived pterosaurs (e.g., *Rhamphorhynchus*, *Pterodactylus*) the entire membrane behind the forelimb (equivalent to the chiropatagium of Wellnhofer, 1975) was actinopatagial and free of the hindlimb, and included a tongue-like, flap-controlling actuator behind the elbow. He termed this derived membrane a brachiopatagium and viewed it as a self-supporting, self-cambering structure. Most of Schaller’s

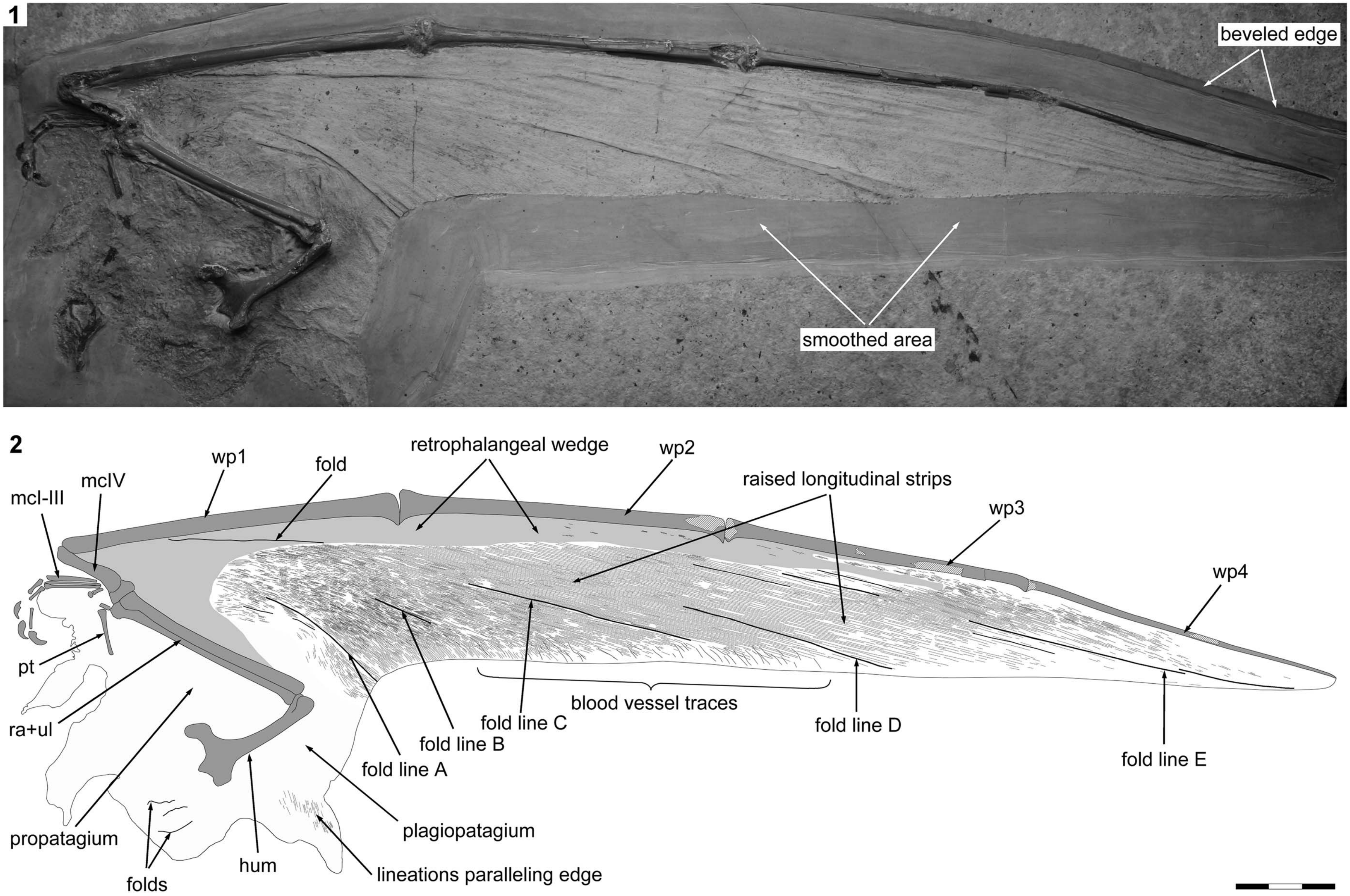

**Figure 1.** Zittel wing of *Rhamphorhynchus muensteri*, BSP 1880 II 8. (**1**) Articulated left wing skeleton and associated soft tissue traces of the patagium in ventral view; (**2**) map of structures and impressions with bones shaded medium gray, retrophalangeal wedge shaded light gray, raised longitudinal strips indicated by thin black lines, folds in the plagiopatagium, dactylopatagium, and retrophalangeal wedge indicated by heavy black lines, and blood vessel traces indicated by dark gray lines. Abbreviations: hum, humerus; mc, metacarpal; pt, pteroid; ra + ul, radius and ulna; and wp, wing phalanx. Scale bar represents 3 cm.

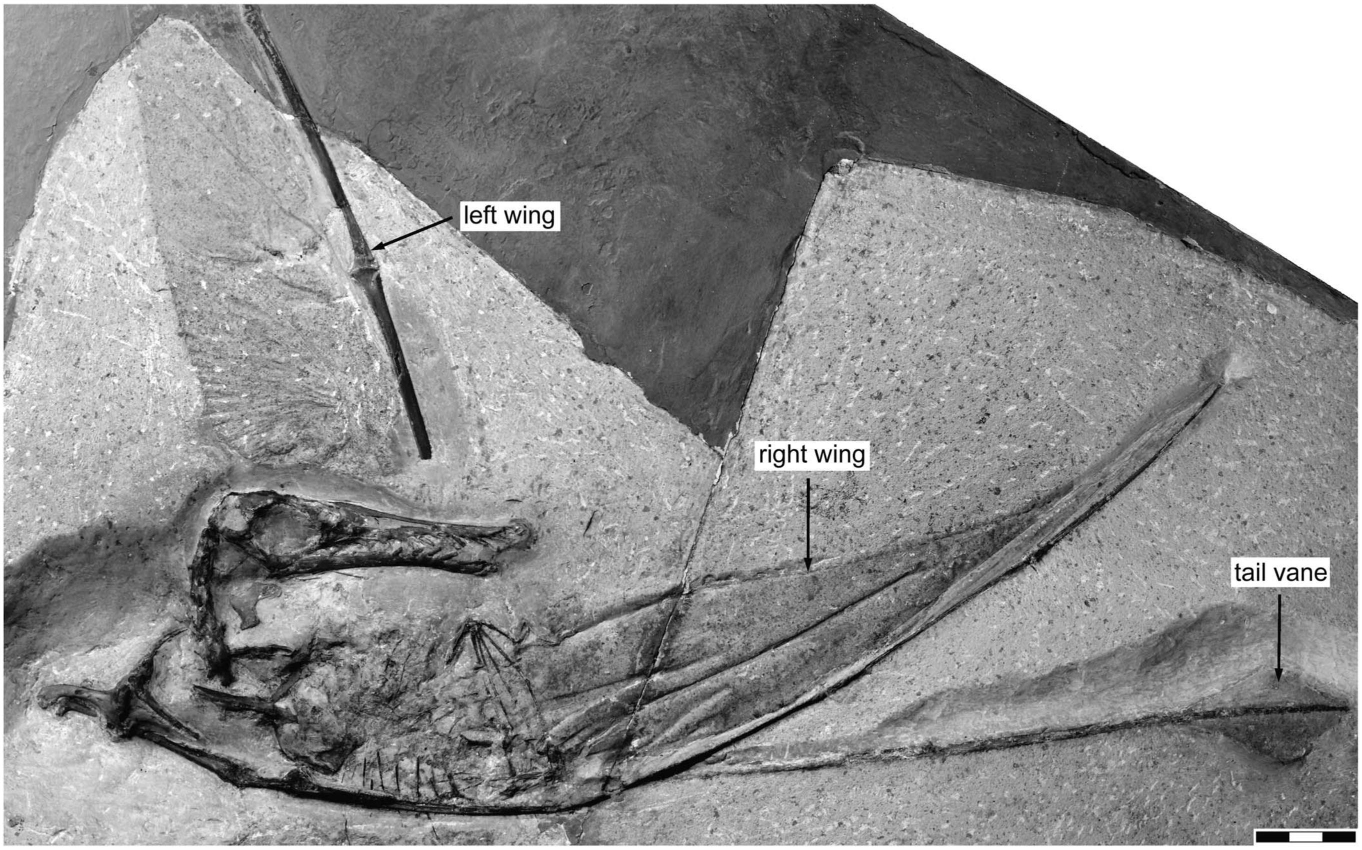

**Figure 2.** Marsh specimen of *Rhamphorhynchus muensteri*, YPM 1778. Nearly complete articulated skeleton and associated soft tissue traces of the patagia and tail vane in ventral view. Scale bar represents 3 cm.

new terms have not gained acceptance, but Wellnhofer (1987) and some subsequent authors (e.g., Bennett, 2000; Frey et al., 2003; Kellner et al., 2010) used the terms brachiopatagium, tenopatagium, and actinopatagium, though not necessarily in Schaller's original sense. Schaller (2007) developed his ideas further and suggested that most pterosaurs had fore and hind wings supported by the fore- and hindlimbs, respectively.

Wellnhofer (1987) described the Vienna specimen of *Pterodactylus antiquus* (Sömmerring 1812) (NHMW 1975/1756/0000) from the Solnhofen Limestone, which is fully articulated and preserves traces of soft tissues of the body and wings. Wellnhofer noted fine parallel striations many of which were made visible by dendritic deposits of manganese and iron oxides in much of the patagium, interpreted the striations as part of the reinforcing system he proposed in his 1975 paper, and reconstructed the reinforcing fibers as present throughout the entire membrane spread between the forelimb, trunk, and hindlimb, which following Schaller (1985), he termed the brachiopatagium. Wellnhofer summarized Zittel's observations of the raised longitudinal strips in the wing of *Rhamphorhynchus* though he referred to them as reinforcing fibers or rays (*Verstärkungsfasern oder -strahlen*), and repeated his earlier description of their size and spacing. He then proposed the term *Aktinofibrillen* (= actinofibrils), which he derived from Schaller's term actinopatagium, for the supposed reinforcing fibers in the Vienna *Pterodactylus* and the Zittel wing, and presented a schematic reconstruction of the cross-section of the brachiopatagium with cylindrical actinofibrils dimensioned according to his measurements from the Zittel wing (i.e., 0.05 mm in diameter and spaced 0.2 mm apart) and lying in the middle of the brachiopatagium (Fig. 3.1).

Pennycuick (1988) was not convinced that the raised longitudinal strips of the Zittel wing represented solid fibers and instead interpreted them as epidermal wrinkles produced by contraction of internal elastic fibers running chordwise from the wing spar to the trailing edge. He noted that fractures across the strips showed no internal structure, and stated that:

> "Although not disputing that the ridges seen in the fossils are composed of matrix material, Wellnhofer [1975] argues that such sharply defined relief could not have been produced unless the particles of matrix were compacted in between fibers of some hard material. He considers that the original fibres would eventually decay, leaving compacted ridges in the matrix." (Pennycuick, 1988, p. 307)

Unfortunately, Wellnhofer made no such argument in his 1975 monograph nor did he make such a statement anywhere else (P. Wellnhofer, personal communication, 2012). Queries of Pennycuick and other colleagues have failed to produce an explanation or alternate source for Pennycuick's statement. I wonder if perhaps the statement resulted from a misreading on Pennycuick's part of the passage in which Wellnhofer (1975, p. 11–12) attributes the relative abundance of articulated *Rhamphorhynchus* wings to their being coarse, leathery, and tough. Pennycuick (1988, p. 308) also noted the parallel striations on the wings of the Vienna *Pterodactylus* as well as a "layer of

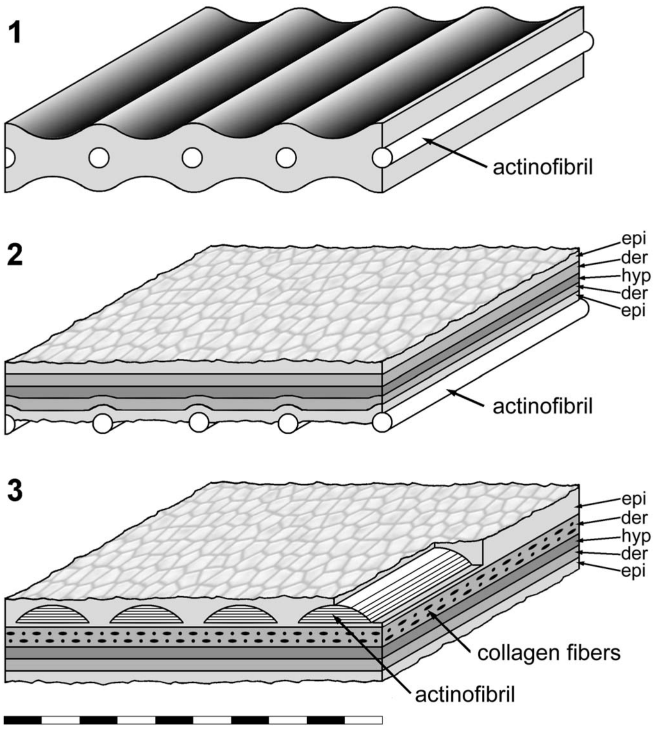

**Figure 3.** Schematic diagrams of cross-sections and dorsal surfaces of the brachiopatagium of *Rhamphorhynchus*. (**1**) Widely spaced cylindrical actinofibrils embedded within the patagium (after Wellnhofer, 1987); (**2**) widely spaced cylindrical actinofibrils on the undersurface of a patagium consisting of dorsal and ventral skins of epidermis (light gray) and dermis (medium gray) surrounding a common hypodermis (dark gray) core (after Padian and Rayner, 1993); (**3**) proposed model with closely spaced broad lenticular actinofibrils within the dorsal epidermis and a layer of collagen fibers within the dorsal dermis forming the functional layer of a dactylopatagium consisting of dorsal and ventral skins of epidermis and dermis surrounding a common hypodermis core. Scale bar represents 1 mm.

calcite that encrusted the original membrane," but dismissed the striations as "bundled-up portions of contracted membrane."

Martill and Unwin (1989) described soft tissues from a small section of a pterosaur specimen preserved in a concretion from the Santana Formation of Brazil, and interpreted them as consisting of the brachiopatagium near the ulna. They described a thin epidermis, a thicker dermis including a vesicular layer they compared to Böhm's (1962) stratum vasculosum of *Gallus*, a layer of amorphous organic matter that they compared to Hildebrand's (1988) stratum spongiosum, and a layer of closely spaced cylindrical structures they interpreted as muscle fibers. No actinofibrils were found. Martill and Unwin also did not find a second epidermis and dermis, which casts doubt on the interpretation of the specimen as wing membrane. Kellner (1996) had access to the remainder of the concretion from which Martill and Unwin (1989) obtained their section and argued that the soft tissues consisted of the skin and underlying musculature of the body wall behind the shoulder joint; in which case they would tell us nothing about the patagium. Unwin (personal communication, 2013) now interprets the layer of muscle fibers as actinofibrils; however, their arrangement (tightly packed in a layer ~5 fibers thick) and position (deep to the dermis, in which case they would not be keratinous) is incompatible with most if not all interpretations of actinofibrils. Regardless, unless a second epidermis and dermis can be identified, any interpretation of the specimen's soft tissues as wing membrane is tenuous.

Padian and Rayner (1993) presented a review of pterosaur wings and agreed with Wellnhofer (1975, 1987) that the raised longitudinal strips of the Zittel wing and the parallel striations of the Vienna *Pterodactylus* were the same, though they referred to them as structural fibers rather than as actinofibrils. They noted that pterosaur patagia would have consisted of dorsal and ventral skins of epidermis and dermis surrounding a common hypodermis core, and argued that the Zittel wing preserved the actual patagium rather than a positive impression of it and therefore that the actinofibrils were external. Furthermore, because the Zittel wing preserves the left wing in ventral aspect, they inferred that the actinofibrils were on the underside of the patagium (Fig. 3.2). Padian and Rayner stated that the actinofibrils were 0.05 mm wide and were spaced from 3 to 8 per mm, and like Wellnhofer (1987) seem to have interpreted actinofibrils as present throughout the patagium (Padian and Rayner, 1993, fig. 14). They stated that some actinofibrils appeared to bifurcate near the trailing edge of the patagium, and suggested that this appearance resulted from the posterior end of actinofibrils having been detached from the underlying membrane and displaced laterally to expose the grooves in which the actinofibrils had lain. They also interpreted the Marsh specimen as preserving actinofibrils. Padian and Rayner noted a narrow band of tissue immediately behind the wingfinger and interpreted it as lying ventral to the actinofibril layer and as possibly involved in the formation of actinofibrils and their attachment to the wing spar. In regard to function, nowhere in Padian and Rayner's paper is it stated or implied that tension within the patagium transmitted lift forces to the wing spar and body or that tension within the patagium enabled actinofibrils to transmit lift forces to the wing spar. Rather, although they did not use the word cantilever, it is implied that actinofibrils cantilevered the membrane behind the wing spar in the same way that feather shafts cantilever the feathers' vanes behind the forelimb in birds: "we argue that the structural fibers played a very similar role to bird feather shafts in transmitting aerodynamic force from the wing [sic] to the bones of the arm" (Padian and Rayner, 1993, p. 144), and "the wing-finger of pterosaurs had relatively little mechanical involvement in wing function" (Padian and Rayner, 1993, p. 140).

Unwin and Bakhurina (1994) described and illustrated soft tissue traces of the wings of *Sordes pilosus* Sharov (1971) from the Upper Jurassic Karabastau Formation of Karatau, Kazakhstan, which included long, straight, closely packed fibers in the chiropatagium behind the third interphalangeal joint and short multi-stranded fibers in the uropatagium. They suggested that the former fibers made the outer part of the wing stiff and relatively inelastic, but did not clearly state whether they interpreted the long and short fibers as the same or different.

Bennett (2000) followed Wellnhofer (1987) in referring to actinofibrils and brachiopatagium, and accepted that the raised longitudinal strips on the Zittel wing were actinofibrils that imparted special properties to the patagium, However, I rejected the interpretation that the entire brachiopatagium bore actinofibrils; rather I interpreted the pterosaur wing as Schaller (1985) had interpreted the wing of *Sordes* with a medial tenopatagial part and a lateral actinopatagial part. Perhaps I should have reverted to Wellnhofer's (1975) term chiropatagium, but the membrane is no more a hand-wing than an arm-wing, and I was aiming for stability. In addition, I used tenopatagium and actinopatagium not as Schaller (1985) had, for types of patagia, but rather for the medial and lateral parts of the brachiopatagium. I accepted Padian and Rayner's (1993) interpretation that pterosaur patagia consisted of dorsal and ventral skins of epidermis and dermis surrounding a common hypodermis core, and also accepted their interpretation that actinofibrils were on the undersurface of the patagia. I noted that superficial actinofibrils would be epidermal and keratinous, and because there is no evidence that they were elastic or that they stretched and contracted I interpreted actinofibrils as formed of a hard keratin that would better resist longitudinal compression. I argued against the previous interpretations of the function of actinofibrils, which I referred to as the stiffening element (Wellnhofer, 1975) and load-bearing element (Padian and Rayner, 1993) interpretations on the grounds that elastic actinofibrils would not stiffen or stabilize the brachiopatagium and keratinous fibers alone would not be stiff enough to resist dorsoventral bending to camber the brachiopatagium and transfer aerodynamic loads to the wing spar. I presented a new interpretation of their function: actinofibrils prevented narrowing of the patagium under tension and redirected spanwise tension to the proximal wing phalanges, reducing loads on the distal wing phalanges. I argued that the combination of actinofibrils and an elastic membrane including collagenous and elastic fibers in the dermis would produce a composite fabric that transmitted lift forces to the wing spar and body by tension, spread the brachiopatagium chordwise, maintained the chord even as tension increased from aerodynamic loading, and redirected spanwise tension in the brachiopatagium into chordwise loads on the wingfinger. This interpretation, which I called the spreading element interpretation, explained the pattern of radiating actinofibrils in the lateral part of the brachiopatagium and their absence from the medial part.

Czerkas and Ji (2002) described the rhamphorhynchoid *Pterorhynchus wellnhoferi* Czerkas and Ji (2002) from the Haifanggou Formation of Inner Mongolia, which preserves a soft tissue cranial crest and extensive traces of a hairy body covering on the neck and trunk. They claimed that it also preserved part of the brachiopatagium with actinofibrils; however, the supposed patagium is a lanceolate leaf with parallel venation coincidentally preserved near the skeleton, so the specimen provides no evidence as to pterosaur patagium structure.

Frey et al. (2003) described the internal structure of the brachiopatagium based on visible and ultraviolet (UV) light examinations of a specimen of *Rhamphorhynchus muensteri*, JME SOS 4784, from the Solnhofen Limestone. They identified three different layers within the patagium: a layer of actinofibrils averaging 0.2 mm in diameter, ranging from 30 to 80 mm in length, and bifurcating near the trailing edge; a layer consisting of bifurcating and merging longitudinal strings that lay ventral to the actinofibril layer and crossed the actinofibrils at angles of 30°–90°; and a vascular layer with one large vessel subparallel to the wing phalanges giving rise to smaller branches and loops. They noted that the large vessel and branches are also preserved on the Vienna specimen of *Rhamphorhynchus* (NHMW 1998z0077/0001) and that traces of them are visible on the Zittel wing under UV illumination. Frey et al. (2003) rejected Kellner's (1996) criticisms of Martill and Unwin's (1989) interpretation of the structure of the patagium in the supposed Santana wing specimen, and conflated Martill and Unwin's (1989) interpretation with their own evidence from JME SOS 4784 in order to conclude that pterosaur brachiopatagium consisted of at least five layers: a thin dorsal epidermis, a spongy subdermis, the actinofibril layer, a layer of muscle fibers that presumably included the longitudinal strings, and a ventral vascular layer; although note that neither dorsal dermis nor ventral epidermis and dermis were mentioned. Frey et al. (2007) expanded the reconstruction in a popular article, suggesting that the spongy subdermis was pneumatic and that contraction of the muscle fibers resisted by actinofibrils would have enabled active control of camber.

Tischlinger and Frey (2010) described the band of soft tissue that Padian and Rayner (1993) had noted just behind the wing phalanges of the Zittel wing on two new specimens of *Rhamphorhynchus muensteri*. They characterized the band of tissue as massive and interpreted it as forming a streamlined transition between the thick wing phalanges and thin patagium, and as representing the:

> "insertion tissue for the aktinofibrills [sic], which probably interwove with the connective tissue of the wedge. Thus, the wedge itself effected force transduction between aktinofibrills and the wing skeleton." (Tischlinger and Frey, 2010, p. 64)

In an extended abstract, Monninger et al. (2012) interpreted the band as dense fibrous connective tissue that reinforced the interphalangeal joints of the wingfinger to keep them fully extended in addition to streamlining the transition between the wing phalanges and patagium. They suggested this was necessary because there was no evidence of strong interphalangeal ligaments. They also argued that there was a trailing edge structure that they termed a trailing edge ligament.

Kellner et al. (2010) described the patagia of the anurognathid *Jeholopterus ningchengensis* Kellner et al. (2010) (IVPP V12705) from the Daohugou Beds of Inner Mongolia. They used the term plagiopatagium for the entire membrane between the fore- and hindlimbs, but followed Bennett (2000) in using tenopatagium and actinopatagium for its medial and lateral parts. They described three types of fibers: small, closely spaced, parallelly arranged fibers up to 0.1 mm thick and 4–8 mm long, which they interpreted as actinofibrils; less abundant, larger, and much longer fibers that they suggested might also be actinofibrils; and short branching hair-like structures they termed pycnofibers. They described two layers of actinofibrils close to the wing phalanges with the more dorsal layer subparallel to the wing phalanges and smaller, thinner, and more closely spaced than the other more ventral layer that was oblique to the wing phalanges. They also stated that in places the specimen had three or more layers of actinofibrils with different fiber orientations, yet seemed to reject the possibility that the appearance of multiple layers resulted from overlapping layers of a folded patagium. Kellner et al. (2010, p. 327) rejected the interpretation that actinofibrils were external and keratinous, instead interpreting them as internal structures that "could potentially shorten or expand and therefore provide more flexibility to the wing membrane," and yet suggested that their model was not incompatible with Padian and Rayner's (1993) load-bearing element interpretation or my spreading element interpretation (Bennett, 2000).

## Materials and methods

The Zittel wing (BSP 1880 II 8) and the Marsh specimen (YPM 1778) were examined with optical microscopes and photographed with an 18 MP digital SLR camera and macro lens at minimum focal distance to produce several vertically overlapping rows of multiple laterally overlapping high-resolution images, which were composited into a single large TIFF photomosaic using Microsoft Image Composite Editor (Version 1.4.4.0, Microsoft Corporation, Redmond, WA). In the case of the Zittel wing, 130 overlapping images were composited into a 422 MB TIFF photomosaic with a resolution of ~91 pixels/mm. The photomosaic images were temporarily divided into smaller sections in separate files that were processed using Paint Shop Pro 8 (Jasc Software, Minneapolis, MN) and Photoshop CS5 Extended (Adobe Systems, San Jose, CA) to map various features of the specimen (e.g., bones, raised longitudinal strips, folds) onto separate layers. Subsequently, the sections and layers were reassembled.

As for terminology, on the limestone slabs places where bones or soft tissues were pressed into the sediment at the bottom of the Solnhofen lagoons and produced a mold of the external surface of the underside of the structures (as a foot pressed into damp sand produces a footprint) are referred to as negative impressions. Similarly, where sediment covered over bones or soft tissues and produced a mold of the external surface of the upper side of the structures are referred to as negative impressions. Thus negative impressions may be on both the lower and upper slabs. Places where soft tissues were pressed into the sediment and produced a negative impression on the lower slab but decayed away so that the sediments that formed the upper slab filled the negative impression on the lower slab and produced an opposite and complementary shape (as plaster poured into a footprint takes a cast) are referred to as positive impressions. In some instances soft tissues may have resisted decay long enough to produce negative impressions on the lower and upper slabs but decayed away to leave a void between the slabs. Where waterborne minerals precipitated and filled the void, they produced a three-dimensional cast of the soft tissues that reproduces the shape of the soft tissues and the external surfaces of their upper and under sides. The term trace is used not in the sense of trace fossils, which typically preserve the interaction of a living organism with sediments (e.g., footprints, burrows), but rather as a more inclusive term for all sorts of evidence of soft tissues (e.g., impressions, brownish carbonaceous organic films, fluorescence under UV illumination).

Following Wellnhofer (1987) and Bennett (2000), the terms propatagium, brachiopatagium, and uropatagium are used to refer to the parts of the patagium anterior to the forelimb, between the fore- and hindlimbs, and behind the hindlimb, respectively. Schaller's (1985) terms plagiopatagium and dactylopatagium are used for the parts of the brachiopatagium behind the brachium through carpus, and behind the wingfinger, respectively, and Fold Line A is arbitrarily used as the dividing line between the plagiopatagium and dactylopatagium. The term actinofibril is restricted to the actual structural elements arranged in a posterolaterally radiating pattern within the dactylopatagium and lateral plagiopatagium that are considered to have imparted special properties to the dactylopatagium. Bennett (2000) thought that the significant difference between the medial and lateral parts of the brachiopatagium of *Rhamphorhynchus* was the presence and absence of actinofibrils and so used Schaller's (1985) terms tenopatagium and actinopatagium for the medial and lateral parts of the brachiopatagium rather than for types of patagia as Schaller had used them. I now think that Schaller's division into plagiopatagium and dactylopatagium better describes the difference between the medial and lateral parts of the brachiopatagium and so will use those terms and will not use tenopatagium and actinopatagium except in their adjectival forms in Schaller's original sense for types of patagia. It is argued below that the raised longitudinal strips of Zittel (1882), which he and subsequent authors interpreted as structural fibers of some sort, are not traces of the actual structural fibers and so should not be called actinofibrils; therefore, I retain Zittel's term. The term striae is used to refer to shallow epidermal grooves such as those that Marsh (1882) noted on the wings of YPM 1778. Prominent ridges or grooves in soft tissue impressions that resulted from the folding of the patagium are referred to as folds, and linear features about which the patagium preferentially folded are referred to as fold lines. The band of soft tissue just behind the wingfinger (Padian and Rayner, 1993; Tischlinger and Frey, 2010; Monninger et al., 2010) is termed the retrophalangeal wedge. Following Wellnhofer (1975), filamentous structures protruding from the skin of *Rhamphorhynchus* are referred to as hair; the term pycnofiber (Kellner et al., 2010) does not apply because none of the filamentous structures seem to be branched.

## Description of the Zittel wing

The Zittel wing (BSP 1880 II 8; Fig. 1) is an isolated left wing exposed in ventral view on the underside of an upper slab, fully articulated with the elbow, wrist, and fourth metacarpophalangeal (MCP) joint flexed more or less as they might be for terrestrial locomotion, which preserves an impression of a seemingly undamaged patagium. The bedding plane of the specimen lay 5–7 mm below the surface of the limestone slab, and in preparing the specimen the finder removed the covering matrix, scraped and smoothed the surrounding matrix for a distance of ~1–2.5 cm, and carved a beveled edge around the smoothed area. Note that there is no evidence that the scraping and smoothing altered the shape of the impression or removed any soft tissue traces. The left wing skeleton is essentially complete and articulated from the humerus to wing phalanx (WP) 4. The individual elements of the carpus are difficult to discern, the preaxial carpal and pteroid are anterior to the carpus with the pteroid directed medially. Metacarpals (Mc) I–III are displaced medially somewhat relative to Mc IV. Two phalanges of digits I–III are displaced near the base of Mc I, and one phalanx seems to be missing. Wing phalanges 1–4 are 105, 99, 90, and 91 mm long, respectively, and the estimated wingspan of the specimen in life using my standard method (Bennett, 2001) is 102 cm. The brachiopatagium has a rounded tip of ~4 mm radius and a gradually increasing chord as preserved of about 27, 39, and 44 mm behind the third through first interphalangeal (IP) joints, respectively, which results in a trailing edge that is rather straight behind WP2–4 before arcing posteromedially toward the hindlimb. Viewed from a moderate distance one can see the bones of the wing skeleton and a series of undulations and occasional prominent folds in the dactylopatagium, but on closer examination the most abundant features are the raised longitudinal strips. Also visible are gouges and tool marks, the retrophalangeal wedge, and blood vessel traces. These features will be described below, and with the exception of the undulations, gouges, and tool marks, they were mapped and are shown in Figure 1.1.

*Medial part of the impression*.—The medial part of the soft tissue impression consists of traces of the propatagium, the plagiopatagium, and probably some of the skin of the lateral trunk. The margins of the impression were cleaned up by the specimen's finder, who scraped and smoothed the limestone, but only the trailing edge of the plagiopatagium near the humerus can be accepted as the actual margin of the wing in life. The area of the propatagium in the angle between the humerus and antebrachium is irregularly textured and provides no information as to the structure or extent of the propatagium. Those parts medial to digits I–III and anterior and medial to the pteroid are stained with iron oxide, and a tongue-shaped flap preserves traces of integumentary hairs highlighted with iron oxide. Therefore, that part may pertain to the skin of the trunk.

The area of the plagiopatagium lies behind the forelimb and extends laterally to contact the dactylopatagium posterior to the MCP joint of digit IV. Comparing the area of the preserved plagiopatagium with that of reconstructions of the skeleton with the wing spread as in flight (e.g., Wellnhofer, 1975, fig. 41; Bennett, 2000, fig. 1) shows that the plagiopatagium, if essentially complete, must have been strongly contracted and/or folded. There are a few ridges within the area that may be overlapping folds, and it is possible that some of the plagiopatagium was folded under the humerus. The texture of most of the plagiopatagium's area differs from that typical of bedding planes of the Solnhofen Limestone and seems to preserve a trace of the patagium though in most places it is indecipherable. Immediately behind the lateral four-fifths of the antebrachium there is a raised area with a loose linear texture and a curving posterior margin that is part of the retrophalangeal wedge. It continues into the angle between the metacarpus and WP1 where the regularity of the texture disappears. The lateralmost parts of the plagiopatagium exhibit some short raised longitudinal strips immediately behind the retrophalangeal wedge and anterior to the trailing edge, but the area between the two has an irregular texture lacking distinct raised strips. Medial to the raised longitudinal strips along the trailing edge, the texture has a distinct linearity with the lines roughly perpendicular to the trailing edge and the shaft of the humerus, but the texture lacks the regularity of raised longitudinal strips. Farther posteromedially and behind a prominent ridge that probably is an overlapping fold, the texture has a pattern of faint regular lineations more or less parallel to the trailing edge continuing posteromedially toward the hindlimb. The lineations are finer and more closely spaced than the raised longitudinal strips of the dactylopatagium.

*Undulations and folds*.—There are undulations and prominent folds in various places on the dactylopatagium, which in most cases are parallel to the raised longitudinal strips. There is a series of gentle undulations behind WP2 and 3, which have a wavelength of ~3 mm and fade away medially, laterally, and posteriorly, and there are gentle undulations with a wavelength of 3–4 mm along the trailing edge of the brachiopatagium behind WP1. There are also several prominent posterolaterally oriented folds indicated by heavy lines in Figure 1.2. They are best seen in the posterior half of the dactylopatagium but the lines along which the patagium is folded presumably continued anteromedially paralleling the raised longitudinal strips. Five of the folds seem to be prominent enough that they are lettered A through E for identification. Note that it is argued below that the folds occurred along genetically controlled fold lines in the dactylopatagium. Folds A and C–E are visible as long, prominent raised linear features, whereas Fold B is shorter and fainter, but it is roughly midway between Folds A and C, and with it included and assuming that the fold lines extended proximally and distally parallel to the raised longitudinal strips the five fold lines divide the dactylopatagium into five sections of roughly equal width. The positions of the fold lines can be described in terms of positions along the wing phalanges and the trailing edge behind the phalanges. Fold Line A extends posterolaterally for some distance from the MCP joint before arcing posteriorly to the middle of the curve where the trailing edge bends toward the hindlimb behind the first IP joint, Fold Line B extends from roughly one-third of the distance along WP1 from its proximal end to the trailing edge behind the mid-point of WP2, Fold Line C extends from roughly the mid-point of WP1 to the trailing edge behind the second IP joint, Fold Line D extends from a point one-fifth along WP2 to the trailing edge behind the mid-point of WP3, and Fold Line E extends from a point three-fifths along WP3 to the trailing edge behind the distal third of WP4. There is also a prominent fold in the retrophalangeal wedge that is highlighted by iron oxide and extends posterolaterally from a point one-third along WP1 to the intersection of the trailing edge of the wedge and Fold Line C. In addition to the undulations and folds, in the lateral part of the dactylopatagium there are features that can be best described as creases where two sections of the dactylopatagium that exhibit concave-up curves meet in a sharp edged convex-up crease.

*Gouges and tool marks*.—There are several prominent gouges (~2.5 × ~5 mm) into the patagium impression near the trailing edge behind the middle third of WP2, the proximal third of WP3, and the proximal third of WP4. None of them shows any evidence of internal structure or permineralized soft tissues, rather they merely expose matrix that has taken the impression. There are also several tool marks gouged into the matrix just behind the distal third of WP4. The matrix near the wing tip has a slightly different character than elsewhere in the area of the dactylopatagium, and I suspect that the finder in preparing the specimen had difficulty identifying and following a separation between the wing impression and the overlying matrix, and made the tool marks in his attempt to do so.

*Raised longitudinal strips*.—The raised longitudinal strips are present across most of the dactylopatagium and a small part of the lateralmost plagiopatagium and lie roughly parallel to the wingfinger in the lateral parts of the dactylopatagium but are angled progressively more anteroposteriorly in the more medial parts. Their shape, spacing, and length are variable across the dactylopatagium. Behind WP2 and 3 the strips seem to be quite long and straight, whereas they are shorter behind WP1 because of their more anteroposterior orientation. At mid-chord behind WP2 and 3, the strips seem to be best developed and evenly spaced at ~5 per mm, whereas close to the wing phalanges and in the more medial parts of the dactylopatagium posterior to WP1 they are more closely spaced and often difficult to follow. The strips are generally not visible where the retrophalangeal wedge is present, though as noted above there appear to be a few visible within the area of the wedge impression behind WP2 and 3. In addition, the strips fade away within ~5–10 mm of the trailing edge of the dactylopatagium and ~3–5 cm of the wingtip.

Mapping the raised strips was difficult because they are poorly defined and faint in many places, and so it was often necessary to arbitrarily decide whether an apparent gap in a raised longitudinal strip resulted from poor preservation of a continuous strip or from one strip ending and another beginning. Several strips seemed to extend continuously from the posterior margin of the retrophalangeal wedge until fading out near the trailing edge, a distance of ~125 mm. The strips are quite straight, though there are occasional jogs to one side or another. The strips do not branch, but their number is increased by intercalation; the spacing between two adjacent strips increasing until a third strip appears midway between the two.

Where best developed, the raised longitudinal strips have a roughly symmetrical cross-section somewhat raised above the surrounding impression, corresponding to the interpretations of previous authors of the strips as positive impressions of subcylindical fibers. However, in places the shape of the strips is asymmetrical, approximating the appearance of a lapstrake or clinker-built boat hull with the raised longitudinal strips forming the exposed angles of the strakes such that the overall appearance of the impression is that of negative impressions of closely spaced broad flat structures arranged en echelon rather than that of widely spaced narrow raised strips. In support of this appearance, there is a small fragment of what appears to be calcite adhering to a groove between two raised longitudinal strips ~1 mm behind a small fold and ~10 mm behind a point about one-third along WP3 (Fig. 4). The fragment is 2.6 mm long and ~0.17 mm wide. Its sides are parallel, its width corresponds well to that of the groove in which it is preserved, and its ends are fractured irregularly suggesting that it represents but a section of a longer structure. Its thickness cannot be measured, but it appears to be less than half its width, thus <0.08 mm. Its superior surface resembles a gabled roof with a median ridge flanked by sloping surfaces extending to the sides of the fragment. It is argued below that the calcitic fragment is a short section of an actinofibril preserved by permineralization or replacement by calcite.

The raised longitudinal strips along Fold Lines C and D seem to be smaller and more closely spaced than generally elsewhere on the dactylopatagium. In addition, part of Fold C is not parallel to, but rather lies at a low angle to, most of the adjacent raised longitudinal strips, whereas a few smaller and more closely spaced strips follow exactly along the fold. Thus that part of the fold line appears to cut across the general pattern of raised longitudinal strips. In addition, along Fold D the raised longitudinal strips posteromedial to the fold seem to converge on the fold line slightly.

Note that Zittel (1882, p. 53) stated that some raised longitudinal strips were more prominent than the rest, marked by reddish brown iron oxide deposits, and resembled ossified tendons. Based on my examinations, no raised strips are significantly larger than the others and Zittel probably was referring to the prominent folds discussed above.

*Retrophalangeal wedge*.—The trace of the retrophalangeal wedge extends along the posterior side of the wing spar from a

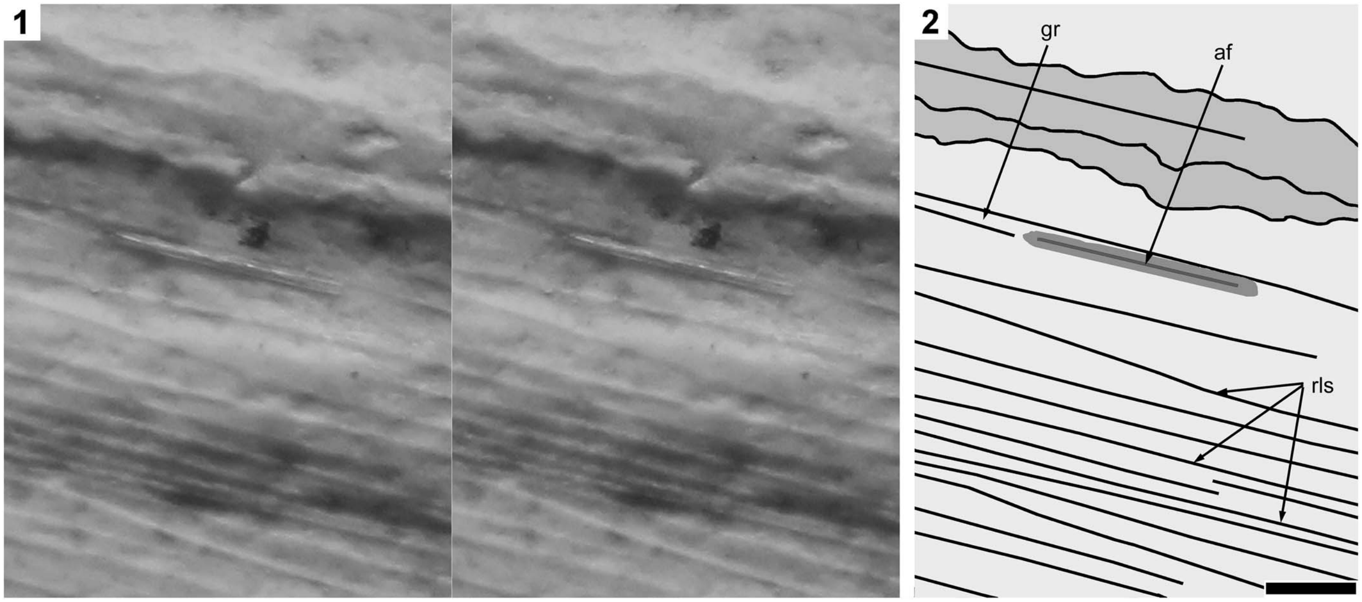

**Figure 4.** Zittel wing of *Rhamphorhynchus muensteri*, BSP 1880 II 8. (**1**) Stereo pair of photographs of the fragment of actinofibril preserved by calcite within a groove forming a negative impression of the actinofibril; (**2**) interpretive drawing with raised longitudinal strips indicated by thin black lines, Fold E shaded medium gray, and the actinofibril fragment shaded dark gray. Abbreviations: af, actinofibril fragment preserved by calcite;; gr, groove; rls, raised longitudinal strip. Scale bar represents 0.1 mm.

point about one-fifth along the antebrachium to a point about three-quarters along WP3 (Fig. 1.2). Its posterior margin is somewhat irregular and the chordwise width of the trace increases evenly to ~8 mm at mid-antebrachium before following an arcing path toward the distal half of WP1 where it is again ~8 mm. The trace continues behind WP2 and 3 with the width varying between ~7–11 mm until it ends or disappears at a point about two-thirds along WP3. The appearance of the trace's end suggests that the wedge continued farther distally but its trace broke away from the slab with the overlying matrix. The texture of the trace is that of loose, coarse fibers, but what can be seen of individual fibers suggests that they were rather short and followed sinuous paths, thus quite different from the adjacent long and parallel raised longitudinal strips. The orientation of the fibers is more or less perpendicular to the antebrachium in the medial part of the trace but parallel to the wing phalanges in the lateral part.

The wedge appears to be a distinct structure that lay on top of the raised longitudinal strips rather than merely being raised longitudinal strips becoming indistinct near the bones of the wing spar because in places, particularly behind the antebrachium and the first IP joint, the posterior margin of the trace forms a step down from the plane of the wedge to that of the raised longitudinal strips posterior to the wedge, and because the orientation of the fibers of the wedge behind WP2 and 3 is not parallel to the slightly oblique posterolateral orientation of the raised longitudinal strips. The prominent fold in the wedge, which extends from a point approximately one-third along WP1 to where Fold Line C intersects the trailing edge of the wedge, supports the interpretation that the wedge tissues were distinct from those that produced the raised longitudinal strips. In the more lateral parts of the trace, there appear to be patches of small raised longitudinal strips within the area of the retrophalangeal wedge, which suggest that the wedge tissue was not particularly substantial.

*Blood vessel traces*.—Within 1 cm of the dactylopatagium's trailing edge behind WP2 and the proximal half of WP3 there are raised features, which have widths that are more variable than the adjacent raised longitudinal strips, are sinuous rather than straight, are sometimes branched, and often cut across the raised longitudinal strips and appear to be superimposed on top of the strips (Fig. 5). These are the features that Padian and Rayner (1993) thought were bifurcating structural fibers and interpreted as structural fibers that had been detached from the underlying membrane and were displaced laterally to expose the grooves in which they had lain. That interpretation is rejected here because some of the raised features are wider than the raised longitudinal strips anteriorly and taper to be narrower than the strips posteriorly, because the raised features cut across the strips at steep angles and nowhere appear to connect to them, and because no grooves in which the supposed cylindrical fibers had formerly lain can be seen. The raised features are interpreted as positive impressions of blood vessels, an interpretation consistent with their branching and variable widths. Note that although Frey et al. (2003, fig. 7A) found traces of the large vessel subparallel to the wing phalanges and its branches under UV illumination in the Zittel wing, no traces of large vessels are apparent under daylight illumination.

## Description of the Marsh specimen

The Marsh specimen (YPM 1778; Fig. 2) is a nearly complete, articulated specimen preserved with soft tissue traces of both wings and the tail vane on the underside of an upper slab consisting of two subrectangular pieces mounted in plaster in a wooden frame. The bedding plane preserves large numbers of small dark calcareous nodules that may be *Saccoma* debris and also exhibits large numbers of light scratches and small shallow gouges that probably resulted from removal of a thin counterpart slab in small pieces. The neck is strongly bent to the left such that the skull is exposed in right lateral view, lying to the trunk's left and roughly parallel to it. The trunk is preserved in ventral view with the sternum, the ventral ends of dorsal ribs, gastralia, prepubes, and the ventral parts of the paired puboischiadic plates of the pelvis exposed. The dorsal, sacral, and anterior caudal vertebrae cannot be seen and are presumably buried in matrix, and the tail is first visible immediately behind the right WP2. The tail is preserved in a nearly straight line and despite some damage from splitting off the counterpart from the part slab and subsequent preparation exhibits the hyperelongate pre- and postzygapophyses and hemal arches well. The tail vane is preserved at an angle to the plane of the slabs so that its left side is exposed to view.

The right wing is complete and flexed such that the wing-finger extends posteriorly along the right side of the trunk before curving to the left and crossing over the proximal caudal vertebrae. The left wing is folded such that the head and

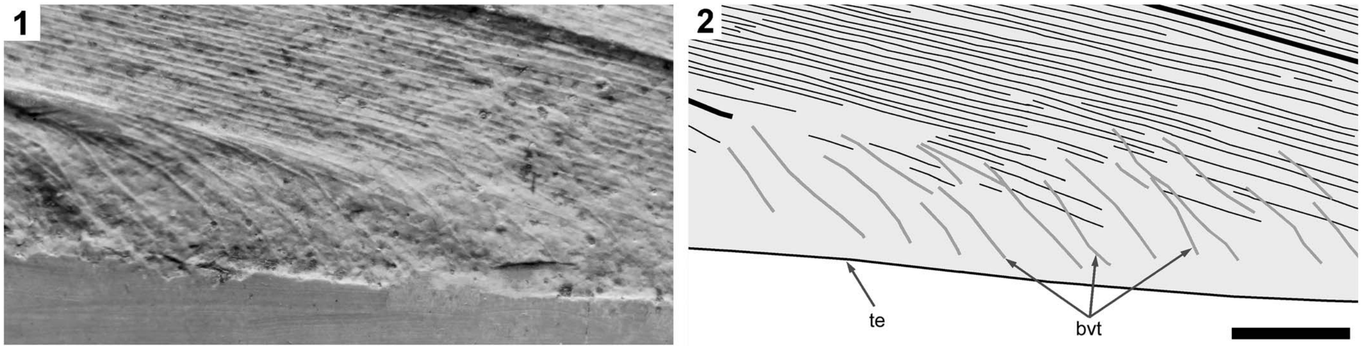

**Figure 5.** Zittel wing of *Rhamphorhynchus muensteri*, BSP 1880 II 8. (**1**) Photograph of blood vessel traces near the trailing edge behind the second interphalangeal joint; (**2**) interpretive drawing with raised longitudinal strips indicated by thin black lines, the trailing edge of the dactylopatagium indicated by medium black lines, Folds C (left) and D (right) indicated by heavy black lines, and blood vessel traces indicated by gray lines. Note the gouge near the trailing edge. Abbreviations: bvt, blood vessel traces; and te, trailing edge. Scale bar represents 5 mm.

deltopectoral crest of the left humerus are visible in the angle between the skull and neck whereas the rest of the humerus, antebrachium, carpus, and metacarpus are presumably buried in the matrix beneath the skull and body, and the wingfinger is extended to the left, roughly perpendicular to the trunk. A deep excavation into the matrix exposes the distal two-thirds of the left WP1 as it rises through the matrix to the specimen's main bedding plane. The left wingfinger extended beyond the margin of the slab such that the distal half of WP2 and WP3–4 are missing. Wing phalanges 1–4 of the right wing are 95, 75, 74, and 80 mm long, respectively, and the estimated wingspan of the specimen in life using my standard method is 86 cm, thus ~85% the size of the Zittel wing. The hindlimbs are presumably buried in matrix except for the pedes that are visible adjacent to the pelvis.

The specimen preserves impressions of the dactylopatagia and the lateralmost parts of the plagiopatagia of both wings; that of the right wing extends from behind WP1 to the wing tip and that of the left from behind WP1 and 2. When the specimen sank to the bottom of the lagoon, it came to lie with the ventral surface of its trunk on the substrate, the right wing under the body with its ventral surface on the substrate, and the left wing flipped over to lie over the body with the brachium through metacarpus folded compactly, the wingfinger extended to the left, and the dorsal surface of the wing on the substrate. As a result, the right wing impression is preserved such that it appears to be exposed in ventral view, whereas the left wing impression is preserved such that it appears to be exposed in dorsal view. The proximalmost part of the impression of the right wing was on a thin layer of matrix that covered the posterior trunk and feet. The matrix was prepared away in places to expose the bones, but the soft tissue impression is still preserved on the matrix between those bones. The right dactylopatagium is partially folded as indicated by several deep furrows. The brachiopatagium has a sharply pointed tip and the chord as preserved is about 13, 40, and 50 mm behind the third through first IP joints, respectively. The left dactylopatagium seems not to have been folded significantly and has a chord as preserved of ~55 mm behind the first IP joint and the trailing edge is gently convex. However, because the brachium, antebrachium, and metacarpus were folded the plagiopatagium was lax and its lateralmost part was folded over the proximal part of the dactylopatagium. The deep excavation around the top of the skull probably cut away the proximalmost part of the soft tissue trace of the left wing. Viewed from a moderate distance the left wing exhibits the wing skeleton and a series of undulations and linear features in the dactylopatagium and the partially folded right wing exhibits more prominent folds. On closer examination and particularly under low angle illumination tool marks, fine striae, and the retrophalangeal wedge are visible. These features are described below, and with the exception of the undulations and tool marks, they were mapped and are shown in Figure 6.

*Undulations and folds*.—There is a series of gentle undulations with a wavelength of ~3 mm along the proximal part of the trailing edge of the left dactylopatagium; however, neither wing exhibits the series of undulations parallel to the wingfinger seen in the Zittel wing. The left wing exhibits three linear features that are not folds but seem to be fold lines corresponding to those of the Zittel wing (Fig. 6.1). Fold Line B is visible behind the retrophalangeal wedge extending posterolaterally in an arc to near the trailing edge behind the first IP joint and its course suggests that its anteromedial end was near the MCP joint. Fold Line C is visible behind WP2 and its course suggests that its anteromedial end was near the proximal end of WP1 and its posterolateral end was near the trailing edge behind the second IP joint. A third fold line that presumably is Fold Line D lies anterior to Fold Line C with its anteromedial end near the first IP joint. There is a fold in the retrophalangeal wedge that extends anteromedially from where Fold Line D intersects the posterior margin of the retrophalangeal wedge. Based on the pattern of the Zittel wing, a Fold Line A might be expected near the proximal end of the impression; however, no evidence of one was found.

The right wing is partially folded and exhibits several folds as prominent furrows that also seem to correspond to the fold lines of the Zittel wing (Fig. 6.2). Fold Line B is visible for a short distance close to the trailing edge and ends behind the middle of WP2. Fold Lines C and D seem to be present but are disturbed at mid-chord by spanwise extraneous folds, one that is behind the proximal three-fourths of WP2, roughly parallel to the trailing edge of the dactylopatagium and connecting laterally with the posterolateral part of Fold Line C, and a second that also parallels the trailing edge of the dactylopatagium and connects the anteromedial part of Fold Line C with the posterolateral part of Fold Line D. The presumed courses of Fold Lines C and D that are not visible are indicated in Figure 6.2 by dashed lines. The extraneous folds may have resulted from post-mortem flattening of the patagium onto the planar substrate in the same way that the spanwise undulations occurred at mid-chord in the Zittel wing. Fold Line E extends from the distal third of WP2 to the trailing edge behind the lateral third of WP4, and is folded such that behind the middle of WP4 the trailing edge is not visible and the edge of the fold forms the posterior margin of the wing impression. Note that the folding of the lateral dactylopatagium at Fold Line E suggests that there is another unseen fold between Fold Lines D and E.

*Striae and other traces*.—Both wings of the Marsh specimen preserve rather smooth surfaces with fine striae that are best viewed under low angle illumination (Fig. 6), and because the right wing preserves an impression of the ventral surface whereas the left preserves an impression of the dorsal surface, striae were present on both surfaces. The left wing exhibits a radiating pattern of shallow linear striae (Fig. 6.1), which although similar to the pattern of the raised longitudinal strips of the Zittel wing are shorter, fewer, and more widely spaced (~8 per 5 mm in the medial left dactylopatagium). In addition, the striae are not as regular as the Zittel wing's raised longitudinal strips and in the posteromedial part of the impression behind Fold Line B they are often sinuous and some appear to branch. The right wing preserves striae similar to those of the left wing, but there are fewer of them. In addition, an impression of what may be the medialmost parts of the dactylopatagium or the plagiopatagium is present in the area between the left tibia and left foot and extending onto the area of the ribs. The impression consists of what seem to be rather straight striae intersecting one another are roughly right angles to produce a

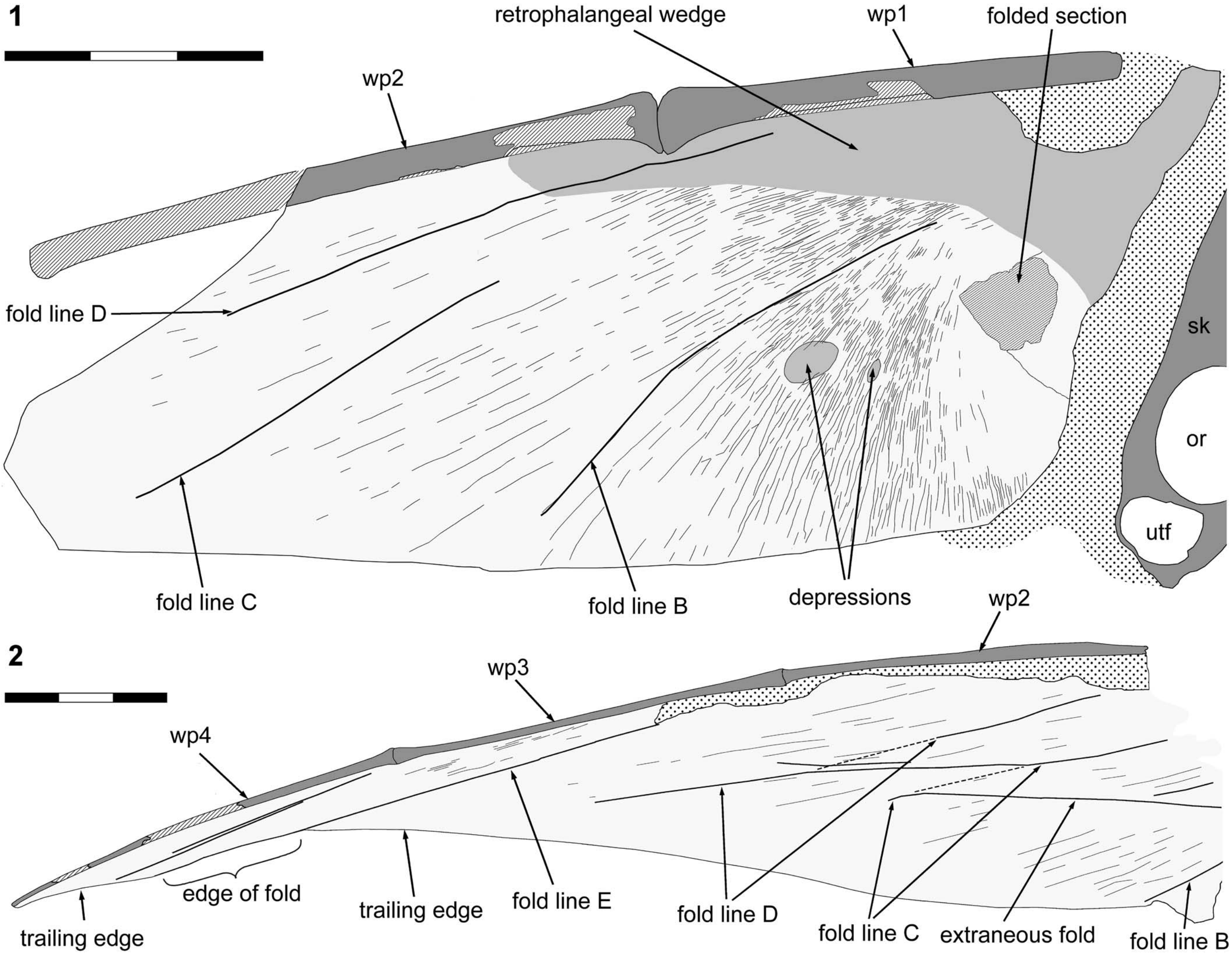

**Figure 6.** Maps of the wing structures and impressions of the Marsh specimen of *Rhamphorhynchus muensteri*, YPM 1778. (**1**) Dorsal surface of the left wing; (**2**) ventral surface of the right wing. Bones are shaded medium gray, the retrophalangeal wedge is shaded light gray, striae are indicated by thin black lines, and fold lines are indicated by heavy black lines. Stippling in (**1**) indicates excavations into the slab to expose the proximal part of WP1 and the dorsum of the skull, and in (**2**) indicates the fractured surface of the wedge of matrix immediately behind the wing phalanges that may represent the retrophalangeal wedge. The dashed lines in (**2**) indicate the presumed course of Fold Lines C and D. Abbreviations: sk, skull; or, orbit; utf, upper temporal fenestra; and wp, wing phalanx. Scale bars represent 3 cm.

pattern of small quadrangular sections; however, it is possible that the appearance of quadrangular sections results from the overlapping of two layers with only parallel lineations each.

As noted by Padian and Rayner (1993), the left wing preserves some irregular disturbances in the form of oval depressions in the soft-tissue impression and presumably were made by rounded objects embedded in, and projecting slightly above, the substrate upon which the specimen lay. The largest disturbance (~5 × 7 mm) distorted the pattern of striae, with some striae bending laterally as if the patagium was stretched over the object and some striae obliterated in the middle of the disturbance (Fig. 7.2), which indicates that the striated surface was soft and compliant. It would be interesting to have access to the counterpart slab in order to determine what caused the disturbances.

The impression of the left wing also preserves a small section of soft tissue trace near its medial edge that has irregular margins and seems to be lying on top of the main impression (Fig. 8). Within the lateral part of the small section there is a pattern of regular closely spaced broad slightly convex structures separated by narrow grooves. The majority of the structures are ~0.12 mm wide with 7–8 per mm, whereas some are broader, ~0.2 mm wide with 5 per mm. The appearance of the structures is markedly different from that of the striae of the main impression and also the loose fibers of the retrophalangeal wedge. The medial part of the small section has a smoother surface that is interpreted as surface epidermis. It is argued below that the linear structures in the lateral part of the small section represent positive impressions of actinofibrils.

*Retrophalangeal wedge*.—The left wing impression preserves traces of the retrophalangeal wedge extending from the medial edge of the impression to behind the proximal quarter of WP2. The trace is ~6.5 mm wide behind the proximal part of WP2 and widens markedly as the posterior margin arcs posteromedially presumably toward the antebrachium. The lateral end of the

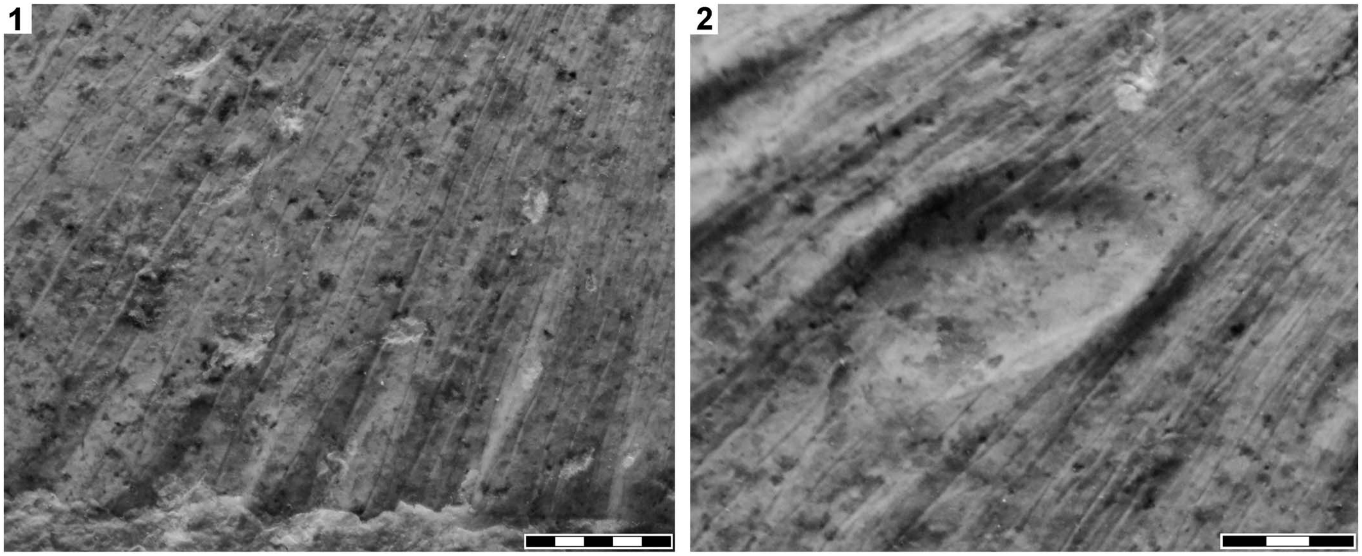

**Figure 7.** Close-up photograph of the dorsal skin impression of the left dactylopatagium of the Marsh specimen of *Rhamphorhynchus muensteri*, YPM 1778. (**1**) Striae in the posteromedial part of the impression with the trailing edge at bottom, undulations near the trailing edge, and six small gouges that resulted from removal of the counterpart; (**2**) the largest depression in the skin impression that distorts and obliterates the pattern of striae. Scale bars represent 5 and 3 mm, respectively.

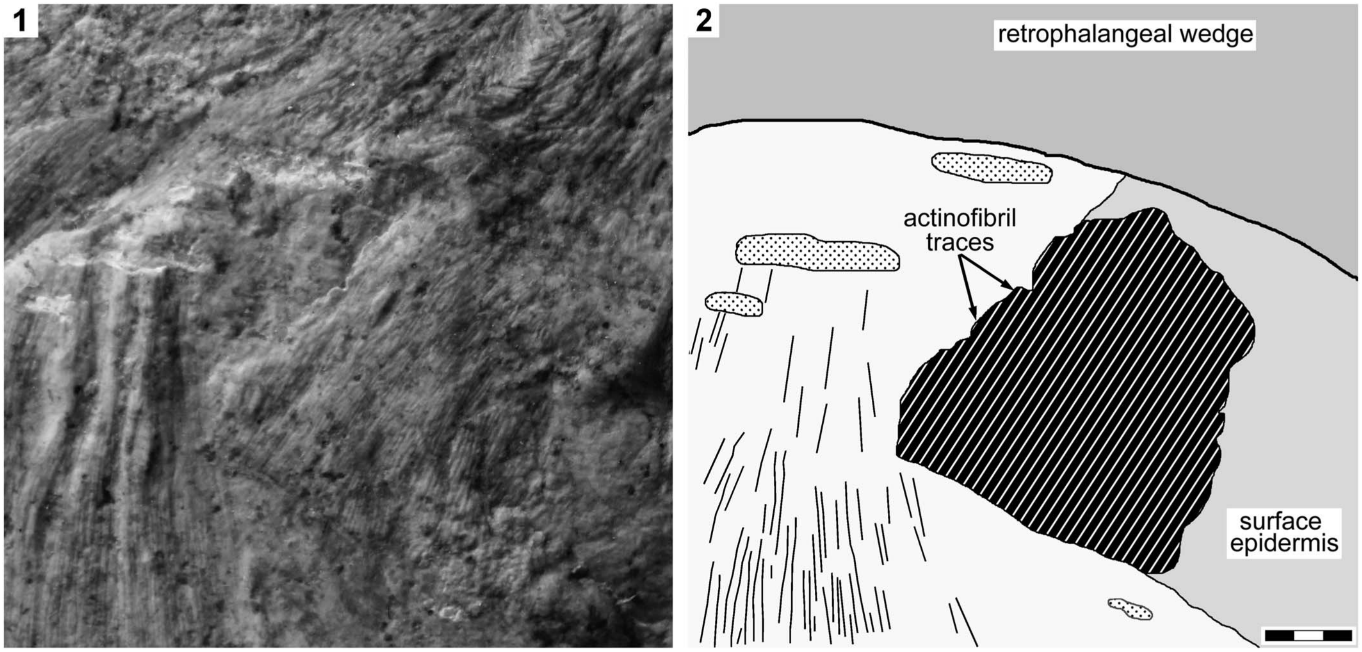

**Figure 8.** Marsh specimen of *Rhamphorhynchus muensteri*, YPM 1778. (**1**) Close-up photograph of the small section of soft tissue traces of folded patagium lying on top of the main impression behind wing phalanx 1 that preserves positive impressions of actinofibrils; (**2**) interpretive drawing with the retrophalangeal wedge shaded dark gray, surface epidermis of the folded patagium shaded medium gray, striae indicated by thin black lines, lateral part preserving actinofibrils darkly hatched with spacing and angle of hatching approximating the size and orientation of the actinofibrils, and gouges into the matrix stippled. Note the irregular fibrous appearance of the retrophalangeal wedge in the upper right. Scale bar represents 3 mm.

trace is truncated by a fracture such that the wedge tissues may have continued farther laterally. There is a distinct groove along the arcing posterior margin of the wedge trace that sets it off from the pattern of striae posterior to it. That part of the trace lateral to the midpoint of WP1 exhibits loose sinuous fibers similar to those of the Zittel wing's retrophalangeal wedge trace, whereas the more posteromedial parts exhibit a combination of loose sinuous fibers and posterolaterally oriented lineations that seem to be a continuation of the pattern of striae posterior to the wedge trace. The right wing does not preserve a clear trace of the wedge, but immediately behind WP2 and the proximal third of WP3 there is a narrow fillet of matrix with a fractured surface that may represent part of the retrophalangeal wedge. Whatever it is, the fillet provides no information about structure of the retrophalangeal wedge.

## Discussion

The Zittel wing and Marsh specimen support Wellnhofer's (1975) observation that the wings of *Rhamphorhynchus* were much more resistant to decay than other soft tissues and so were probably coarse, leathery, and tough. However, the plagiopatagium is less often preserved than the dactylopatagium (e.g., largely absent in the Marsh specimen and most other specimens that preserve traces of the brachiopatagium), and when it is preserved as in the Zittel wing, it provides little information about its structure and so it probably was not significantly more resistant to decay than other soft tissues. Therefore, it seems that Wellnhofer's characterization as coarse, leathery, and tough probably applies primarily to the dactylopatagium. The plagioplatagium and dactylopatagium will be discussed separately, and the dactylopatagium will be considered first.

The soft tissue impressions of the dactylopatagia of the Zittel wing and Marsh specimen are distinctly different from one another, the Zittel wing being dominated by raised longitudinal strips whereas the Marsh specimen is dominated by fine striae that are clearly not impressions of raised longitudinal strips, and this even though the impressions of both specimens are associated with articulated wing skeletons preserved on the underside of upper slabs (the *hangende Platte* of Barthel, 1978) formed by sediments laid down on top of the wing skeletons and their soft tissues. In order to reconcile the differences and properly interpret the raised longitudinal strips, it is necessary to consider the manner in which each specimen preserves what it preserves.

Soft-tissue traces in the Solnhofen Limestone may be produced in various ways. In some cases, soft tissues are preserved as organic films that usually appear as brownish deposits under visible light and often fluoresce under UV light. The isolated *Archaeopteryx* feather and *Pterodactylus antiquus* specimens BSP 1929 I 18 (Döderlein, 1929b; Bennett, 2013a) and BSP 1883 XVI 1 and MCZ 1505 (Wellnhofer, 1970; Bennett, 2013a) are examples of such preservation. In other cases, the surface structure of the soft tissues that came to lie on the substrate is preserved as a negative impression on the lower slab, which in turn produced a complementary positive impression of those soft tissues on the upper slab. An excellent example of this is seen in the feathers of the Berlin *Archaeopteryx* (Rietschel, 1984), but among pterosaurs the occipital lappet of *Pterodactylus antiquus* (Wellnhofer, 1970; Bennett, 2013a) is preserved as a negative impression on the lower slab (MCZ 1505) and a positive impression on the upper slab (BSP 1883 XVI 1). Lastly, soft tissues that resisted decay may be permineralized or replaced by calcite to produce a three dimensional cast of their structure, which if removed will expose negative impressions of the upper and lower surfaces of the soft tissues on the upper and lower slabs, respectively. In pterosaurs, the cartilage in joints and the incompletely ossified articular ends of long bones are commonly replaced with calcite, which often obliterates the morphology; however, keratinous structures such as claw sheathes (e.g., *Archaeopteryx*, Wellnhofer, 2009) and the horny covering of the cranial crest (e.g., holotype of *Ctenochasma porocristata* Buisonjé 1981, JME SOS 2179; Buisonjé, 1981; Bennett, 2002) may also be preserved in this manner. It is not clear whether the soft tissues that resisted decay lasted long enough for there to be some permineralization or they decayed completely leaving a void in the sediments in which a calcite cast formed, but for convenience this type of preservation will be referred to hereafter as replacement by calcite.

The Marsh specimen exhibits a combination of preservation as an organic film and as an impression. The organic film is rather faint and does not seem to provide useful information as to the structure of the brachiopatagium whereas the impression is a positive impression of soft tissues including fine striae and fold lines on both wings. Padian and Rayner (1993, fig. 9) described and illustrated the left wing as preserving clearly visible structural fibers, yet there are no raised longitudinal strips like those of the Zittel wing and the striae cannot represent actinofibrils because they lack the straightness and regularity of the Zittel wing's raised longitudinal strips and are much more widely spaced (~8 striae per 5 mm in the Marsh specimen's medial left dactylopatagium vs. ~5 strips per mm in the larger Zittel wing). Moreover, the fact that the impressions of the dorsal surface of the left wing and the ventral surface of the right wing both exhibit striae demonstrates that the striae cannot be traces of structural fibers that were present on only the ventral surface of the wing. Instead, their size and shape indicate that the striae are wrinkles in an otherwise rather smooth epidermis. However, there are two areas on the left wing impression that differ from the smooth epidermis; one just behind WP1 is interpreted as preserving a trace of the retrophalangeal wedge whereas the other near the medial edge of the left dactylopatagium is interpreted as a small section of folded patagium sitting on top of the main impression (Fig. 8).

In the case of the Zittel wing, there is evidence of all three types of preservation. The plagiopatagium exhibits a combination of preservation as an organic film and as a positive impression of soft tissues on an upper slab. The organic film is present in the medialmost parts of the plagiopatagium and preserves traces of fine hairs that covered the body whereas the positive impression seems to reflect a strongly contracted tenopatagial membrane and does not provide information as to its structure or properties other than the fact that it was capable of much contraction. The preservation of the dactylopatagium is more complex. In the central area of the dactylopatagium (i.e., posterior to the retrophalangeal wedge, >1.5 cm anterior to the trailing edge, and behind WP1–3) the presence of the small calcitic fragment preserved within a groove between two raised longitudinal strips behind the middle of WP3 (Fig. 4) demonstrates that there was soft tissue preservation of resistant structures by replacement by calcite, with calcite casts presumably formerly covering the entire central area of the dactylopatagium. As a result, the pattern of raised longitudinal strips bounding broad grooves must be interpreted as a negative impression of closely spaced broad flat structures rather than as a positive impression of widely spaced cylindrical structures. In addition, the lapstrake appearance of part of the central area is consistent with a negative impression of closely spaced broad flat structures but inconsistent with a positive impression of widely spaced cylindrical structures.

Two reviewers stated that they prefer to interpret the raised longitudinal strips of the Zittel wing as preserving a positive impression rather than a negative impression. This is not surprising given that the human mind tends to interpret concave faces as convex (i.e., the hollow mask illusion, Gregory, 1997), and that the illusion is not limited to faces and the interpretation of objects as convex or concave is influenced by our knowledge of, or assumptions as to, the structure of the

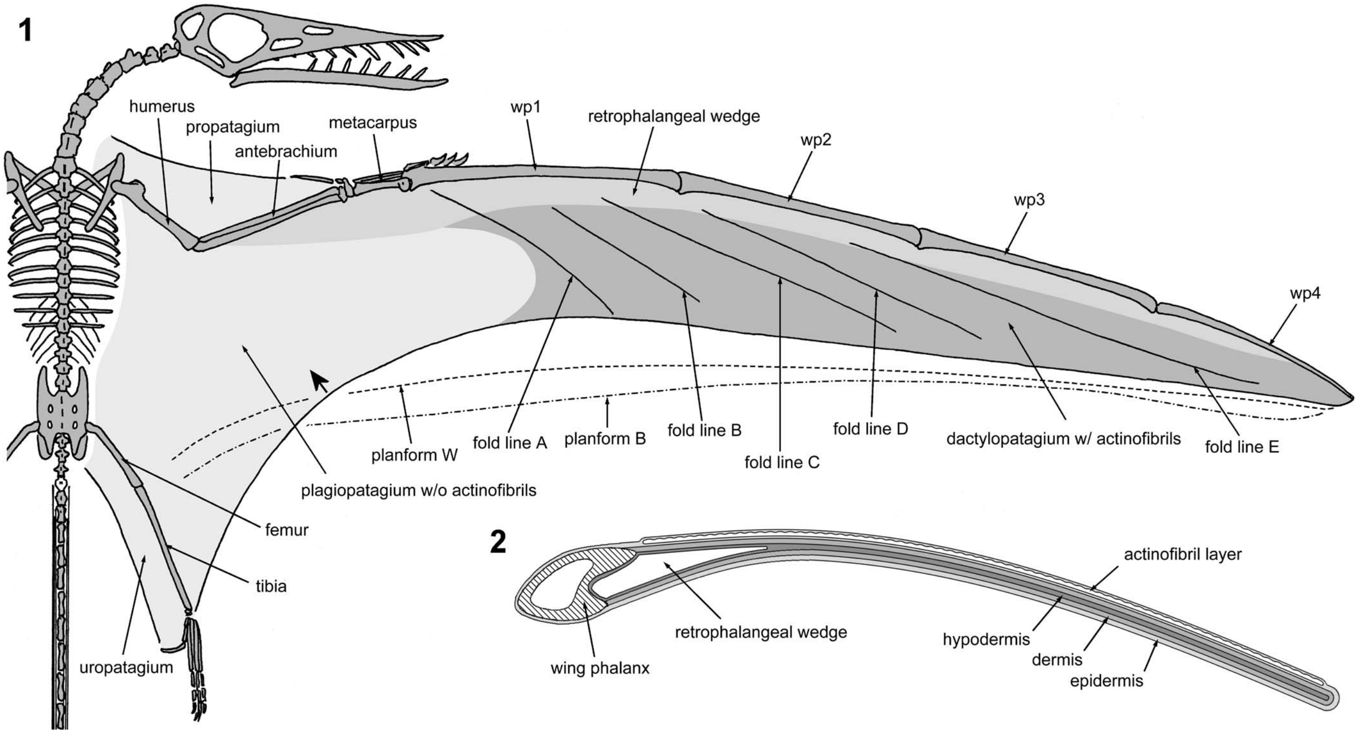

**Figure 9.** Reconstructions of the wing of *Rhamphorhynchus muensteri* based on the Zittel wing, BSP 1880 II 8, and Marsh specimen, YPM 1778. (**1**) Wing planform and structure proposed here with the extent of the tenopatagial (light gray) and actinopatagial (dark gray) parts and the pneumatic retrophalangeal wedge (medium gray) indicated, the dashed and dashed-and-dotted lines indicate the reconstructed planforms W and B after Wellnhofer (1975) and Bennett (2001), respectively, and the large arrow by the trailing edge behind the antebrachium indicates possible contraction of the plagiopatagium; (**2**) cross-section of the dactylopatagium behind wing phalanx 2. Within the patagium the vertical thickness of tissue layers is exaggerated. The wing phalanx (cross-section after Gross, 1937, fig. 3E) is hatched, its pneumatized medullary cavity is unshaded, and the patagium consists of upper and lower skins of epidermis (light gray) and dermis (medium gray) surrounding a common hypodermis (dark gray) core. An unshaded actinofibril layer lies within the dorsal epidermis, and anteriorly there is an unshaded pneumatized retrophalangeal wedge within the hypodermis. Abbreviation: wp, wing phalanx.

object (Hill and Bruce, 1993, 1994; Johnston et al., 1992; Kleffner and Ramachandran, 1992; Langer and Bülthoff, 2001). In the case of the Zittel wing, the natural tendency would be to interpret it as a positive impression, and the knowledge that all previous pterosaur workers have interpreted it as such surely has influenced all pterosaur workers since Zittel who have studied the specimen. I know that that knowledge influenced me. I examined the Zittel wing in 1988, 1993, 2008, and 2011 and consistently interpreted it as a positive impression until I forced myself to study its every square millimeter in order to map the wing, and noticed the lapstrake appearance and discovered the calcitic fragment in a groove between two raised strips, which seem to have been overlooked by all previous workers. Thereby was I only reluctantly convinced that the central area of the Zittel wing is a negative impression.

The calcitic fragment and lapstrake appearance make sense within the context of the central area of the dactylopatagium preserving a negative impression of closely spaced broad flat structures replaced by calcite. Such preservation indicates that the closely spaced broad flat structures were keratinous, and therefore they were actinofibrils, the actual structural elements arranged in a posterolaterally radiating pattern in the pterosaur wing that are considered to have imparted special properties to the patagium. I cannot conceive any explanation for the presence of the calcitic fragment in the context of preservation of a positive impression of widely spaced cylindrical structures.

The negative impression of closely spaced broad actinofibrils is present only in the central area of the dactylopatagium. Anteriorly it ends at the posterior margin of the retrophalangeal wedge trace where there is a distinct step down from the wedge to the raised strips and grooves posterior to it. There is no evidence of preservation of resistant structures by replacement by calcite anterior to the step, so the trace of the retrophalangeal wedge might be interpreted as a positive impression. Posteriorly and laterally the negative impression in the central area fades out within ~5–10 mm of the trailing edge and ~3–5 cm of the wingtip. The fading suggests that the actinofibrils grew thinner near the trailing edge and wingtip. Within the transition zone along the trailing edge, blood vessel traces are preserved as positive impressions (Fig. 5) that appear to be superimposed on the faint pattern of actinofibrils either because the actinofibrils were too thin to produce much of a negative impression in the area or because the raised longitudinal strips along the trailing edge actually represent a positive impression of the ventral surface of the actinofibril layer. There also should be a transition from positive impression to negative impression associated with the transition from plagiopatagium to dactylopatagium; however, the appearance of the impression grades smoothly from the positive impression of the plagiopatagium to the negative impression of the central area of the dactylopatagium over a distance of several centimeters and no specific transition point can be discerned.

One reviewer requested a "coherent taphonomic model for the preservation of wing membrane impressions in the

Solnhofen Limestone." Therefore I offer the following speculations as to how some specific features of the Zittel wing and Marsh specimen might have been preserved. The wing impressions of the Zittel wing and Marsh specimen were both covered by a thin layer of matrix that formed a counterpart that was chipped away to fully expose the impressions on the upper slabs. The counterpart of the Marsh specimen seems to have come off in many small pieces as shown by the large number and rather close spacing of the gouges (Fig. 2). Whereas the main impressions of both wings of the Marsh specimen preserve positive impressions of smooth epidermis and wrinkles that were impressed into the sediments that formed lower (i.e., counterpart) slab, the two areas on the left wing that differ from the smooth epidermis require more complicated explanations. In the case of the impression interpreted as the retrophalangeal wedge, it presents the appearance of loose sinuous fibers like those of the retrophalangeal wedge trace of the Zittel wing and is separated from the adjacent epidermis impression by a distinct groove. The lateral part of the wedge trace consists entirely of the sinuous fiber impressions whereas in the medial part the sinuous fiber impressions are superimposed on a pattern of posterolaterally oriented striae. The superimposition might be interpreted as evidence that the retrophalangeal wedge and its sinuous fibers were a distinct structure that in life lay on top of the epidermis behind the wing spar and so was pressed into the bottom sediments that took the negative impression of the wing; however, that seems unlikely. An alternative interpretation relies on the probability that the anterior part of the dactylopatagium that included the retrophalangeal wedge was more substantial than the posterior part and so took longer to decay, and the fact that the wedge is interpreted below as a cancellous pneumatic structure that could have trapped and molded sediments as it decayed. The trapped and molded sediments would have lain on top of the negative impression of the epidermis in the bottom sediments, and as covering sediments formed the upper slab and took the positive impression of the epidermis they would also have taken an impression of the sediments trapped and molded by retrophalangeal wedge. As such, the impressions of the sinuous fibers of the retrophalangeal wedge on the upper slab would seem to be negative impressions of the sediments trapped within and molded by the decaying retrophalangeal wedge tissues but not necessarily positive impressions of the wedge's internal structure. The lateral end of the wedge trace ends abruptly behind the proximal quarter of WP2, perhaps because sediments did not get into the wedge distal to that point. Note that the narrow fillet of matrix with a fractured surface behind WP2 and the proximal third of WP3 of the right wing may also consist of sediments that were trapped within the retrophalangeal wedge.

The small section of soft tissue trace that appears to be lying on top of the main impression near the medial edge of the left dactylopatagium indicates that at least that part of the soft tissue impression consisted of more than one layer. This could have occurred if the medial part of the patagium was folded, perhaps along Fold Line A, such that the lateral plagiopatagium overlapped the medial dactylopatagium lateral to Fold Line A and sediments got in between the two layers of patagium before preservation so as to form a thin layer of sediment lying on top of the main impression and preserving an impression of the folded layer. When the counterpart was split off the part slab, the small section of sediment bearing the impression of the folded patagium adhered to the main slab rather than splitting off with the counterpart. The small section appears to preserve a positive impression of closely spaced broad slightly convex structures separated by narrow grooves in its lateral part and smoother surface epidermis in its medial part. The positive impression of broad convex structures compares well with, and is complementary to, the negative impression of closely spaced broad actinofibrils in the Zittel wing, and so it is interpreted as a positive impression of actinofibrils. In the context of the reconstruction of the wing presented below, in which actinofibrils were not on the wing surface but rather were covered by a thin layer of surface epidermis, it seems that the part of the surface epidermis that covered the actinofibrils was ripped off or fell off or rotted away so as to expose the actinofibrils before the small section's impression formed.

In the case of the Zittel wing, the counterpart seems to have come off in larger pieces, perhaps as a result of greater preparation skill on the part of the finder. According to Zittel (1882; quoted above), the finder removed all of the counterpart to fully expose the impression, producing gouges and tool marks and making the specimen more attractive but less scientifically informative. Removal of the counterpart could have exposed the layer of actinofibrils preserved by replacement by calcite in the central area of the dactylopatagium. It is probable that chipping off the counterpart would have damaged the dull, pale calcite layer in places and exposed the remarkable pattern of raised longitudinal strips on the underlying matrix, in which case the finder would have prepared away the rest of the damaged calcite layer in order to expose the entire pattern of strips, thereby increasing the specimen's visual appeal and monetary value. Alternatively, much of that layer might have adhered to the counterpart and come away with it as the counterpart was chipped off, in which case the finder would have removed whatever of the calcite layer remained on the slab so as to increase the specimen's visual appeal and monetary value. Whichever happened, it is remarkable that the tiny calcitic fragment was left to demonstrate that soft tissues preserved by replacement by calcite had once covered much of the impression; however, it was probably overlooked because it was very short and in a relatively narrow groove.

Preservation of resistant structures by replacement by calcite is rare in the Solnhofen Limestone except in the case of cartilage in joint capsules, and so one might ask why keratinous actinofibrils were preserved in the Zittel wing when no keratinous feathers have been so preserved in any specimen of *Archaeopteryx*. I expect that the exact set of circumstances and conditions that permitted such replacement by calcite was rare. Wanderer (1908) described the Dresden specimen (SNSD-MMG BaJ 2210) as agreeing with the Zittel wing in all details, but based on my examinations although the specimen does preserve traces of actinofibrils from the medialmost dactylopatagium, the preservation is quite different in manner and quality from the preservation of the both Zittel wing and Marsh specimen (description of the Dresden specimen may be undertaken elsewhere). Thus the Zittel wing is the only 1 (<1%) out of the ~108 *Rhamphorhynchus* specimens in museum collections monographed by Wellnhofer (1975) that exhibits replacement of actinofibrils by calcite. At such a rate, we might have to collect ~90 more specimens of *Archaeopteryx* before finding one with feathers preserved by replacement by calcite.

The Zittel wing's preservation of the retrophalangeal wedge is similar to that of the Marsh specimen with impressions of sinuous fibers and a distinct posterior margin proximally. The preservation differs from the Marsh specimen in that the posterior margin behind the wing phalanges forms a distinct step down from the plane of the wedge trace to the strips and grooves of the actinofibril impression. This suggests that the matrix formed of sediments trapped within the cancellous spaces of the wedge is for the most part still adhering to the upper slab and did not break off with the counterpart. However, distally where the wedge trace is truncated, the matrix seems to have split off with counterpart. Preservation of blood vessels as positive impressions along the trailing edge, whether superimposed on a faint negative impression of the dorsal surface of actinofibrils or a faint positive impression of the ventral surface of the actinofibrils, could have resulted if the ventral epidermis and dermis rotted away before the vessels, which were then pressed into the lower sediments to produce a negative impression upon which the upper slab's positive impression was formed.

Previous authors interpreted the raised longitudinal strips of the Zittel wing as structural fibers in or on the brachiopatagium though most did not explicitly state whether they interpreted the strips as actual actinofibrils preserved through permineralization or as positive impressions of actinofibrils. The strips cannot be actual structures, permineralized in place, because as noted by Pennycuick (1988) that is contradicted by the fact that gouges into the specimen do not preserve any evidence of internal structure or permineralized soft tissues, but rather show normal matrix. That fact would not preclude the possibility that the strips were positive impressions of structures pressed into the substrate on which the pterosaur carcass came to rest, but the fact that the Marsh specimen, though preserving positive impressions of the dorsal and ventral surfaces of the patagia, does not preserve raised longitudinal strips demonstrates that that is not the case.

Padian and Rayner (1993) interpreted the brachiopatagium as consisting of dorsal and ventral skins of epidermis and dermis surrounding a common hypodermis core (Fig. 3.2). At a minimum the core would have included blood and lymph vessels and nerves, but might also have included other connective tissues, muscle fibers, and other structures. Padian and Rayner (1993) interpreted actinofibrils as keratinous, and Bennett (2000) concurred because their pattern is inconsistent with tensile structures and the Vienna *Pterodactylus* (NHMW 1975/1756/0000) shows that they resisted longitudinal compression, which collagen, elastin, and muscle fibers would not. Their relative resistance to decay, which resulted in preservation by replacement by calcite in the Zittel wing, also supports the interpretation that they were keratinous. If actinofibrils were keratinous, they must have been epidermal, which argues against Wellnhofer's (1987; Fig. 3.1) and Frey et al.'s (2007) interpretations of fibers in the middle of the brachiopatagium, and because there is no evidence of two layers of actinofibrils in any specimen of *Rhamphorhynchus*, the actinofibril layer was presumably part of either the dorsal or ventral epidermis. Padian and Rayner (1993) interpreted actinofibrils as on the ventral epidermis and the retrophalangeal wedge as ventral to the actinofibril layer; however, the fact that the Marsh specimen does not preserve evidence of actinofibrils on the skin's surface and does provide evidence that the retrophalangeal wedge was internal shows that that cannot be the case. In addition, the fact that the blood vessel traces and the retrophalangeal wedge are preserved as positive impressions that appear to be superimposed on actinofibril traces around the margins of the dactylopatagium of the Zittel wing shows that actinofibrils could not have been part of the ventral epidermis. Blood vessels would not be superficial to the epidermis, but rather would have been within the common hypodermis, and therefore the fact that they were ventral to the actinofibril layer shows that the actinofibril layer was part of the dorsal epidermis.

A reconstructed cross-section of the dactylopatagium based on the above interpretation of the Zittel wing and Marsh specimens is shown in Figure 3.3. The structure is similar to the interpretation of Padian and Rayner (1993) in that it has upper and lower skins of epidermis and dermis surrounding a common hypodermis core, but the actinofibril layer was within the dorsal epidermis and not on its surface and the common hypodermis contained the retrophalangeal wedge in addition to the blood and lymph vessels and nerves needed to support the dermis and epidermis (Fig. 9.2). Whereas Wellnhofer (1975) and Padian and Rayner (1993) thought that raised longitudinal strips were actinofibrils that were ~0.05 mm in diameter and spaced up to 0.2 mm apart, it is now apparent that the grooves between raised longitudinal strips are negative impressions of broad flat actinofibrils up to 0.2 mm wide and the raised longitudinal strips represent narrow bands (~0.05 mm wide) of tissue between the actinofibrils. Because actinofibrils were not on the skin's surface, it is probable that they were basal within the dorsal epidermis and were covered by an unspecialized epidermis that was continuous with the epidermis of the narrow intervening bands between the actinofibrils.

The reconstruction presented here is compatible with the negative impressions of actinofibrils preserved between the raised longitudinal strips of the Zittel wing and its calcitic fragment, compatible with the skin impressions of the dorsal and ventral surfaces of the wings of the Marsh specimen, and compatible with the small section of brachiopatagium lying on top of the medial part of the left wing trace of the Marsh specimen that preserves a positive impression of closely spaced broad actinofibrils exposed when the covering layer of unspecialized epidermis was lost (Fig. 8). The reconstruction is also compatible with the findings of Frey et al. (2003), who reported that JME SOS 4784 preserves a dorsal actinofibril layer that would have been part of the dorsal epidermis, an intermediate layer of fibers that was present only where there were actinofibrils and would have been collagen fibers within the dorsal dermis, and a ventral blood vessel layer that would have been within the common hypodermis. It is also compatible with the fact that Frey et al. (2003) described actinofibrils as 0.2 mm wide, the same as the width of the negative impressions of actinofibrils in the Zittel wing and much greater than the 0.05 mm width of the raised longitudinal strips. However, the reconstruction presented here is incompatible with reconstructions (Frey et al., 2003; Frey et al., 2007) based on conflations of

Frey et al.'s (2003) evidence with the interpretation of Martill and Unwin (1989). The layer of collagen fibers described by Frey et al. (2003) seems to be arranged as Bennett (2000) suggested collagen fibers would be to redirect spanwise tension in the more medial parts of the brachiopatagium anteriorly to the proximal wing phalanges. Thus, the actinofibril and collagen fiber layers were within the dorsal epidermis and dermis, respectively, and together they formed a dorsal skin that was the primary functional and structural part of the dactylopatagium, whereas the ventral epidermis and dermis were presumably unspecialized.

*Actinofibrils*.—Actinofibrils probably were modified epidermal scales that formed in place as part of the dorsal epidermis of the dactylopatagium. In order for this to occur, the stratum basale of the dorsal epidermis of the dactylopatagium would have been divided into broad germinative strips of fibril keratinocytes separated by narrow intervening strips of unspecialized keratinocytes, with the fibril keratinocytes synthesizing and accumulating hard keratin such as is found in claw sheathes and the unspecialized keratinocytes synthesizing and accumulating the softer keratins of unspecialized epidermis. An initial embryonic layer of fibril keratinocytes probably formed during the late embryonic development of the individual, and as the individual grew the fibril germinative strip increased in length and width. The added area of fibril keratinocytes might have been symmetrically distributed around the previous layer of fibril keratinocytes such that the thickest part was in the center of the actinofibril. However, it is also possible that the added keratinocyte area was not symmetrically distributed in much the same way that the development of the dermal shields on the carapace of box turtles (*Terrapene*; Zangerl, 1969) and the plastron of mud turtles (*Kinosternon*; Mosimann, 1956) is asymmetrical such that the embryonic shield is toward one edge of the dermal shield. If the added area was biased toward the posterolateral end of the germinative strip, then the thickest part of the actinofibril would be toward the anteromedial end of the germinative strip, which would be consistent with the fact that in the Zittel wing the raised longitudinal strips are tall and sharply defined in the more anterior and medial parts of the dactylopatagium and indistinct to absent near the trailing edge and wing tip, and the fact that thicker anteromedial ends would be better suited to the function of resisting compressive loads and redirecting tensile loads to the proximal wing phalanges.

Actinofibrils formed deep in the epidermis would not have been shed and replaced during the lifetime of the individual, so the rate of cell division in the stratum basale of the fibril germinative strip need only have been high enough to keep up with the growth of the individual and produce a sufficiently stiff actinofibril. The layer of unspecialized surface epidermis that covered over the actinofibrils might have been formed by having the stratum basale of the intervening strips spread laterally over the actinofibrils and merge with that of adjacent intervening strips to cover the actinofibrils and form a continuous sheet of unspecialized stratum basale that produced the surface epidermis or by having the developing keratinocytes from the intervening strips spread laterally and merge to cover the actinofibrils and form a continuous sheet of surface epidermis. The rate of cell division in the unspecialized stratum basale would have been high enough to produce a surface epidermis that could have been shed or lost through abrasion.

In Figure 3.3, actinofibrils are shown as having cross-sections equivalent to a plano-convex lens. Such a cross-section would result if the actinofibrils were built up through the addition of multiple planar layers of keratinocytes produced by a planar germinative strip as the animal grew from embryo to adult. The cross-section could also have approximated a biconvex lens or a plano-convex lens with a flat external surface if the germinative strip was concave rather than planar, or could conceivably have taken other shapes if the rate of addition of keratinocytes was not uniform across the width of the fibril germinative strip. Note that the gabled roof appearance of the calcitic fragment suggests that the germinative strip was V-shaped.

The widths and lengths of actinofibrils are variable across the dactylopatagium. In the central area posterior to WP2 and 3, actinofibrils were ~0.2 mm wide, whereas anteriorly, close behind the wing phalanges they were narrower as they also seem to be in the more medial parts of the dactylopatagium posterior to WP1. In the medialmost part of the dactylopatagium and in the adjacent lateral plagiopatagium the raised longitudinal strips are short, closely spaced, and less regular than elsewhere, which suggests that the actinofibrils were shorter and narrower than elsewhere. However, it is possible that that appearance is partly a result of the manner of preservation of the patagium, such that the actinofibrils may have been longer and more regularly arranged than the appearance of the raised strips suggests. Note that there may have been a limit to the permissible width of actinofibrils if the unspecialized stratum basale or the developing keratinocytes of the adjacent intervening strips were to merge and form a continuous sheet of surface epidermis covering the actinofibrils. In the middle of the dactylopatagium behind WP2 and 3 actinofibrils seem to be quite long and straight. A special case of varying width seems to be found in the actinofibrils that are adjacent to the prominent fold lines in the dactylopatagium. In the case of Fold Line C, the actinofibrils immediately on either side of the fold line are narrow and their raised longitudinal strips less prominent than most strips whereas the actinofibrils a short distance on either side of the fold line are of normal breadth and prominence.

While mapping the raised longitudinal strips of the Zittel wing I did not see any evidence that the grooves between them, and thus the actinofibrils that had occupied the grooves, were not continuous longitudinally. The only possible evidence of discontinuity was in places where a raised strip seemed to jog to one side; however, that might merely represent a local change in the width of the germinative strip rather than the posterolateral end of an anteromedial actinofibril abutting the anteromedial end of a more posterolateral actinofibril. Thus it is probable that individual germinative strips and actinofibrils extended unbroken from the wing spar to the trailing edge, which in the Zittel wing could be up to 125 mm long. It seems that there would be no difficulty and no disadvantage in having such long actinofibrils, though there probably also would be no disadvantage to having shorter ones if their ends were staggered.

As noted by Padian and Rayner (1993) there are many places on the Zittel wing where a raised longitudinal strip was intercalated between two adjacent strips. These instances might represent the posterolateral end of an anteromedial actinofibril abutting the anteromedial ends of two more posterolateral actinofibrils so as to accommodate the radiating pattern of actinofibrils on the dactylopatagium while limiting the maximum width of individual actinofibrils. However, there is no evidence that such actinofibrils ended adjacent to one another and the instances could also represent the branching of one germinative strip into two. Frey et al. (2003) stated that in JME SOS 4784 actinofibrils bifurcated near the trailing edge but did not provide photographs or diagrams so it is not clear if this is what they were describing. Note that Padian and Rayner (1993) also stated that some structural fibers appeared to bifurcate near the trailing edge of the dactylopatagium, but this was because they misinterpreted branching blood vessel traces as structural fibers.

*Skin surface*.—The Marsh specimen preserves positive impressions of the dorsal and ventral surfaces of the dactylopatagium that show that the epidermis was smooth except for fine striae that are best observed under low angle illumination. The striae form a posterolaterally radiating pattern that loosely reflects the posterolaterally radiating pattern of the underlying actinofibrils. The sections of epidermis bounded by striae do not appear to have been heavily keratinized. This is shown by the distortions of their pattern associated with the oval depressions in the Marsh specimen's left wing (Fig. 7.2), and so the surface epidermis seems to have formed a soft, compliant covering of the dorsal and ventral surfaces of the wings. Interestingly, the Marsh specimen seems to have been largely ignored by pterosaur workers because its preservation of traces of a smooth skin with only fine striae differed markedly from the raised longitudinal strips of the Zittel wing and so was deemed less informative.

*Undulations and fold lines*.—The undulations in the Zittel wing indicate that the dactylopatagium was lax, which is to be expected because the wing was no longer attached to the trunk. The series of undulations behind WP2 and 3 probably resulted because the wingfinger was unloaded and flattened into the plane of the substrate, whereas when spread as in flight the curvature of the wingfinger and tension within the brachiopatagium would have taken up the slack, eliminating the undulations. Similarly, the undulations along the trailing edge behind WP1 in the Zittel wing and the left wing of the Marsh specimen would have flattened out when the brachiopatagium was under tension. The sharp edged creases of the Zittel wing, which are also evident in BSP 1907 I 37, indicate that the membrane was somewhat stiff and suggest that it had some natural camber, at least in the distal part of the dactylopatagium. The stiffness of the dactylopatagium is also evident in the deep furrows along the fold lines on the right wing of the Marsh specimen, which because the impression is a positive impression of the ventral surface of the patagium represent places where two sections of the dactylopatagium lying on the substrate resisted compression perpendicular to the long axes of the actinofibrils within the plane of the patagium and were pushed up into ridges along fold lines.

It is not clear how extensible Wellnhofer (1975, 1987) thought the brachiopatagium was, but Padian and Rayner (1993, fig. 15A) thought it was significantly extensible perpendicular to the long axes of actinofibrils and Bennett (2000) thought it was as extensible as bat patagium perpendicular to the long axes of actinofibrils within the limits of a load-bearing collagen fiber network. However, the stiffness and resistance to compression perpendicular to the actinofibrils noted above plus the remarkable uniformity of the widths (~0.05 mm) of the raised longitudinal strips representing the strips of unspecialized epidermis between the actinofibrils indicate that the dactylopatagium was essentially inextensible. A significantly extensible membrane would not exhibit any stiffness, and it is probable that an extensible membrane, even a lax one, would exhibit some variation in the width of the intervening strips. The gentle undulations seem to represent the only significant shortening that could occur in the dactylopatagium. Thus, the dactylopatagium was somewhat stiff and inextensible.

Because the dactylopatagium was somewhat stiff and inextensible, it was necessary to fold it in order to store it compactly. The dactylopatagium would have folded up somewhat like a traditional folding hand fan consisting of a sector of paper supported by slender slats pivoting around a single point. The Zittel wing, Marsh specimen, and other specimens such as BSP 1907 I 37 exhibit a consistent pattern of prominent fold lines, of which five have been identified by letters. In both specimens described here Fold Line B extends from roughly one-third of the distance along WP1 from its proximal end to the trailing edge behind the mid-point of WP2, Fold Line C extends from roughly the mid-point of WP1 to the trailing edge behind the second IP joint and in part cuts across the regular pattern of raised longitudinal strips in the Zittel wing and the pattern of striae that reflects the pattern of underlying actinofibrils in the Marsh specimen, Fold Line D extends from a point one-fifth along WP2 to the trailing edge behind the mid-point of WP3. and Fold Line E extends from a point three-fifths along WP3 to the trailing edge behind the distal third of WP4. The similarity of the positions and shapes of the folds and the deviations from the pattern of actinofibrils suggest that the folds were not merely the result of incidental folding of a uniform patagium but rather were genetically controlled lines of increased flexibility that enabled the otherwise somewhat stiff dactylopatagium to fold consistently and compactly. It is not clear how the dactylopatagium folded up along each of the fold lines, but the folding along Fold Line E of the right wing of the Marsh specimen indicates that the patagium posteromedial to the fold line folded up and over the patagium anterolateral to the line. Presumably there was another fold close behind Fold Line E that brought the patagium down and backward.

One reviewer seemed to think that a wing with a somewhat stiff and inextensible dactylopatagium would present a different appearance when folded as proposed here than a wing with an elastic membrane bearing widely spaced cylindrical fibers furled by contraction of the membrane, and furthermore suggested that no pterosaur specimen preserves evidence of the proposed fan folding. Bennett (2000; fig. 3) discussed and illustrated the sort of folding proposed here, with the dactylopatagium folded into a narrow band alongside the wingfinger just as is seen in specimens such as BSP 1938 I 503 (Wellnhofer, 1975, pl. 4, fig. 1). I find that the majority of specimens with soft tissue preservation of wing membranes present an appearance that is consistent with both fan folding of a stiff dactylopatagium and contractive furling of an elastic dactylopatagium; however, the right wing of the Marsh specimen presents an appearance that is consistent with fan folding but not consistent with contractive furling (Fig. 6.1). The outer part of the dactylopatagium is folded along Fold Line E such that the edge of the fold rather than the trailing edge of the dactylopatagium forms what looks like the trailing edge of the wing behind the middle third of WP4. I cannot conceive of a manner in which contractive furling could produce such an appearance.

It is possible that the idea of genetically controlled fold lines was arrived at independently by others: Monninger et al. (2010, p. 52) commented in an abstract that actinofibrils were “the guiding structure for formation of ... folds.” However, it is not clear to me whether they meant merely that folds were parallel to the long axes of actinofibrils, which had been noted before (Padian and Rayner, 1993; Bennett, 2000) or if they meant that specific variation in the size and pattern of actinofibrils controlled the location of the folds.

*Retrophalangeal wedge*.—Previous authors noted the retrophalangeal wedge immediately behind the wing spar, but interpreted it as only behind the wingfinger (Padian and Rayner, 1993; Tischlinger and Frey, 2010; Monninger et al., 2012) whereas the Zittel wing shows that it extended proximally almost to the elbow, and the wedge’s arcing posteromedial margin on the Marsh specimen also suggests it extended behind the antebrachium. Various functions have been proposed for the retrophalangeal wedge including: (1) streamlining the transition between the thick wing spar and thin brachiopatagium (Padian and Rayner, 1993; Tischlinger and Frey, 2010; Monninger et al., 2012), (2) containing generative tissue that produced the actinofibrils (Padian and Rayner, 1993), (3) anchoring the actinofibrils to the wing spar and transferring lift forces from the actinofibrils to the wing spar (Padian and Rayner, 1993; Tischlinger and Frey, 2010; Monninger et al., 2012), and (4) reinforcing the IP joints and preventing their flexion (Monninger et al., 2012).

Faced with the problem of explaining the development of cylindrical keratinous fibers on the ventral surface of the epidermis, Padian and Rayner (1993) suggested that the retrophalangeal wedge contained the generative tissues from which the fibers grew like fingernails, posterolaterally in a radiating pattern to be abraded away at the trailing edge. This suggestion is not supported because as discussed above actinofibrils developed in place within the epidermis, and so no concentrated mass of generative tissue was necessary.

Padian and Rayner (1993) viewed the brachiopatagium as essentially cantilevered behind the wing spar with the actinofibrils transferring lift forces anteromedially to the wing spar. Such a structure would require that the actinofibrils were anchored to the wing spar in such a way that the lift forces could be transferred to the spar, and Padian and Rayner (1993, fig. 12) suggested that local tension in the wedge was important in the force transference. The suggestion that the wedge was involved in anchoring the actinofibrils and transferring aerodynamic forces to the wing spar is not supported because actinofibrils formed as part of the epidermis would be securely attached to the underlying dermis, which in turn could have been securely attached to the periosteum of the bones of the wing spar, so no broad wedge of tissue would be necessary to transmit forces. However, a planar rather than interwoven array of actinofibrils alone or as part of composite of actinofibrils and an elastic membrane would not have been stiff enough to transmit lift forces. McGowan (1991) noted that cylindrical actinofibrils 0.05 mm in diameter would be too slender to resist bending forces, and though the actual actinofibrils were broader than previously thought, they were probably little thicker and little better suited to resist bending out of the plane of the patagium. This is clearly shown by the presence of the Zittel wing’s undulations and fold lines; a patagium flexible enough to undulate and fold compactly would not be stiff enough to transfer lift forces as Padian and Rayner (1993) proposed. The dactylopatagium must have been tensioned between the plagiopatagium medial to it and the wingfinger anterior to it, and lift forces must have been transferred medially and anteriorly by tension in the collagen fiber layer. Note that other authors who have viewed the dactylopatagium as self-supporting and self-cambering with actinofibrils transmitting lift forces (Schaller, 1985; Frey et al., 2007; Tischlinger and Frey, 2010; Monninger et al., 2012) have not provided evidence or argumentation that actinofibrils were stiff enough to resist bending and transfer lift forces to the wing spar or that the layer of collagen fibers did not transfer such loads to the wing spar and body by tension. Frey et al. (2007) suggested that intrinsic muscle tissue ventral to the actinofibrils contracted to bend the actinofibrils to camber the dactylopatagium, but did not provide any evidence that there were muscle fibers associated with the actinofibrils or collagen fibers.

The suggestion that the retrophalangeal wedge consisted of dense fibrous connective tissue that reinforced the IP joints and prevented them from flexing is not supported because the wedge extended proximally behind the MCP joint of digit IV, because the wedge was as well developed behind the middle of the wing phalanges as behind the IP joints, and because such reinforcement was unnecessary. Monninger et al. (2012) stated that there is no evidence of strong IP ligaments, which may be true in the case of *Rhamphorhynchus* because of the small size and immaturity of most specimens, but Bennett (2000) described prominent IP ligament attachment scars in mature individuals of *Pteranodon* so there is evidence that pterosaurs had strong IP ligaments in their wingfingers. Even without that evidence, the extant phylogenetic bracket (Witmer, 1995) informs us that pterosaurs had IP ligaments. Pterosaurs, like their extant relatives (e.g., lepidosaurs and birds), exhibit the osteological correlates of synovial joints in their wingfingers (e.g., expanded articular ends with complementary surfaces, different bone texture on the articular ends indicating that they were covered by articular cartilages), and so it can be concluded that the synovial joints of pterosaurs included a fibrous joint capsule with parts thickened into ligaments to hold the bones together and control their movements. Moreover, IP ligament attachment scars on most pterosaur wing phalanges would be relatively smaller and less prominent than those of their non-volant relatives because of the large radius of the joint surfaces and the extremely limited movement allowed by the joint. In the case of a typical ginglymoid IP joint, the joint surfaces have a small radius and allow considerable flexion and extension, and so the IP ligaments must attach to a small area around the center of joint rotation on the medial and lateral sides of the proximal phalanx, resulting in prominent attachment scars. In all pterosaurs except anurognathids (Bennett, 2001, 2007), the joint surfaces have a large radius and allowed almost no flexion and extension, and so the ligaments need not have attached to a small area but rather could attach to broad areas resulting in less prominent scars. Lastly, dense fibrous connective tissue though strong in tension is not suited to resist compression, and so a band of dense fibrous connective tissue (or even cartilage) behind the IP joints would not be suited to preventing flexion of the joints.

Having rejected other proposed functions of the retrophalangeal wedge, only a streamlining function remains. The retrophalangeal wedge would have streamlined the airflow over the wing, reducing drag (Palmer, 2010). Note that the wedge is widest behind the carpus and MCP joint where the wing spar is thickest, and tapers out proximally where streamlining of the elbow might be more difficult because the wedge would be on the extensor side of the joint and perhaps because it would be well behind the leading edge of the wing where streamlining might be less important. It is possible that there was also a streamlining structure medial to the elbow, but if so the Zittel wing does not preserve any trace of it.

Various tissues might have formed the retrophalangeal wedge; however, most pterosaurs, including *Rhamphorhynchus* (Bonde and Christensen, 2003), exhibit extensive skeletal pneumaticity, which was presumably evolved to displace marrow and lighten the skeleton. Therefore, it is unlikely that the wedge would have been formed of dense connective tissues that would add significantly to the mass of the wing if a lighter alternative were available. It is probable that the wedge was an extra-skeletal pneumatic feature. If, as reconstructed here, the dorsal and ventral surfaces of the wedge were in contact with the dorsal and ventral dermis (Fig. 9.2), then the wedge could be a pneumatic diverticulum bounded by thin epithelia and connected to the intra-skeletal pneumatic spaces. It could deflate and collapse when the wing was folded and inflate when tension in the dactylopatagium pulled the dorsal and ventral skins taut. The facts that the Zittel wing preserves a separate fold line in the retrophalangeal wedge and that there are places where raised longitudinal strips can be seen in gaps in the wedge are consistent with the wedge being a pneumatic diverticulum bounded by thin epithelia.

It is possible that the unusual wing phalanx cross-sections seen in *Rhamphorhynchus* (Fig. 9.2) and *Nesodactylus* with streamlined anterodorsal and ventral surfaces but markedly concave posterior surfaces reflect the presence of the retrophalangeal wedge. It is conceivable that other rhamphorhynchoid pterosaurs that did not have such wing phalanx cross-sections did not have pneumatized retrophalangeal wedges behind their wing phalanges. However, it is unlikely that *Rhamphorhynchus* and *Nesodactylus* were the only taxa with intrapatagial pneumatized structures to streamline the wing cross-section.

*Vascular supply to the brachiopatagium.*—Frey et al. (2003) described and illustrated vasculature within the dactylopatagium of *Rhamphorhynchus* as consisting of one large vessel subparallel to the wing phalanges that gave rise to smaller branches and loops that in turn sent off small branches, and noted that the Zittel wing preserved some vessel traces visible under UV illumination. The pattern is similar to that supplying the small intestine in humans, in which a large superior mesenteric artery gives rise to multiple smaller intestinal arteries interconnected by looping arcades that in turn send off still smaller vasa recta, and the positive impressions of the small vessels along the trailing edge correspond to the vasa recta. Note that if the Zittel wing originally preserved physical traces of the large vessel and loops in addition to those visible under UV illumination, they would have been ventral to the actinofibril layer and lost when the counterpart was chipped off.

There is no evidence that the dactylopatagium contained any muscle tissues and no reason to think that it did. Rather the dactylopatagium seems to have consisted of little more than two layers of skin and only enough hypodermis containing vasculature and nerves needed to support those two layers. Therefore, the dactylopatagium probably was rather inactive metabolically, such that it is unlikely to have required high levels of perfusion to supply its tissues with oxygen and nutrients. The presence of large vessels suggests that the patagium was important in thermoregulation (Frey et al., 2007), in which case it could have been used to lose heat by radiation and convection or absorb heat for warming after a night's cooling. Note that it is not clear whether the vessel traces of JME SOS 4784, NHMW 1998z0077/0001, and the Zittel wing represent arteries, veins, or artery-vein pairs, and so there is no evidence of separation of the arterial and venous supplies, which would be necessary to prevent countercurrent heat exchange if the dactylopatagium was to be used for thermoregulation.

*Plagiopatagium.*—The Zittel wing presents a plagiopatagium that may not be complete, but certainly is contracted considerably from its extent in flight. That contraction is indirect evidence that the plagiopatagium was extensible such that it would have behaved much as bat patagium does, extending spanwise and chordwise when appropriately tensed and contracting so as to be stored compactly when relaxed. The Zittel wing provides no direct evidence as to the structure of the plagiopatagium except for the fine lineations that are parallel to the trailing edge. The fine lineations are smaller than the raised longitudinal strips associated with actinofibrils and their orientation is inconsistent with keratinous elements that would resist longitudinal compression. Rather their orientation is consistent with collagen and/or elastin fibers that would bear tensile loads within the patagium. The Marsh specimen provides no information about the plagiopatagium except for the indirect evidence that there are essentially no traces of the plagiopatagium despite well-preserved traces of the brachiopatagia and the tail vane, which suggests that the dactylopatagium was a soft tissue that was not more resistant to decay than most of the body's soft tissues.

*Trailing edge tendon?*—Bramwell and Whitfield (1974, p. 543–544) modeled pterosaur wings with and without a collagenous load-bearing trailing tendon and preferred the model without, whereas Pennycuick (1988) suggested that a trailing edge tendon was present. Padian and Rayner (1993) argued against a trailing edge tendon on the grounds that there is no evidence for one, that the tip of the dactylopatagium was rounded whereas a load-bearing tendon would follow a straight line to the tip, and that a tendon was unnecessary. In addition, Bennett (2000) noted the curved fourth wing phalanges of some pterosaurs (e.g., *Pteranodon*) could not have borne the tensile loads that a trailing edge tendon would apply.

Recently, Monninger et al. (2012) described what they interpreted as a trailing edge tendon in a specimen of *Rhamphorhynchus*. They reconstructed it as extending from wing tip to ankle and suggested that it stabilized the trailing edge and contributed to camber control, but they did not explain how it would have functioned. I do not doubt that some pterosaur specimens preserve linear trailing edge features of some sort; however, the mere presence of a linear trailing edge feature in the brachiopatagium does not indicate that the feature was a discrete load-bearing structure. The actinofibril layer, the collagen fiber layer of the dorsal dermis, and the hypodermis each must have had a posterior margin, and the dorsal and ventral epidermis and dermis must have been continuous with one another, respectively, most of which need not have been coincident with each other or the posterior margin of the dactylopatagium, and all of these could have produced a linear trailing edge feature in a fossil preserving patagial soft tissues.

A load-bearing trailing edge tendon would be compatible with a wing in which the patagium was subjected to chordwise tension between the wing spar and tendon and the tendon rather than the patagium bore spanwise tension. However, it is incompatible with the interpretation presented here of a somewhat stiff inextensible dactylopatagium and would place significant limitations on the shape and control of a tenopatagial plagiopatagium. It makes more sense to interpret the plagiopatagium as carrying spanwise tensile loads by way of collagen, elastin, and intrinsic muscle fibers spread across the chord of the plagiopatagium, which would provide greater control of the area and three dimensional shape of the plagiopatagium. Proponents of a load-bearing trailing edge tendon should provide evidence or argumentation for the presence and properties of the tendon and against alternative interpretations, and explain how it might have functioned within the context of the pterosaur patagium and flight.

*Wing planform and flight.*—*Rhamphorhynchus* has largely escaped the attentions of aerodynamicists, who prefer to concentrate on the largest of pterosaurs, and there have been few reconstructions of the wing planform of *Rhamphorhynchus* (Fig. 9.1). Wellnhofer (1975) described the wing planform as narrow and scythe-like and illustrated it with the trailing edge following a smooth arc from the wing tip to near the hip joint. Padian and Rayner (1993) did not illustrate the planform, but presented schematic illustrations that showed a narrow and scythe-like wing similar to that illustrated by Wellnhofer. Bennett (2000) reconstructed the planform with the trailing edge following an S-curve from the wing tip to the proximal tibia based on the assumption that the dactylopatagium was extensible perpendicular to actinofibrils and with the patagium extended such that the length of the medialmost actinofibrils determined its chord posterior to the MCP joint. Here the planform is reconstructed based on the interpretation that the dactylopatagium was essentially inextensible and that the trailing edge of the plagiopatagium followed an arc of essentially constant radius to attach near the ankle as has been shown by Elgin et al. (2011). The planform of the plagiopatagium is quite broad chordwise whereas that of the dactylopatagium is significantly narrower than previously thought. Note that there is no evidence that the trailing edge followed an arc of essentially constant radius, and if the trailing edge arc had a small radius behind the proximal antebrachium and increasing radii laterally to the dactylopatagium and posteriorly to the ankle, then the plagiopatagium would have a narrower chord and less area. In that case, control of the posterior part of the plagiopatagium by rotation of the femur about its axis for pitch control could have been more or less independent of the control of the area and shape of the rest of the plagiopatagium.

One reviewer objected that the wing reconstruction proposed here could not function in flight because wing area could not be reduced “to less than 50% of the fully extended area” whereas bats and birds can do so. Padian (1983a, 1983b, 1985, 1987a, 1987b, 1991) argued against bat-like interpretations of pterosaurs as erroneous, but the bird-like interpretation of pterosaurs advocated in their place has proved to be similarly erroneous (e.g., pterosaurs were plantigrade quadrupeds [Lockley et al., 1995; Bennett, 1997a, b; Unwin, 1997] with the hindlimb fully involved in the wing [Elgin et al., 2011]). Pterosaurs were probably neither bat-like nor bird-like and differed from bats and birds as much as bats and birds differ from one another; therefore, there is no reason to think that pterosaur wings must have been functionally similar to bat and bird wings. It is true that many birds can reduce wing area in flight; however, some birds (e.g., diomedeids, trochilids, spheniscids) do not reduce wing area significantly, and neither do insects including large (e.g., *Titanus*, *Ornithoptera*, the extinct *Meganeuropsis* [Beckemeyer and Hall, 2007]) and heavy species (e.g., *Goliathus*). Likewise, man-made ornithopters ranging from von Holst’s (1957) model of *Rhamphorhynchus* and MacCready’s model of *Quetzalcoatlus* (Brooks et al., 1985; Cowley, 1986) to Festo’s Smartbird gull-like ornithopter (Mackenzie, 2012) have demonstrated that the ability to alter wing area is not necessary for flapping flight. Thus, the reviewer’s objection is baseless.

Although the ability to reduce wing area is not necessary for successful flapping flight, the wing reconstruction proposed here would allow wing area to be altered. Contraction of intrinsic muscle fibers arranged subperpendicular to the trailing edge in the plagiopatagium could pull the trailing edge anteriomedially (large arrow in Fig. 9) reducing its chord and area. In addition, as discussed by Bennett (2000, p. 281–282), flexion of the shoulder, elbow, and wrist would reduce wingspan, and contraction of collagen, elastin, and intrinsic muscle fibers in the plagiopatagium could reduce its area. It would also be possible to maintain tension on the medial margin of the dactylopatagium so as to keep it spread even if the plagiopatagium was lax and passively contracted. The only control envisioned by Bennett (2000) that would not be possible with the new interpretation would be decreasing the area of the dactylopatagium in flight.

*Other pterosaurs.*—Both Wellnhofer (1987) and Pennycuick (1988) noted linear features in the wings of the Vienna *Pterodactylus* (NHMW 1975/1756/0000). Wellnhofer interpreted them as similar to what he thought was preserved on the Zittel wing, i.e., widely spaced cylindrical structures embedded within a bat-like extensible membrane. Pennycuick (1988,

p. 308) noted that the surface of the wing impression was different from that of the surrounding matrix and suggested it was covered by a layer of encrusting calcite. Based on my examinations, the Vienna *Pterodactylus* exhibits closely spaced broad actinofibrils similar to those of the Zittel wing preserved by way of calcification with dendritic deposits of manganese and iron oxides in the intervening strips (Bennett, 2013b); however, a detailed description of the wings of the Vienna *Pterodactylus* is beyond the scope of this paper and will be undertaken elsewhere.

The wings of *Sordes pilosus* described and illustrated by Unwin and Bakhurina (1994) included long, straight, closely packed fibers in the dactylopatagium that are clearly actinofibrils. Their preservation is consistent with the interpretation of actinofibrils as closely spaced broad keratinous structures in a somewhat stiff and inextensible dactylopatagium. Unwin and Bakhurina (1994, fig. 2c) did not provide measurements, but based on their figure the actinofibrils, though somewhat variable in width, were ~0.11 mm wide and spaced 6–7 per mm. *Sordes* had an estimated wingspan of 65 cm (Unwin and Bakhurina, 1994), but if scaled up to the size of the Zittel wing the actinofibrils would be ~0.17 mm wide and spaced 3.8–4.5 per mm, quite close to the measurements of the Zittel wing's actinofibrils. Note that advocates of widely spaced cylindrical actinofibrils on or in an extensible elastic patagium might interpret the close spacing of the actinofibrils as evidence of the contraction of the elastic membrane in order to furl the wing; however, it is also consistent with the interpretation presented here, and the actinofibrils are much wider (>2 times absolute width and >3 times relative width) than the Zittel wing's raised longitudinal strips that some may still wish to interpret as actinofibrils. Unwin and Bakhurina (1994) did not describe fibers of any sort in the plagiopatagium, but described shorter fibers from the uropatagium, which they interpreted as having unraveled in some cases. They did not make it clear whether they interpreted the short fibers as homologous with the actinofibrils preserved in the lateral dactylopatagium of *Sordes*. Bennett (2000) argued that the short fibers were not homologous with the actinofibrils of the dactylopatagium and suggested that they were elastic fibers, but I now wonder if they might not be the branching integumentary structures that Kellner et al. (2010) termed pycnofibers.

Kellner et al. (2010) identified two types of fibers in the patagia of *Jeholopterus*, and suggested that one and possibly both were actinofibrils. They suggested that actinofibrils could shorten or expand to provide flexibility and that such actinofibrils would not be incompatible with Padian and Rayner's (1993) load-bearing element interpretation or my spreading element interpretation (Bennett, 2000); however, extensible actinofibrils are incompatible with the latter two interpretations. Unfortunately, Kellner et al. (2010) did not provide illustrations or diagrams of fiber orientation and distribution, and they made no attempt to determine whether one or both of the two fiber types was homologous with the actinofibrils of the Zittel wing, JME SOS 4784 (Frey et al., 2003), or the Vienna *Pterodactylus*, so their description adds little to our knowledge of pterosaur wings. However, based on their description it is probable that the short Type A fibers that were interpreted as actinofibrils are not actinofibrils but rather are collagenous tensile fibers like the longitudinal strings Frey et al. (2003) noted in JME SOS 4784, whereas the Type B fibers that were interpreted as possibly also being actinofibrils are keratinous actinofibrils. Note, however, that because anurognathids are the likely sister group to all other pterosaurs and possess wingfinger IP joints capable of flexion and extension unlike all other pterosaurs (Bennett, 2007), it is possible that the structure of the patagium of *Jeholopterus* and other anurognathids was distinctly different from that of other pterosaurs.

*Bennett's (2000) spreading elements interpretation.*—Bennett (2000) accepted that actinofibrils were widely spaced cylindrical structures on an elastic patagium and argued that they resisted longitudinal compression to prevent chordwise narrowing and redirected spanwise tension anteriorly to reduce loads on the distal phalanges. The present interpretation that the dactylopatagium did not include an extensible elastic membrane that would tend to narrow chordwise when under spanwise tension appears to negate the importance of preventing chordwise narrowing, but it is the presence of the closely spaced actinofibrils that would have made the dactylopatagium inextensible and determine its chord and area. The proposed function of redirecting spanwise tension from the plagiopatagium into more chordwise tension on the proximal wing phalanges would still be important for reducing the loads applied to the distal phalanges and allowing slender distal phalanges to bear the loads placed on them.

One reviewer simultaneously expressed doubt that keratinous actinofibrils would function to resist compressive loads and acceptance that they would function to redirect tensile loads anteriorly to proximal wing phalanges. Those views are incompatible because actinofibrils could not have redirected tension without resisting longitudinal compression. Bennett (2000) discussed and illustrated this with what were termed strut and cable systems including struts representing actinofibrils. If actinofibrils could not resist any compression, they would when loaded in compression shorten until the lines of tension ran straight between their attachments to the body wall and hindlimb medially and the wing phalanges laterally, and so would not redirect tension at all. If actinofibrils could resist compression, they would not shorten significantly when loaded in compression and the lines of tension between their attachments to the body wall and hindlimb medially and the wing phalanges laterally would be bent by the actinofibrils, and the tension would be redirected to proximal wing phalanges rather than borne on distal ones. Perhaps the reviewer took my statements that actinofibrils would resist compression to suggest that they were subjected to and could resist compressive forces other than or exceeding those that tension within a tensed dactylopatagium would subject them to. However, I have never suggested that the role of keratinous actinofibrils was in resisting the sort of compressive loads that would be placed on them if one were to snatch a *Rhamphorhynchus* out of the air, put one's thumb on the midshaft of WP1 and one's index and middle fingers on the trailing edge behind WP1, and squeeze. In such a situation, the longitudinal compressive forces would exceed those which could be resisted by actinofibril and collagen fiber composite, the actinofibrils would bend, and the plane of the dactylopatagium would wrinkle and fold. However, Bennett (2000) argued that in the context of the roughly planar dactylopatagium loaded in tension as in flight, actinofibrils would resist longitudinal compression and would be prevented from bending within the plane of the patagium by the collagen fibers of the dorsal dermis. If actinofibrils consisted of collagen or elastin rather than keratin, if they could “shorten or expand and therefore provide more flexibility to the wing membrane” as Kellner et al. (2010) suggested, then they would not have been able to resist longitudinal compression, would not redirect tension in the patagium, and would not prevent chordwise narrowing of the patagium under spanwise tension, and there would no explanation for their radiating pattern in the dactylopatagium.

## Conclusions

This paper has shown that the Zittel wing of *Rhamphorhynchus*, probably the most influential specimen preserving traces of the structure of the pterosaur patagium, has been misinterpreted since its first description, and actinofibrils were closely spaced broad keratinous structures within the dorsal epidermis. The findings, when combined with evidence from other specimens, indicate that the dactylopatagium was narrow, inextensible, and somewhat stiff, which when combined with the streamlining of the pneumatic retrophalangeal wedge would produce a highly efficient airfoil more like that of sailplanes than the membranous wings of bats. That dactylopatagium was combined with a broad extensible plagiopatagium to produce a unique wing structure and planform.

Various aspects of the present interpretation have been suggested before: Wellnhofer (1975) interpreted the patagium as coarse, leathery, and tough; Padian and Rayner (1993) interpreted actinofibrils as keratinous; and Unwin and Bakhurina (1994) interpreted the dactylopatagium as stiff and relatively inelastic. However, the general acceptance of Zittel’s (1882) incorrect interpretation that the wing included widely spaced cylindrical fibers inhibited progress toward a reinterpretation. It is interesting to consider that Marsh’s (1882) interpretation of his specimen as preserving folds and wrinkles was correct, and yet for 130 years Marsh’s interpretation was largely ignored in favor of Zittel’s. Also interesting is the fact that Pennycuick (1988, p. 307) presented an essentially correct interpretation of the raised longitudinal strips of the Zittel wing while incorrectly attributing it to Wellnhofer (1975) and rejecting it.

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