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The extent of the pterosaur flight membrane

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The shape and extent of the membranous brachioptagium in pterosaurs remains a controversial topic for those attempting to determine the aerodynamic performance of the first vertebrate fliers. Various arguments in favour of the trailing edge terminating against either the torso or hip, the femur, the ankle, or different locations for various taxa, has resulted in several published reconstructions. Uncertainty over the correct model is detrimental to both aerodynamic and palaeoecological studies that are forced to simultaneously consider multiple and highly variable configurations for individual taxa. A review of relevant pterosaur specimens with preserved soft tissues or impressions of the wing membrane, however, strongly suggests that the trailing edge of the wing extended down to the lower leg or ankle in all specimens where the brachiopatagium is completely preserved. This configuration is seen across a phylogenetically broad range of pterosaurs and is thus likely to have been universally present throughout the Pterosauria. Support for opposing hypotheses where the trailing edge terminates against the body, hip, or knee are based on several specimens where the wing membrane is either incomplete or has undergone post-mortem contraction. An ankle attachment does not rule out a high aspect ratio wing as the curvature of the trailing edge and the ratio of the fore to hind limbs also play a major role in determining the final shape of the membrane.

Key words: Reptilia, Pterosauria, flight, wings, patagium, Mesozoic.

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Introduction

The pterosaurs were prehistoric flying reptiles that dominated the skies for much of the Mesozoic Era (Late Triassic to the end Cretaceous). They were the first vertebrates to develop true powered flight and included the largest flying animals of all time, with wing spans in excess of 10 metres (Witton 2008). While several studies have considered the aerodynamic characteristics of the group (e.g., Bramwell and Whitfield 1974; Stein 1975; Brower 1980, 1982, 1983; Chatterjee and Templin 2004) further work is required to better understand the aerodynamics of the pterosaurian wing and the consequences of altering its material and structural compositions. Such studies, however, cannot proceed in the absence of a consensus on the shape and extent of the wings.

Previous aerodynamic and palaeoecological based studies have been divided over the shape and surface area of the main wing membrane by the use of either a "bird-like" model, where the proximal portion of the trailing edge attaches to the body, or a "bat-like" model where it is integrated with the hind limbs. The result of this divergence is that the conclusions of aerodynamic studies utilising a narrow chord (Brower 1980, 1982, 1983; Chatterjee and Templin 2004) will differ from those with a broader chord (Hankin and Watson 1914; Kripp 1941; Heptonstall 1971; Bramwell and Whitfield 1974; Stein 1975; Wilkinson et al. 2005) regardless of any other similarities between the methods or taxa under investigation. As both aspect ratio and wing load have important implications for ecology in bats and birds (Hazelhurst and Rayner 1992), which can be equally applied to pterosaurs (McGowan and Dyke 2009; Witton 2008), the resolution of the wing shape in pterosaurs benefits not only those seeking to investigate their aerodynamic characteristic but also those with an interest in determining pterosaur life habits.

Powered flight appears to have been the primary method of locomotion in all pterosaurs where the flight surface is primarily comprised of a single uninterrupted membrane, the "brachiopatagium," with the leading edge being formed by the bones of the forelimb (Fig. 1). Within the context of this manuscript we use the term wings inclusively to refer to all the bones of the forearm and the primary flight membrane that spans between the most distal point of the forearm to where it is associated with the lateral margin of the body or hind limb. The distal portion of the brachiopatagium was controlled by the elongated fourth digit (wing-finger) that was able to flex anterioposteriorly about the wing metacarpal, folding the wing during terrestrial locomotion, diving, or fast gliding flight. For the purpose of this study all orientations are given for an animal in its estimated gliding position, with the wing fully extended as illustrated in Fig. 1. Within the patagia itself a radiat-

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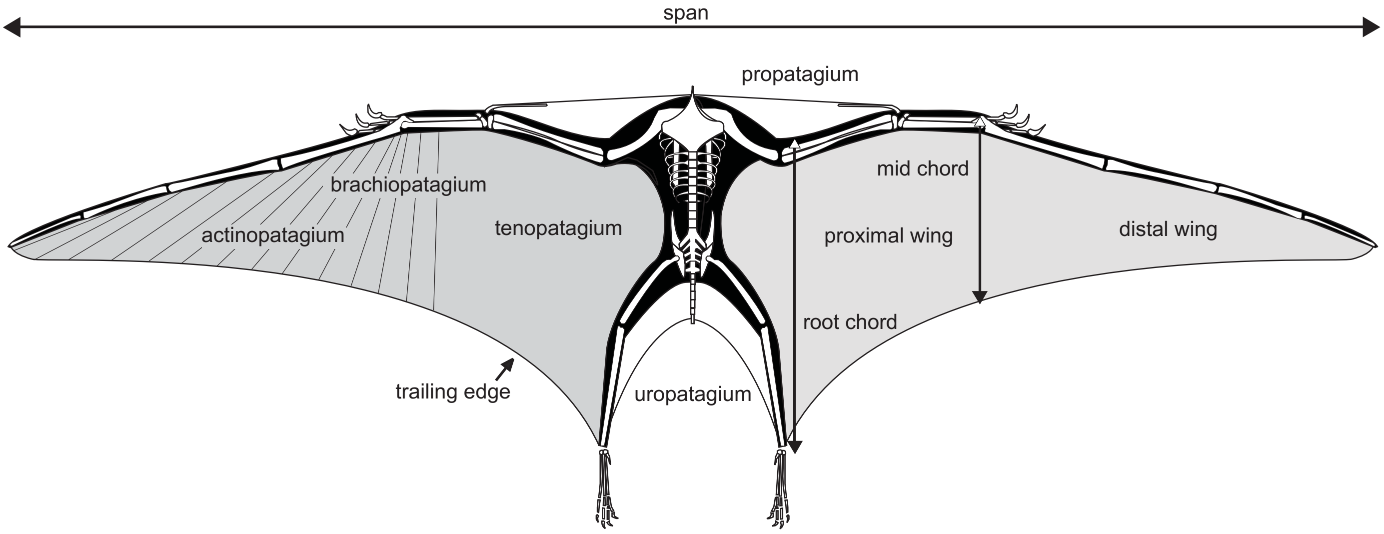

Fig. 1. Schematic sketch of *Pterodactylus* as viewed in its inferred flight position from ventral view (adapted from Wellnhofer 1970). The three flight membranes are illustrated with the brachiopatagium, the focus of this work, being shaded in grey. All terminology is applied to the animal in this position and the size of any specific chord is here generally defined as being narrow or broad, large or small. While the root chord should generally also include the chord of the propatagium for the purpose of this paper it is restricted to the brachiopatagium.

ing pattern of structural actinofibrils developed for both controlling the local camber and spreading the wing distally (Bennett 2000). The distribution of these elements gives rise to the major divisions of the brachiopatagium, the distal, fibril dense actinopatagium, and the proximal tenopatagium, containing fewer fibrils (Schaller 1985).

In addition to the brachiopatagium two separate, and much smaller, membranes are also proposed to take an active role in flight, these being the fore-wing or "propatagium" and the tail wing or "uropatagium" (also sometimes referred to as the "cruorpatagium"). While the shape of the pro- and uropatagia may also be considered controversial, the former is reliant on the orientation and mobility of the pteroid bone (see Bennett 2007a; Palmer and Dyke 2009; and Wilkinson 2008 for contrasting interpretations), while the latter also hinges on the use of an important skeletal element, the fifth pedal digit. While the authors acknowledge that both the propatagia and uropatagia are important for the construction of an accurate flying model of a pterosaur, they are not considered further here.

The primary focus of this paper is thus to evaluate the fossil evidence and identify the proximal attachment of the brachiopatagium so that future aerodynamic studies do not have to simultaneously consider radically different wing configurations. It also aims to ensure that unsupported wing reconstructions, common throughout the current literature, are not repeated in future works.

Institutional abbreviations.—BPM, Beipaio Paleontolgical Museum, Beipaio, China; BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; GMV, Geological Museum of Nanjing, Nanjing, China; IGM, Universidad Nacional Autónoma de México Instituto Geología de Mexico, Mexico City, Mexico; IVPP Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, China; JME, Jura-Museum, Eichstätt, Germany; MCSNB, Museo Civico di Scienze Naturali Bergamo, Bergamo, Italy; NHMW, Naturhistorisches Museum Wien, Vienna, Austria; SMNK, Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe, Germany; YPM, Yale Peabody Museum, New Haven, USA.

Current problems: "bird" versus "bat"-like wings

Reconstructions of the wing membrane are divided between the so called "bird" (narrow chord) and "bat-like," (broad/ankle chord) configurations (Fig. 2). In the former the membrane extends to the torso or hip (Brower 1980, 1982, 1983; Padian and Rayner 1993; Peters 2001), while in the latter it is associated with the hind limb at about the knee (Martill and Unwin 1989) or ankle (e.g., Unwin and Bakhurina 1994; Frey and Martill 1998; Frey and Tischlinger 2000; Tischlinger and Frey 2002; Frey et al. 2003; Witton 2008). Variable configurations for individual species must also remain a possibility (Wellnhofer 1991; Dyke et al. 2006). The inferred extent of the wing has been influenced by a number of factors including historical interpretations, the mode of terrestrial locomotion, and the degree of soft tissue preservation in specimens; each of which will be considered separately.

Historical considerations

Although life restorations of pterosaurs are known as early as 1800 (Taquet and Padian 2004) it was the reconstruction of Sömmerring (1812) that was to become the best known and most widely circulated in the early years of pterosaur re-

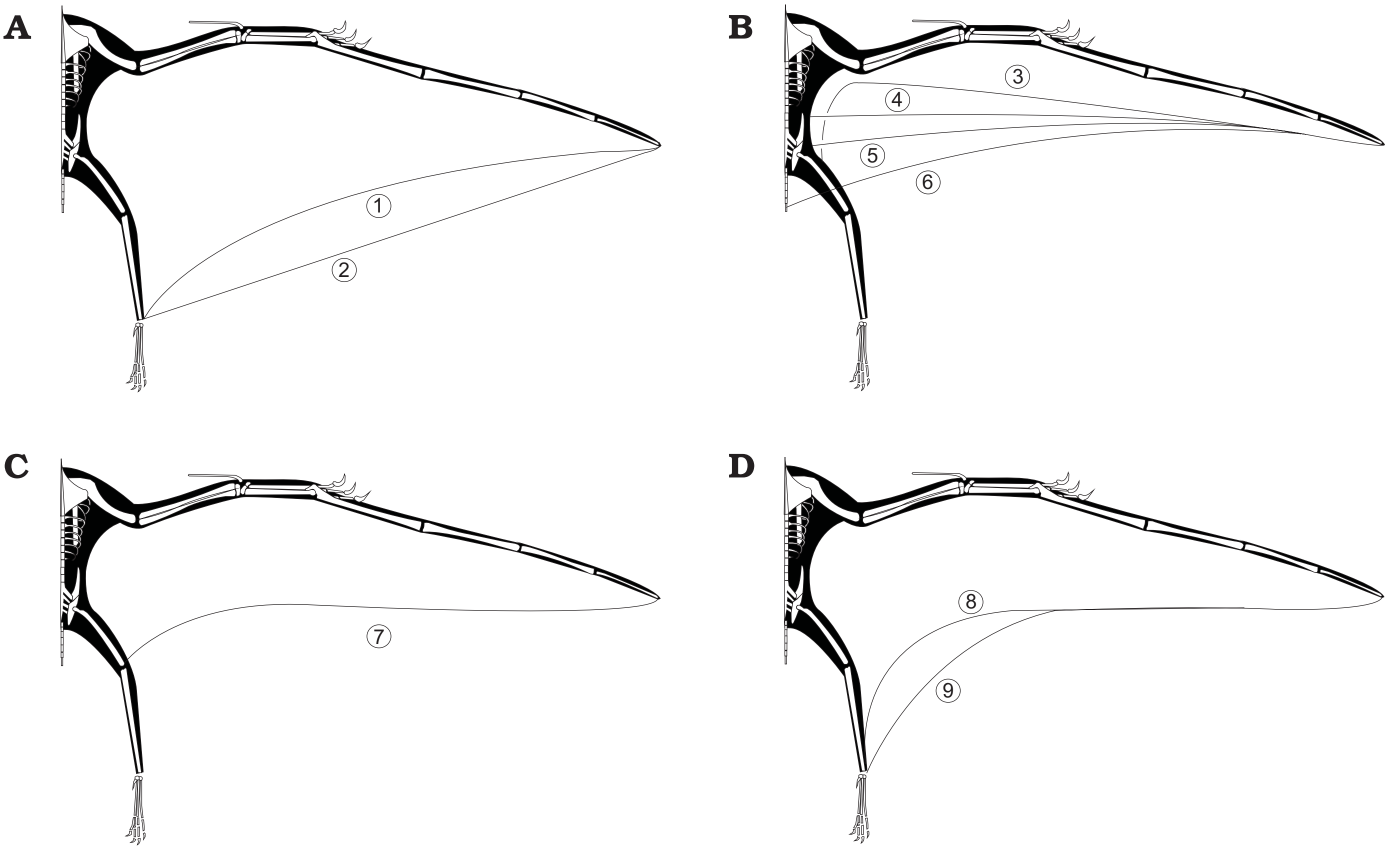

Fig. 2. Various configurations of the pterosaur main wing. **A**. The traditional "bat-like" interpretation adopted by Sömmerring 1812 (1) and Marsh 1888 (2). **B**. The "bird-like" model where the membrane was free of the legs and attached to the body after Peters 2001(3), Padian and Rayner 1993 (4, 5), or tail Bennett 1987(6). **C**. The "*Pterodactylus* model" where the membrane, based on specimen NHMW 1975/1756, attached around the knee (7). **D**. A more recent "bat-like" wing model (8, 9) where the membrane attaches to the ankle (Unwin and Bakhurina 1994; Frey and Martill 1998; Frey and Tischlinger 2000; Tischlinger and Frey 2002; Frey et al. 2003).

search. His belief that pterosaurs were a form of extinct bat, ignoring the fossil evidence laid down by Collini (1784) and Cuvier (1801)—dismissing the reptilian quadrate, the elongated fourth metacarpal and reconstructing the thorax and pelvis based on the skeleton of a bat—must have been the dominant reason why the wing membrane extended to the hind limbs in his restoration. While later authors would accept the reptilian nature of pterosaurs contra to that of Sömmering (1812), his illustration of a "bat-like" membrane remained the accepted configuration for much of the 19th and 20th centuries.

The appearance of the first fossils preserving part of the membranous wing seventy years later did little to alter this view when in 1882 Zittel and Marsh each independently published on different exceptionally preserved fossils of *Rhamphorhynchus*. Despite the absence of the body, Zittel (1882) interpreted the membrane in his specimen as being associated with the hind limbs during life. Restorations from the 19th century illustrate that the flight apparatus in pterosaurs was more or less universally accepted to have been "bat-like" (e.g., Marsh 1882; Zittel 1882; Williston 1897; also see Seeley 1901: fig. 58). However, in his classic book "Dragons of the Air," Seeley (1901) criticised his colleagues for restoring more of the wing membrane than the fossil specimens preserved, stating that "I should have preferred to carry it [brachiopatagium] no further down the body than the lower part of the back there being no fossil evidence in favour of this extension so far as specimens have been described" (Seeley 1901: 165). Although later works such as Jaekel (1910) and Strömer (1913) also kept the hind limbs of *Rhamphorhynchus* free from the brachiopatagium, a majority of restorations produced during the first quarter of the 20th century continued to carry the membrane down to the lower hind limb or ankle (e.g., Abel 1919, 1925; Hankin and Watson 1914—*Pteranodon*; Stieler 1922—*Dorygnathus*; Wiman 1923—*Dorygnathus*; Wiman 1925—*Pterodactylus*). Williston, in his 1911 paper, included an extensive wing surface for *Nyctosaurus*, which stretched from the ankle as far forwards as the head, and stated "that the membrane extended to the tarsus on the peroneal side of the legs I think now hardly admits of doubt; the animals would hardly have been "*flugfähig* [volant]" were the legs wholly free, since the membrane would have been too narrow to serve as a parachute….." (Williston 1911: 704).

Although this ankle chord configuration was widely accepted and would later be adopted by several studies into

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pterosaur flight dynamics (e.g., Bramwell and Whitfield 1974; Stein 1975) there was little fossil evidence during this period to suggest that this, or indeed any other model, was correct. The holotype of *Pterodactylus antiquus* preserves no trace of a membrane and therefore the restorations of Hermann (Taquet and Padian 2004) and Sömmerring (1812), amongst others, are fictional. Neither were the first specimens preserving a membrane of much assistance, as the "Zittel Wing" (BSPG 1880 II 8) is an isolated wing with no trace of the body, though Padian and Rayner (1993) argued that it would have extended no further caudally than the hip. The *Rhamphorhynchus* specimen (YPM 1778) of Marsh (1882) is also of little use as the proximal portion of the membrane is not preserved. No traces of a membrane have ever been found in any specimen of *Dorygnathus*, *Pteranodon* or *Nyctosaurus* and therefore the early reconstructions of Marsh (1882) and Williston (1897) cannot be tied to any fossil evidence. Lastly Williston's (1911) assumptions that pterosaurs would not have been flight worthy were the legs free of the flight membrane is also untrue, as has been demonstrated by a significant increase in our understanding of aerodynamics and several recent studies on the subject (e.g., Brower 1980, 1982, 1983; MacCready 1985; Chatterjee and Templin 2004). Therefore while a "bat-like" configuration has historically been the accepted model it was not explicitly tied to any fossil evidence and appears to have been sustained primarily through a historical bias and a lack of any evidence to the contrary.

"Bird-like" configuration

Many of these points were raised by Padian (1983, 1985, 1987) who challenged the traditional "bat-like" model and argued that the wing was far less extensive and more "bird-like" in profile. Padian (1983) supported this by observing that several fossils of *Rhamphorhynchus* "clearly show that the hind limb was free of the wing and that the wing extended no further back along the body wall than the pelvis" (Padian 1983: 219); reiterating the concerns of Seeley (1901). It was subsequently argued that previous workers were mislead into reconstructing an ankle chord as post-mortem contractions had caused the trailing edge of the membrane to coincidentally lie in the same plane as the wing (Padian and Rayner 1993). Padian and Rayner (1993) also noted that an ankle membrane would have required a trailing edge structure, a feature which has never been identified, and that with an appropriate form and the actinofibrils providing a sufficient camber there was no need for the brachiopagium to attach to the hind limbs. The hind limbs would have been of limited use in cambering a high aspect ratio wing as their influence would have been restricted to only the most proximal region of the membrane.

The narrow chorded configuration was adopted by Rayner (1990) and was also incorporated into several aerodynamic experiments (Brower 1980, 1982, 1983; MacCready 1985; Chatterjee and Templin 2004). It was also used, along with other configurations, by Hazlehurst and Rayner (1992) in their study of pterosaur ecology. Other studies followed in a similar style by presenting a model where the hind limbs were also free from any role in flight. Bennett (1987) argued that the brachiopatagium might have attached to the lateral face of the tail, having found a pair of elongate caudal rods in *Pteranodon* and possibly *Nyctosaurus* too, although he subsequently rejected this idea (Bennett 2001). Peters (2001), based on his own photographic observations, reconstructed the trailing edge of the brachiopatagium as extending only slightly caudal to the elbow before turning sharply and attaching to the femur (Fig. 2B, configuration 3).

Due to their common association, a narrow chorded model may perhaps be viewed as being inseparable from bipedal locomotion in pterosaurs although this is not suggested to be the case. Bipedal locomotion in pterosaurs was argued for by Padian (1983) but this has been challenged and rejected by several workers (e.g., Unwin 1987, 1988; Wellnhofer 1988); although a parasagittal orientation of the hind limbs was later demonstrated to be possible (Bennett 1990, contra Wellnhofer 1988). Bennett (1997) more recently rejected bipedal locomotion in pterosaurs by noting that: the metatarsals were spreading and unfused; the foot was not symmetrical with a reduction of the medial and lateral digits, unlike other cursorial digitigrade animals; and the metatarsophalangeal joints did not permit sufficient extension. The assumption that these observations, having been made on large pterodactyloids, were equally applicable to more basal pterosaurs was later confirmed by Clark et al. (1998) in a specimen of *Dimorphodon weintraubi* (IGM 3494). Although Padian (2003, 2008) subsequently acknowledged that pterodactyloid pterosaurs must have adopted a quadrupedal stance as a result of ichnological evidence and the increasing length of the fourth metacarpal he argued that this evolved secondarily from a bipedal ancestry and non-pterodactyloid pterosaurs may themselves have been bipedal.

The arguments for and against a bipedal mode of locomotion are not considered further here as we do not regard them as being of direct relevance in determining the extent of the main wing (for a full discussion see Padian 2008). It is sufficient to state that it is now universally accepted that pterodactyloids were quadrupedal and thus would have been free to have extended a membrane to the ankle. Even if non-pterodactyloid pterosaurs (or pterosaur ancestors) were bipedal it is widely accepted that the brachiopatagium was flexible, elastic and could have been folded to a large degree so there is no clear reason to expect it to hinder terrestrial locomotion to any great degree.

Membrane-preserving fossils

The shape and extent of the brachiopatagium can only be resolved by a comprehensive review of the fossil evidence that, despite their relative rarity, contains a significant number of specimens in which the wing membrane can be observed. Although many of these have been described individually by separate authors and used in isolation to infer details of the brachiopatagium, when considered together they present a clearer picture of the wing configuration. The most useful of these include: *Anurognathus* (private collection, see Bennett 2007b) and *Jeholopterus* (IVPP V 12705), representing the Anurognathidae; *Eudimorphodon* (MCSNB 8950a), *Rhamphorhynchus* (e.g., JME SOS 4784) and *Sordes* (PIN 2585/3) for other non-pterodactyloid pterosaurs; *Beipiaopterus* (BPM 0002), *Pterodactylus* (NHMW 1975/1756), *Eosipterus* (GMV 2117), and to a lesser degree a number of indeterminate azhdarchoids (e.g., SMNK PAL 3830, 3900, 6404) for the pterodactyloids.

The extensive preservation of soft tissue belonging to the wing appears to be relatively more common for *Rhamphorhynchus* than for any other pterosaur taxon. However, despite the relatively large number of individuals having been documented with membrane preservation, only a minority of these are of much use for the purpose of this study. These include the specimens figured by Padian and Rayner (1993: fig. 3) as contra to their claims that these clearly show the hind limb to be free of a membrane, the proximal portion of the trailing edge in each specimen is either obscured or detached. While we rightly acknowledge that these were some of the best specimens available at that time, they cannot be used to infer details of the wing other than that the distal portion of the wing was narrow, as in no specimen does the trailing edge of the membrane contact the body wall in a natural state. This is also the situation observed in the "Zittel Wing" (BSPG 1880 II 8) as despite its exceptional preservation, the absence of the body means that it is of little value for determining the extent of the wing membrane, having been interpreted as supporting a trailing edge attachment to both the ankle (Zittel 1882) and the torso (Padian and Rayner 1993). Arguably the only specimen of *Rhamphorhynchus* that preserves the proximal portion of the wing in association with the hind limb is that of *R. muensteri* (JME SOS 4784), commonly referred to as the "Dark Wing". The detail of preservation here is superior to these other specimens and allows for ultra-violet light to pick out muscle facia and a vascular system within the wing itself (see Frey et al. 2003). Importantly the proximal portion of the left wing is complete and demonstrates that the membrane curved sharply caudally on approaching the body to attach by the ankle (Figs. 3A, 4A).

The holotype of *Sordes pilosus* (PIN 2585/3) preserves several extensive membranous surfaces and has been the focus of a number of publications since its original description by Sharov (1971) (e.g., Unwin and Bakhurina 1994; Unwin 1999). While identifying the full length of the trailing edge of the wing in photographs is often difficult, the brachiopatagium was described as being narrow distally and becoming broader towards the proximal portion with a trailing edge that terminates about the ankles (Unwin and Bakhurina 1994: figs. 3E, 4E). Bakhurina and Unwin (2003) later reconstructed the wing membrane of *Eudimorphodon ranzii* (MCSNB 8950a) noting that the hind limbs, foot and 5th toe, together with preserved patches of membrane, showed an almost identical disposition to that seen in the holotype of *Sordes* (Figs. 3F, 4F). The patterns of fibres observed between the hind limbs were interpreted as patagial fibres with the same orientation and spacing viewed in the uropatagium of *Sordes* and therefore the reconstruction of the wings of *E. ranzii*, and very likely all basal pterosaurs, are directly comparable to that of *S. pilosus*. The wing shape of *Sordes* was disputed by Peters (1995, 2001) who questioned the trailing edge identified by Sharov (1971), suggesting that it may have been an organic smear bounded by breaks in the bedding plane, and having identified a "possible alternate trailing edge…..just posterior to the elbows" (Peters 2001: 285). He also argued that post-mortem disturbance was evident in this specimen and that the movement of the fore and hind limbs had created the illusion of an ankle wing. Dyke et al. (2006) later cautioned against applying a *Sordes*-like configuration universally because the hind limb proportions were suggested to be atypical for even its closest relatives. The completion of more extensive databases, however, indicates that this concern is incorrect and nothing unusual is noted in its limb proportions (RAE personal observation 06/2010).

Within the Anurognathidae the exceptional preservation of the specimens of *Jeholopterus ningchengensis* (Figs. 3B, 4B) and *Anurognathus ammoni* (Figs. 3D, 4D) indicate that the membrane, or the impression of the wing and its associated fibres, were also associated with the hind limb down to the ankle (Wang et al. 2002; Bennett 2007b; Kellner et al. 2009). While a second specimen of *Jeholopterus* (Ji and Yuan 2002) is also known it does not show an ankle attachment but rather the trailing edge is clearly seen to extend from the first wing-finger phalanx to the proximal margin of the humerus (Fig. 5B). This forms a wing of an impossibly narrow chord that does not even contact much with the wing finger and is a clear example of the extent to which a flexible membrane can contract post-mortem.

The preservation of extensive wing membranes in pterodactyloid pterosaurs appears to be less common than for non-pterodactyloids taxa. In one exceptional *Pterodactylus* specimen (the "Vienna specimen", NHMW 1975/1756) a very narrow wing membrane is preserved and implies a femoral attachment of the brachiopatagium (Figs. 3C, 4C). However, the original extent of the membrane is unclear as its narrow chord suggests a large degree of post-mortem contraction while soft tissue structures preserved adjacent to the tibia, observed under UV light (Tischlinger and Frey 2002), suggest that the trailing edge did not truly terminate about the knee. Rather it is likely that the membrane extended further distally along the limb towards, or even as far as the ankle (Helmut Tischlinger personal communication 6/2008).

The pterodactyloid *Beipiaopterus chenianus* (Lü 2002, 2003) preserves a long patch of membrane adjacent to its femur and a configuration similar to that found in non-pterodactyloid pterosaurs can be observed in the holotype specimen of *Eosipterus* (Figs. 3E, 4E; Ji and Ji 1997). Although

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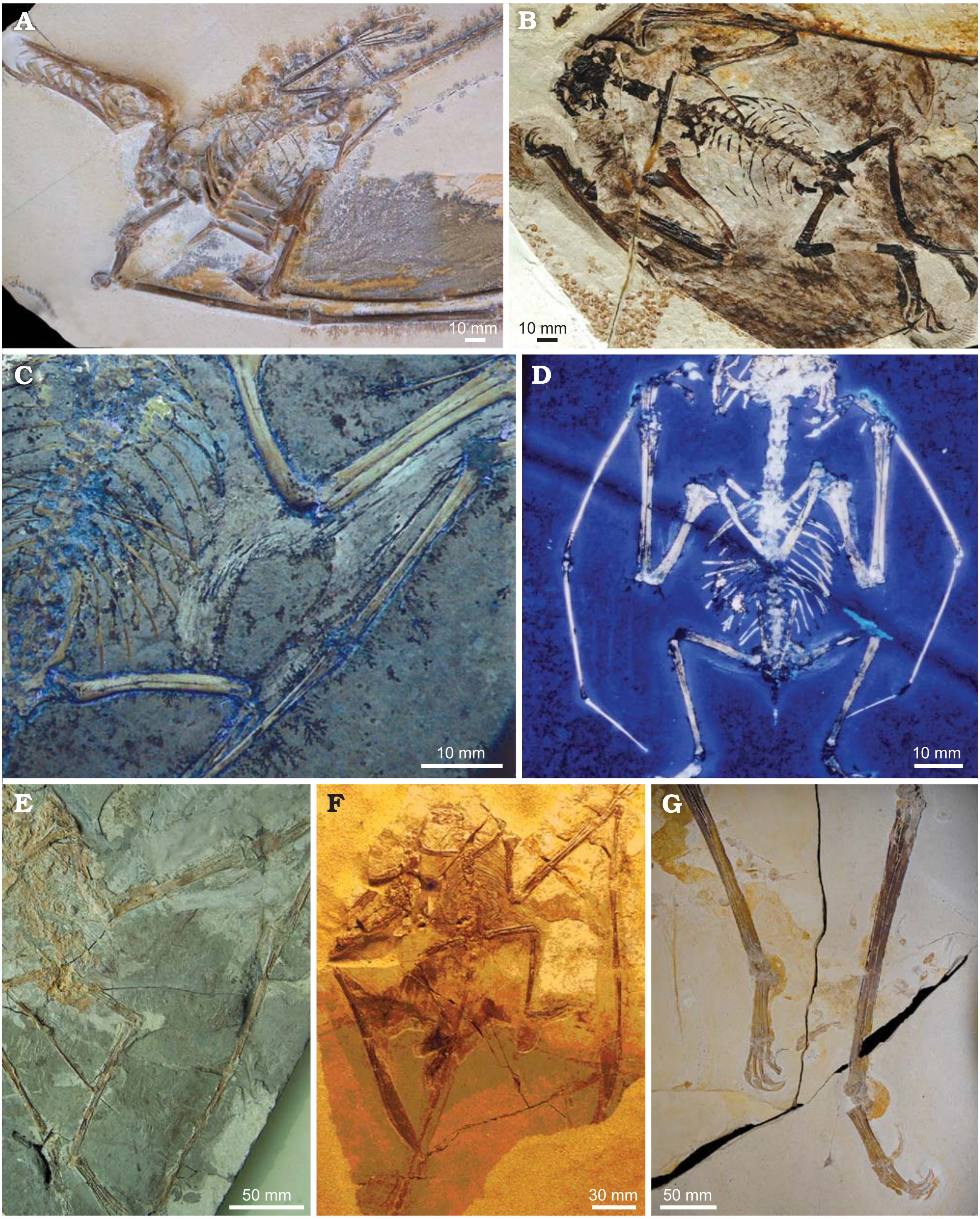

Fig. 3. Selected photographs of pterosaur specimens displaying soft tissue preservation around the hind limbs and/or ankles. **A**. *Rhamphorhynchus muensteri* (Goldfuss, 1831), the "Dark Wing", JME SOS 4784, Eichstätt region (Upper Jurassic), Germany. **B**. *Jeholopterus ningchengensus* Wang, Zhou, Zhang, and Xu, 2002, IVPP V 12705, Lower Yixian Formation (Early Cretaceous), China. **C**. *Pterodactylus kochi* (Wagner, 1837), "Vienna specimen", NHMW 1975/1756, Solnhofen Limestone (Upper Jurassic), Germany. **D**. *Anurognathus ammoni* Döderlein, 1923, private specimen (Bennett 2007b), Solnhofen Limestone (Upper Jurassic), Germany. **E**. *Eosipterus yangi* Ji and Ji, 1997, GMV 2117, Lower Yixian Formation (Early Cretaceous), China. **F**. *Sordes pilosus* Sharov, 1971, PIN 2585/3, Karatau Formation (Upper Jurassic), Kazakhstan. **G**. Tapejarid indet., SMNK PAL 3830, Crato Formation (Early Cretaceous), Brazil.

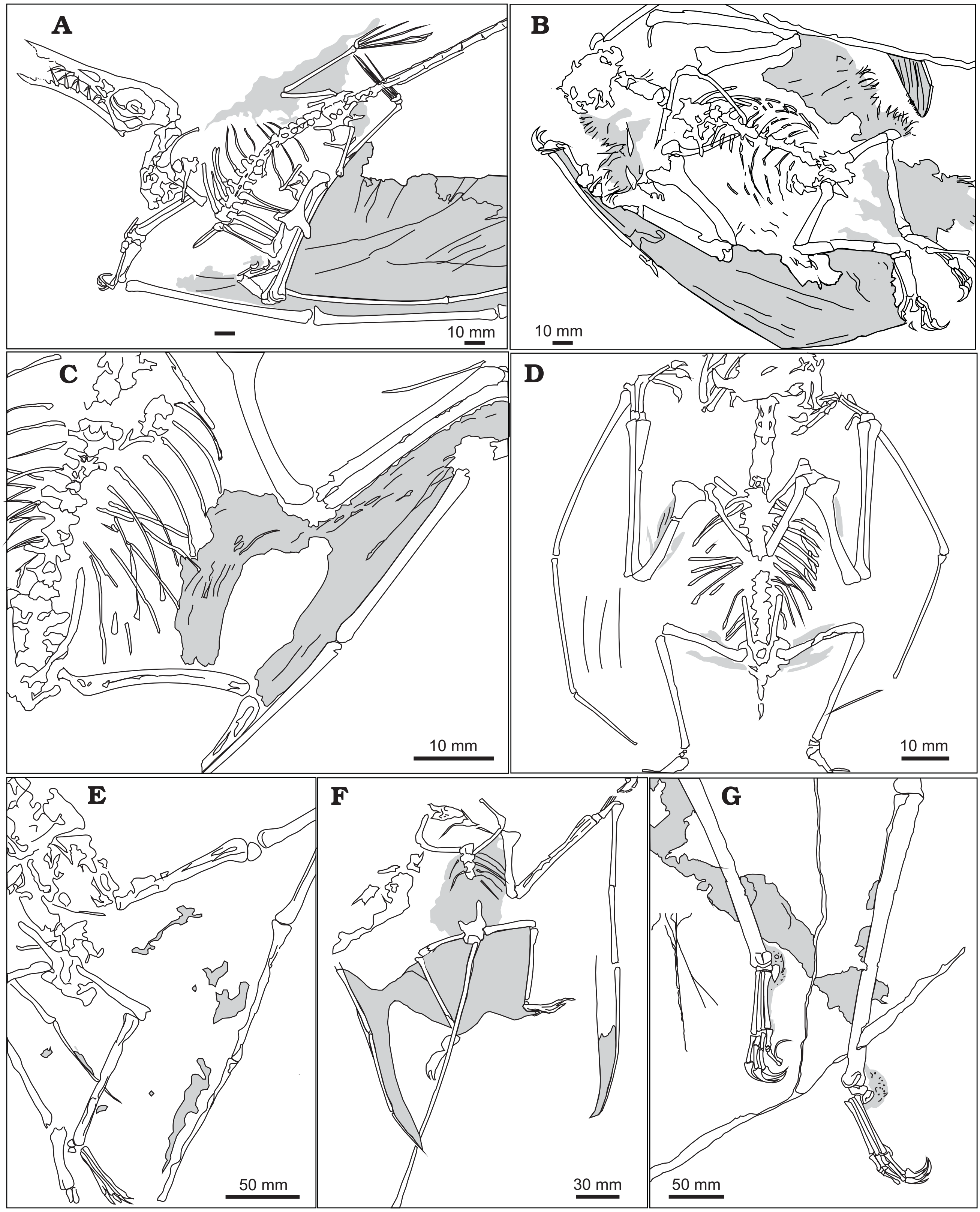

Fig. 4. Line drawings of the pterosaur specimens depicted in Fig. 3 or specific points of interest. Tissue belonging to the wings is marked in bold outlines. **A**. *Rhamphorhynchus muensteri*, the "Dark Wing", JME SOS 4784, Eichstätt region (Upper Jurassic), Germany. **B**. *Jeholopterus ningchengensus*, IVPP V 12705, Lower Yixian Formation (Early Cretaceous), China. **C**. *Pterodactylus kochi*, "Vienna specimen", NHMW 1975/1756, Solnhofen Limestone (Upper Jurassic), Germany. **D**. *Anurognathus ammoni*, private specimen (Bennett 2007), Solnhofen Limestone (Upper Jurassic), Germany. **E**. *Eosipterus yangi*, GMV 2117, Lower Yixian Formation (Early Cretaceous), China. **F**. *Sordes pilosus*, PIN 2585/3, Karatau Formation (Upper Jurassic), Kazakhstan. **G**. Tapejarid indet., SMNK PAL 3830, Crato Formation (Early Cretaceous), Brazil.

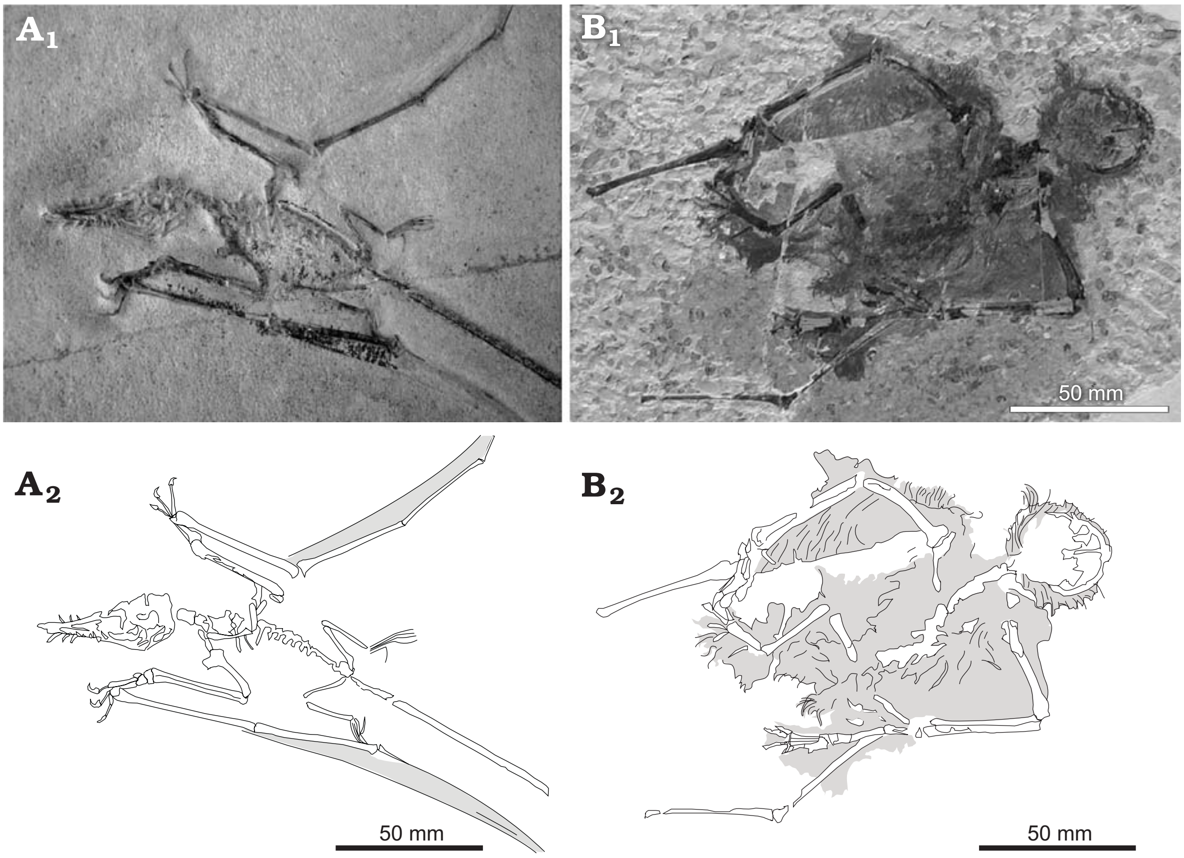

Fig. 5. Photographs and line drawings of selected specimens showing a pronounced contraction of the wing. **A**. *Rhamphorhynchus longicaudus* (Münster, 1839), BSPG 1938 I 503a, Solnhofen Limestone (Upper Jurassic), Germany; photograph (A_1), explanatory drawing (A_2). **B**. *Jeholopterus* sp. (Ji and Yuan 2002), Lower Yixian Formation (Early Cretaceous), China; photograph (B_1), explanatory drawing (B_2). Tissue belonging to the wings is marked in bold outlines in A_2 and B_2.

the flight membrane was not specifically mentioned by Ji and Ji (1997) we confirm that the brachiopatagium extends to about the middle part of the tibia (DWEH personal observation 10/2008). However, the wing membranes of *Eosipterus* require further preparation, being partially obscured by matrix, and that exposed does not include a termination point. The attachment point of the trailing edge was thus probably located more caudally than the mid-tibia, and may well have been at the ankle.

A number of azhdarchoid limb elements from the Crato Formation of NE Brazil are associated with soft tissues from the wings but in the absence of any cranial or axial elements. Frey et al. (2003) described a basal azhdarchoid SMNK PAL 3830 (Figs. 3G, 4G) where a membrane trace extends from the metacarpal region to the ankle of the respective hind limb. Two more specimens (SMNK PAL 3900 and 6409, see Unwin and Martill 2007) also consist of the fore and hind limbs preserved in close association along with a goethitic trace representing part of the brachiopatagium. A fourth specimen (SMNK PAL 3855) preserves no visible soft tissue, however, both the fore and hind limbs are preserved in a comparable manner suggesting that they sank together. In the case of these specimens the soft tissue traces are too extensive to be regarded as anything other than the wing membrane and in the SMNK PAL 3830 preserve traces of folding structures and actinobrils; known only from the brachiopatagium. Although the subsequent specimens do not preserve direct evidence about the attachment location of the tenopatagium it is difficult to explain the presence of corresponding limb elements, settling separate to the torso, without invoking a configuration where they where bound together by a flight membrane.

Discussion

In all exceptionally preserved pterosaur specimens where the proximal portion of the membrane is present, the original descriptions confirm and/or support an attachment to the ankle (e.g., *Anurognathus ammoni*, *Beipiaopterus chenianus*, *Eosipterus yangi*, *Eudimorphodon ranzii*, *Jeholopterus ningchangensis*, *Rhamphorhynchus muensteri*, *Sordes pilosus*). Several azhdarchoid pterosaurs (i.e., SMNK PAL 3830, 3855, 3900, 6409) are also interpreted here as having their limb elements connected by an extensive membrane due to the observed state of the fossil specimens (Frey et al. 2003; Unwin and Martill 2007). Although several of these observations are in no way immune to criticism, as it can be argued that without any

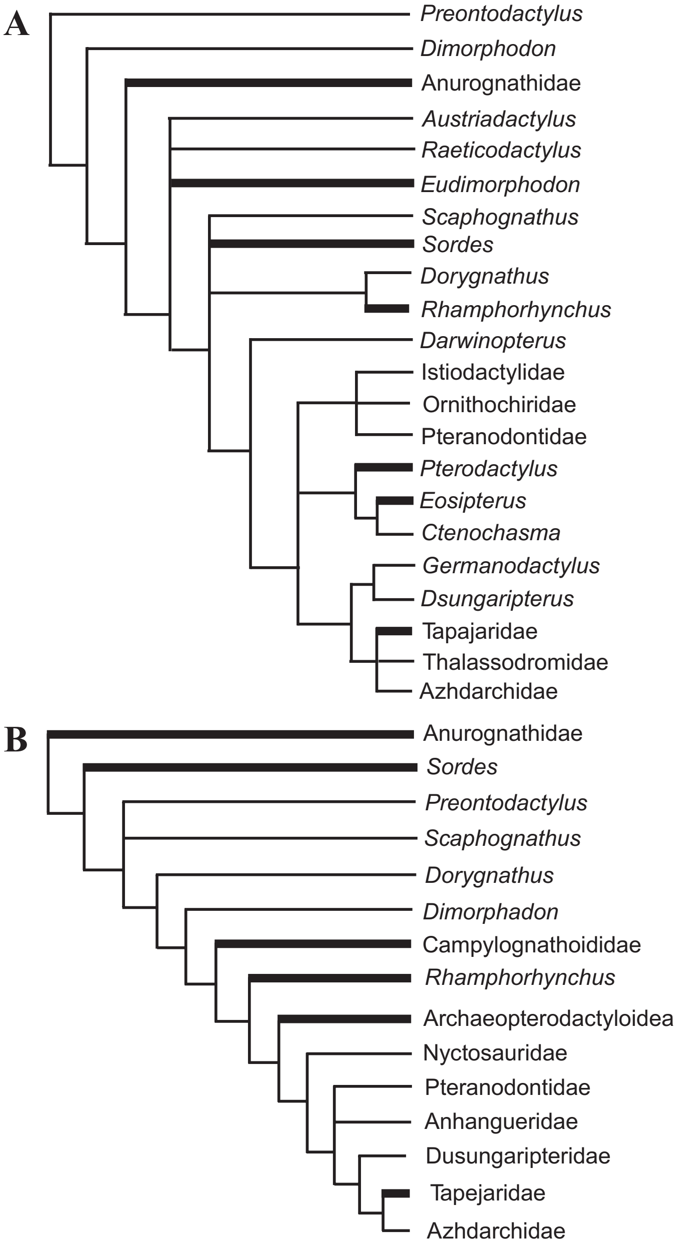

Fig. 6. Two contrasting pterosaur phylogenies. **A**. Phylogeny from Lü et al. (2009). **B**. A simplified version of that presented by Wang et al. (2005). Thick black lines indicate species or groups of taxa for which the fossil evidence supports an ankle attachment of the wing.

actinofibrils it is not always possible to know whether the tissue belongs to that of the wing of the membrane, we note that it is unlikely that tissue from the body has here been misinterpreted as belonging to the brachiopatagium. The majority of the presented specimens preserve fibres and wrinkles, known only from the wing membrane, and/or a clear trailing edge that itself strongly suggests the trace must be regarded as part of the wing. Where none of these features are present the membrane traces are located lateral to the body and between the fore and hind limbs, or are too extensive in their coverage to have belonged to anything other than the flight membrane. The ankle attachment is therefore the best configuration supported by direct soft tissue evidence, although a knee attachment as suggested by the Vienna *Pterodactylus*, or tibia as with *Eosipterus* in any case confirms that the tenopatagium was associated with the hind limbs.

To the best of the authors' knowledge no specimens exist that conclusively show an attachment to the torso or hip. This is contrary to the configuration argued for by Padian and Rayner (1993) who figured several specimens of *Rhamphorhynchus* to support the hypothesis that the hind limbs were free from the wing membrane. As noted above, and is evident from their own figures, these specimens do not preserve the proximal portion of the wing membrane and thus cannot be used support a "bird-like" wing, particularly as more extensive membranes are now known (Frey et al. 2003). While Padian and Rayner (1993) had earlier argued that the post-mortem contraction of the wing membrane was responsible for the misidentification of an ankle attachment in some specimens we instead suggest that these contractions can be used to reject a hip or torso attachment. No preserved wing will ever be broader than during life, but instead may appear to be much narrower due to post-mortem effects (Fig. 5). The comparison of two specimens of *Jeholopterus* sp. (Ji and Yuan 2002; Wang et al. 2002) indicates that considerable post-mortem contraction of the flight membranes was possible and demonstrates the extent to which contractions of the membrane can deform the original shape and/or surface area of the wing (Fig. 5B). While this comparison highlights a rather extreme example of wing contraction, lesser examples are likely to be wide spread throughout the fossil record. To ensure that the most extensive membrane preserved is taken as the minimum for any particular taxa, specimens of the same genus must be compared with other, more recent discoveries whenever possible. We suggest that contraction of the membrane is also responsible for some of the exceptionally narrow chords observed in specimens of *Rhamphorhynchus* (e.g., BSPG AS I 772, BSPG 1938 I 503a; Fig. 5A) and support this by comparative observations with many other specimens of the taxon, particularly the "Dark Wing" specimen and to a lesser extent, the "Zittel Wing". We also argue that the intrinsic flexibility of the membrane (Frey et al. 2003) must be considered when confronted with a preserved wing as any folded or contracted example will inevitably produce a significant underestimate of its true extent if simply taken at face value (see e.g., Bennett 2000).

Despite continuing conflicts between major phylogenies (e.g., Kellner 2003; Unwin 2003; Wang et al. 2005, 2009; Bennett 2007b; Andres and Ji 2008, Andres et al. 2010) the presence of an ankle attachment is supported in a variety of pterosaurian taxa (Fig. 6) demonstrating that an ankle attachment of the wing was widespread across the full range of the Pterosauria. Although Kellner (2003) and Bennett (2007b) both considered the anurognathids to be the most basal pterosaurs, which would confirm an ankle wing as a basal characteristic, the more recent study of Andres et al. (2010) instead places them as the sister-group to the Pterodactyloidea. Accepting a more derived placement of the Anurognathidae

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does not alter the idea of a basal pterosaurian ankle wing as *Eudimorphodon ranzii* (MCSNB 8950a) occupies a position low down on the tree in all phylogenies (Kellner 2003; Andres et al. 2010) and has been inferred to have a wing extent similar to *Sordes* (Bakhurina and Unwin 2003). Although Dyke et al. (2006) voiced concern about "*Sordes*-like" pattern being universally adopted, these have proven to be unfounded and *Sordes* itself is not unusual in this respect for non-pterodactyloid pterosaurs; in any case a similar configuration can be observed in other pterodactyloid and non-pterodactyloid pterosaurs. The presence of an extensive ankle wing as a basal feature is not unexpected as such a configuration would have been beneficial to early pterosaur ancestors and an arboreal leaping origin of flight in the Pterosauria (Bennett 1997).

When considering the arguments of Padian (2008) that basal pterosaurs were bipedal rather than aboreal in habit we argue for a decoupling of the biped/quadruped hypotheses and the attachment of the trailing edge of the wing membrane. Regardless of which gait pterosaurs used, the flexibility of the brachiopatagium would not have impeded terrestrial locomotion, particularly if the wing was folded.

Additional support for a universally broad wing attachment has been suggested by an observed "high knee" style of preservation common in many pterosaurs. The suggestion here is that post mortem shrinkage of the patagium would have pulled the hind limbs upwards into its observed resting position. Although this position is commonly viewed in bats (RAE personal observation, 02/2009) it is not restricted to animals where a membrane would have attached to the hind limbs as it can also be observed in many fossil birds, including the holotype specimens of *Liaoxiornis delicates*, *Eoenantiornis buhleri*, *Longipteryx chaoyangensis*, *Yanornis martini*, and *Prototeryx fengningensis* (Zhang et al. 2007). Furthermore this position is also observed in the carcasses of extant birds and mammals and is instead linked to damage of the proximal portion of the cerebellar cortex, where decerebellate rigidity causes the limb to flex in such a way (Faux and Padian 2007). The "high knee" style of preservation is thus the result of the central nervous system just prior to the animals' death and not as a result of a contracting flight membrane.

One of the principle reasons for resolving the confusion surrounding the extent of the wing membrane in pterosaurs is to more accurately assess their aerodynamic performance, the results of which can vary significantly depending on the chosen configuration. Wing area, aspect ratio and wing loading are all important parts of several mathematical equations used to estimate flight performance, although more straightforward comparisons of these variables with extant animals are also useful for inferring ecological or palaeobiological aspects. When discussing the narrow chorded wing of pterosaurs Padian and Rayner (1993: 108) stated that "were the wings to extend to the ankle the animals aspect ratio and wing load would be significantly lower than those of comparable piscivorous birds". Although a high aspect ratio wing is the most efficient configuration for fast gliding, piscivorous birds and aerodynamic studies of pterosaurs with a "bird-like" wing have shown that they would have been slow, manoeuvrable and highly competent fliers (e.g., Brower 1980, 1982, 1983; MacCready 1985; Chatterjee and Templin 2004), experimental results should not and cannot be used to contradict the fossil evidence where it exists. As demonstrated above this provides unanimous support for the integration of the hind limbs with the tenopatagium. We also note that the above concerns of Padian and Rayner (1993) need not be problematic for pterosaurs and stress that if these taxa adopted a configuration like *Rhamphorhynchus*, where the trailing edge curved sharply to the ankle only towards the proximal most portion of the wing, then the difference in overall wing characters would not be too great (Fig. 2D, configuration 8). As previously noted the long fore arms and short hind limbs that typify these taxa would naturally result in a high aspect ratio/higher wing load configuration even if the trailing edge extended as far down as the ankle, as we argue it should be reconstructed.

Conclusions

The resurgence of interest in the aerodynamic abilities of pterosaurs is a welcome step forward following a prolonged absence of focused research; however, future experiments must not be hampered by a lack of knowledge or uncertainty when reconstructing the flight apparatus. While some variables, such as mass and mass distribution, will invariably remain contentious, others, such as the shape and extent of the brachiopatagium can instead be resolved (or at least heavily constrained) by a review of the fossil specimens. We separate the ankle chord configuration presented here from the traditional "bat-like" reconstruction, which is now widely accepted to have lacked support from fossil specimens and to have been based on incorrect historical interpretations and a supposed aerodynamic "need" for a broad chord. By contrast the ankle chord configuration presented here is based solely on individual specimens where a clear association between the membrane and the hind limbs can be observed. Based on the available specimens the only configuration supported by fossil evidence is that of an ankle or lower hind limb attachment of the proximal trailing edge (Frey et al. 2003; Witton 2008). In the absence of conflicting evidence for specific specimens or taxa we argue that the null hypothesis should become that of an ankle attachment.

The "bird-like" model remains an unsupported interpretation of the wing shape in pterosaurs as none of the specimens cited by Padian and Rayner (1993) preserve the proximal section of the brachiopatagium. As an ankle attachment is observed in the "Dark Wing" specimen proponents of a narrow chord wing must first present fossil evidence against an ankle attachment in this specimen and why, as the most extensive membrane in the taxon, it cannot be considered the standard configuration for *Rhamphorhynchus*. While we argue that the bipedal/quadrupedal debate can be separated from the extent of the brachiopatagium, as it would not interfere with terrestrial locomotion if it was folded, pterodactyloid pterosaurs are now universally accepted to have been quadrupedal and so would have been free to extend the membrane to their ankles. Since its proposal only the interpretations of Peters (1995, 2001) have provided any new support for the "bird-like" model based on fossil evidence. Peters' (1995, 2001) studies of the membrane in *Jeholopterus*, *Sordes*, and *Eudimorphodon* along with their subsequent reconstructions where the trailing edge extends only just caudal to the elbow are, however, extremely controversial (Unwin and Bakhurina 1995), and appear to have been based solely on photographs rather than first hand observations. While working from photographs is not uncommon and at times unavoidable the conclusions of Peters (2001) arise from an improper use of graphic manipulation that exploits the poor resolution of photographs and allows the boundaries between blocks of pixels to be interpreted as "patterns". This methodology is subjective and produces false and often fantastical images that have no value to science in general (see Bennett 2005). Thus without substantial evidence to the contrary, the narrow wing model must be rejected and should not be considered as a viable alternative to an ankle chord model. The presence of the brachiopatagium extending to the ankle in a variety of distantly related taxa is central to our argument that pterosaurs probably never radically altered the attachment of the trailing edge of the wing throughout their evolutionary history. In this respect the authors are in agreement with Witton (2008) that changes in the lengths of the fore and hind limbs was the driving mechanism for altering pterosaur wing shape.

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