



Evolution of the Pterosaur Pelvis

Authors: Elaine S. Hyder, Mark P. Witton, and David M. Martill

Source: Acta Palaeontologica Polonica, 59(1) : 109-124

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: <https://doi.org/10.4202/app.2011.1109>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-o-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Evolution of the pterosaur pelvis

ELAINE S. HYDER, MARK P. WITTON, and DAVID M. MARTILL



Hyder, E.S., Witton, M.P., and Martill, D.M. 2014. Evolution of the pterosaur pelvis. *Acta Palaeontologica Polonica* 59 (1): 109–124.

Pterosaur pelvic girdles are complex structures that offer a wealth of phylogenetic and biomechanical information, but have been largely overlooked by pterosaur anatomists. Here, we review pterosaur pelvic morphology and find significant differences that correlate well with pterosaur clades identified in some phylogenetic analyses. We find that the length and orientation of the iliac processes, position of the acetabulum, extent of the ischiopubic plate and presence of supraneural fusion in adult individuals are taxonomically informative. Ontogenetic changes in pelvic morphology dictate that osteologically mature specimens are required to assess the development of many of these characteristics. We suggest that pelvic characters can readily be incorporated into pterosaur phylogenetic analyses and may assist in resolving the controversial interrelationships of this group. Distinctive pterosaur pelvic morphotypes suggest considerable differences in stance, locomotory kinematics and hindlimb functionality across the group.

Key words: Pterosauria, pelvis, phylogeny, terrestrial locomotion.

Elaine S. Hyder [elainesh1@aol.com], Mark P. Witton [mark.witton@port.ac.uk], David M. Martill [david.martill@port.ac.uk], School of Earth and Environmental Sciences, University of Portsmouth, Burnaby Building, Burnaby Road, Portsmouth, PO1 3QL, UK.

Received 8 September 2011, accepted 24 April 2012, available online 4 May 2012.

Copyright © 2014 E.S. Hyder et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

Pterosaur pelvises have received only sporadic attention from researchers. Although the pelvic anatomy of some taxa has been described in detail (e.g., Williston 1903; Wellnhofer 1991b; Bennett 1995, 2001; Sayão and Kellner 2006; Padian 2008), and their functional morphology discussed with respect to pterosaurian terrestrial capabilities (e.g., Padian 1983a; Wellnhofer 1988; Bennett 1990; Fastnacht 2005), they have almost entirely been ignored in studies of pterosaur evolution. Recently published phylogenetic studies have barely utilised pelvic data or ignored it altogether, despite their anatomical complexity, which suggests that they may provide useful phylogenetic signals. Several phylogenies (e.g., Kellner 2003; Lü 2009; Wang et al. 2009) present no pelvic characters at all, while just three pelvic characters were scored by Unwin (2003), describing six discrete states. These have been replicated almost identically by Andres and Ji (2008), Andres et al. (2010) and Lü et al. (2010), though the latter authors added two additional states, bringing the total to eight. Butler et al. (2011) added only one additional state to Unwin's (2003) pelvic characters.

The underuse of pterosaur pelvic anatomy in phylogenetic studies may be a consequence of several factors. Many pterosaur pelvises are incomplete or so poorly preserved that

interpreting their complex morphology is problematic or controversial (e.g., Wellnhofer 1974 vs. Padian 1983a), and higher quality pelvic remains are often found in isolation or associated with undiagnostic remains that are of little use in phylogenetic studies (e.g., Bennett 1990; Fastnacht 2005; Sayão and Kellner 2006). This situation has improved in recent years with the pelvises of named taxa becoming better known (e.g., Young 1964; Wellnhofer 1988, 1991b; Frey and Martill 1994; Kellner and Tomida 2000; Bennett 2001; Veldmeijer 2003) and, with improved knowledge of pterosaur anatomy, many incomplete specimens with associated pelvises have been referred to major clades (Bennett 1990; Fastnacht 2005; Sayão and Kellner 2006).

These recent improvements in our knowledge of pterosaur pelvises suggest that, while sharing a general form, considerable variation in pelvic morphology exists between different taxa. The potential implications of this are twofold: (i) pterosaur pelvises may carry phylogenetic signatures that could be incorporated into studies of pterosaur evolution, and (ii) the pelvis probably played different functional and mechanical roles in different groups (i.e., differing roles in locomotion, trunk mechanics and support, internal anatomy, reproductive functionality etc.). Here, we assess both of these possibilities with an overview of pterosaur pelvic evolution presented in the phylogenetic model of Lü et al. (2010), and we present functional hypotheses that may have influenced its devel-

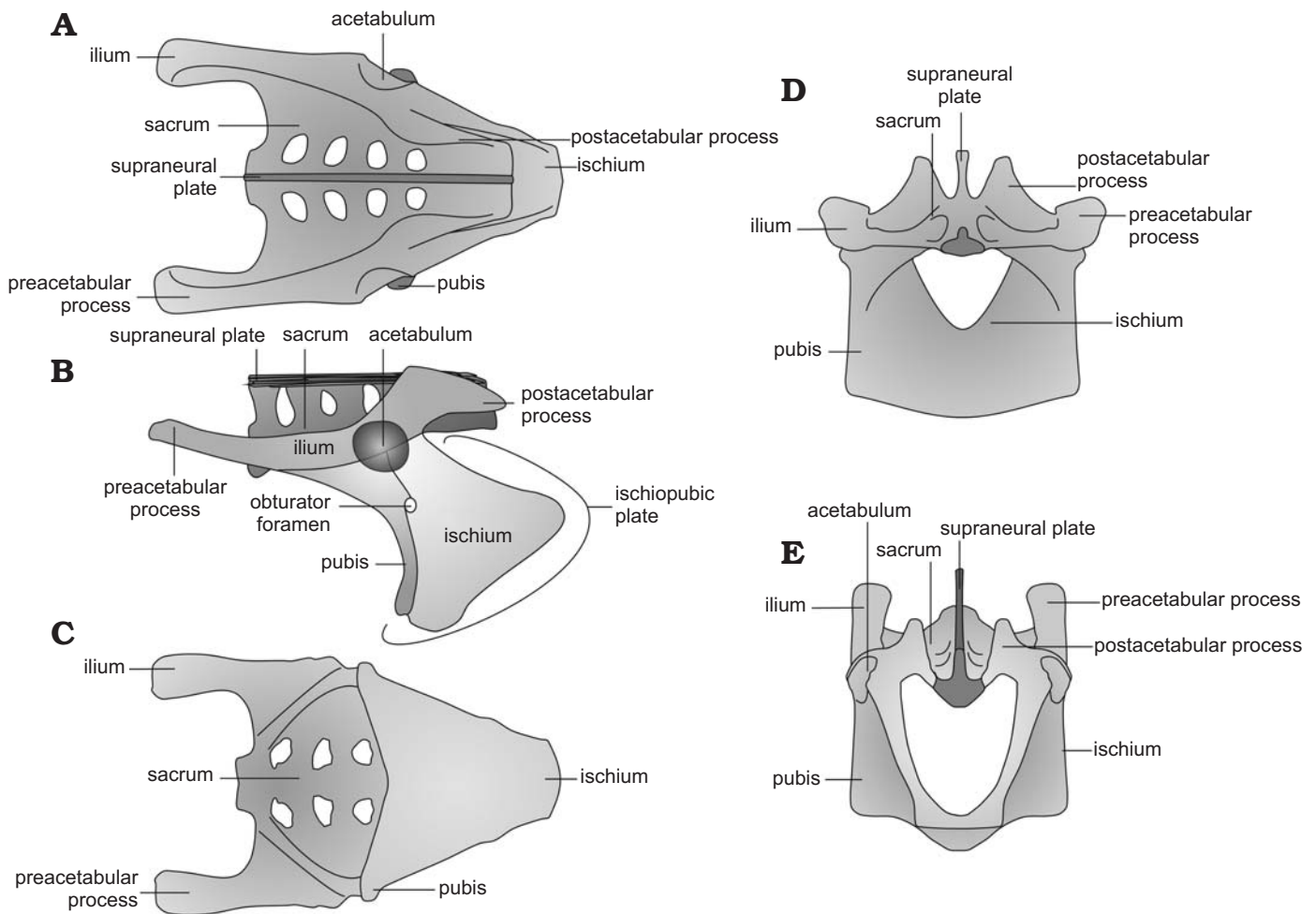


Fig. 1. Generalised pterosaur pelvic anatomy, demonstrated by *Coloborhynchus spielbergi* (RGM 410880), in dorsal (A), lateral (B), ventral (C), anterior (D), and posterior (E) views. Redrawn from Veldmeijer (2003).

opment. We compare the Lü et al. (2010) model of pelvic evolution to those of other pterosaur phylogenies to test for congruence between pelvic morphotypes and clade content, which acts as a useful test for homoplasy within models of pterosaur evolution. Our findings suggest that there is considerable scope for future systematic and functional analyses of pelvis, but we refrain from presenting a cladistic analysis based on the pterosaur pelvis here. A broader analysis of pterosaur phylogeny with detailed pelvic characters is clearly needed, but is beyond the scope of this review.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; BSP, Bayerische Staatssammlung für Paläontologie, Munich, Germany; CM, Carnegie Museum, Pittsburgh, Pennsylvania, USA; CTES-PZ, Palaeozoological Collection, Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste, Corrientes, Argentina; DFMMh, Dinosaurier-Freilichtmuseum Münchhagen/Verein zur Förderung der Niedersächsischen Paläontologie, Münchhagen, Germany; FHSM, Fort Hayes State Museum, Kansas, USA; GMN, Geological Museum of Nanjing, Nanjing, China; GMV, Geological Museum of China, Beijing, China; IVPPV, Institute of Vertebrate Pale-

ontology and Paleoanthropology, Beijing, China; IMCF, Iwaki Coal and Fossil Museum, Iwaki, Fukushima, Japan; JMESOS, Juramuseum (Solnhofen Sammlung, Eichstätt; KUVV, Natural History Museum, University of Kansas, Kansas, USA; MCSNB, Museo Civico di Scienze Naturali of Bergamo, Bergamo, Italy; MFSN, Museo Friulano Di Storia Naturale, Udine, Italy; MHIN-UNSL-GEO-V, Museo de Historia Natural de la Universidad Nacional de San Luis, San Luis, Argentina; MNHN, Museum National d'Historie Naturelle, Paris, France; MOZ, Museo Prof. Olsacher, Zapala, Neuquen, Argentina; NHMUK, Natural History Museum, London, UK; NSM-PV, Institute of Vertebrate Palaeontology, National Science Museum, Tokyo, Japan; QMF, Queensland Museum, Brisbane, Australia; RGM, Rijksmuseum van Geologie en Mineralogie, Leiden, The Netherlands; SMNK, Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe, Germany; SMNS, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; UNC, University of North Carolina, Carolina, USA; YPM, Yale Peabody Museum, New Haven, Connecticut, USA; ZINPH, Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia; ZMNH, Zhejiang Museum of Natural History, Zhejiang, China.

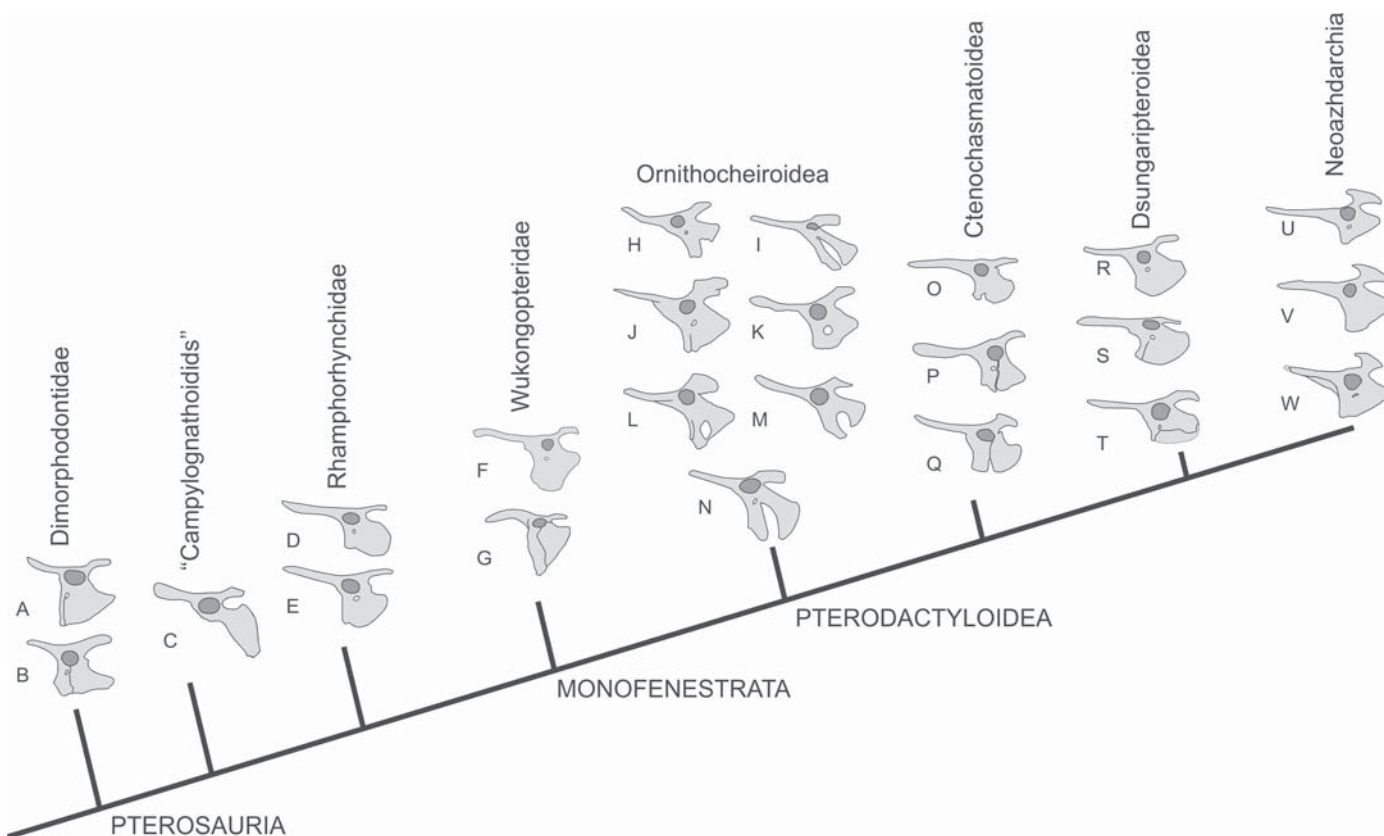


Fig. 2. Plotting of well-preserved pterosaur pelvises into the phylogeny of Lü et al. (2010). A, *Dimorphodon macronyx*; B, *Peteinosaurus zambellii*; C, *Campylognathoides liasicus*; D, *Rhamphorhynchus muensteri*; E, *Dorygnathus banthensis*; F, *Darwinopterus linglongtaensis*; G, *Darwinopterus robustodens*; H, "Queensland pterosaur"; I, Ornithocheiridae indet.; J, *Pteranodon* sp.; K, *Nyctosaurus gracilis*; L, *Coloborhynchus spielbergi*; M, *Arthurdactylus conandoylei*; N, *Anhanguera santanae*; O, "Pterodactylus" *longicollum*; P, *Cynorhamphus suevicus*; Q, *Pterodactylus antiquus*; R, *Herbstosaurus pigmaeus*; S, *Germanodactylus rhamphastinus*; T, *Dsungaripteroidea* indet.; U–W, *Neozhdarchia* indet. See Figs. 4–8 and Appendix 1 for specimen numbers.

Material and methods

Although the anatomy of several pterosaur pelvises is known from exquisite, three dimensionally-preserved remains (Fig. 1), the majority are difficult to interpret. Even those associated with otherwise excellently preserved material are incompletely or poorly preserved, obscured by other bones or preserved in orientations that limit morphological analysis. The latter is particularly common: pterosaur pelvises are frequently preserved in dorsal or ventral orientations that seem to show comparatively little morphological variation compared to pelvises preserved in lateral view. For these reasons, we do not attempt to review all pterosaur pelvic specimens here, but focus on well-preserved pelvises seen in lateral view. In our opinion, these provide the most substantial and significant morphological data of the pelvic elements. The pterosaur literature was trawled for descriptions and illustrations of such pelvises and direct observations were made on pterosaur pelvises in the collections of NHMUK, SMNK, IVPP, and BSP (see Appendix 1 for a full list of specimens).

To place our findings in a phylogenetic context, we present our results in the cladistic framework of Lü et al. (2010; Fig. 2), following recent work suggesting that the dataset

behind this analysis yields the most reliable current pterosaur phylogeny (Andres 2007; Unwin and Lü 2010). Although presenting our results in this way may be seen as making a priori assumptions about pelvic morphotypes, we find that pelvic development shows very little, if any, homoplasy using this phylogenetic model. This cannot be said for other recent pterosaur phylogenies (principally Andres and Ji 2008; Dalla Vecchia 2009; Wang et al. 2009; Andres et al. 2010; Butler et al. 2011), consideration of which can be found in the discussion of our results.

Considerations of intraspecific variation

Pterosaur pelvic morphology is known to reflect likely ontogenetic (Bennett 1993, 1995) and sexual (Bennett 1992; Lü et al. 2011) variation. These can only be determined in part because pterosaur growth sequences and reliable inferences of sexual dimorphism are rare, but some such differences may be apparent even with the limited datasets available and, using the criteria explored below, we exclude some pelvic remains from our analysis.

Descriptions of immature and adult pterosaur specimens (Wellnhofer 1970, 1991b; Bennett 1993, 1995; Kellner and Tomida 2000; Veldmeijer 2003; Wang et al. 2008) suggest

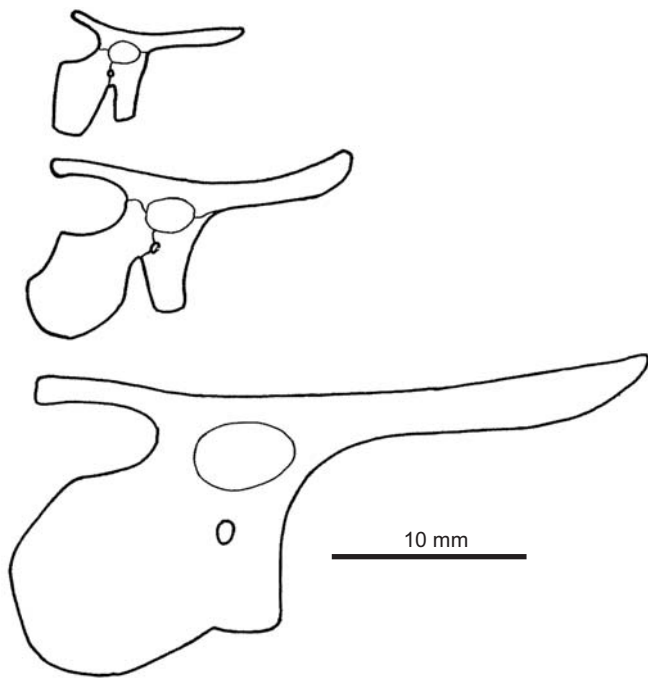


Fig. 3. Ontogenetic changes in the pelvis of *Rhamphorhynchus muensteri* (modified from Bennett 1995).

that young individuals have pelves generally similar to those of adults, but with slightly different proportions, greater suture definition between pelvic bones and, generally, simpler bone morphs (Fig. 3). This seems to reflect increasing ossification of cartilaginous processes in mature individuals (Bennett 1995). Reduced ossification in juveniles is consistent with the ossification sequences of modern precocial bird skeletons, where the synsacrum is one of the last parts of the skeleton to fully ossify (e.g., Hogg 1982), and this may suggest why the pelvic region is poorly preserved in many immature pterosaurs. Pterosaur pelvic bones ossify before fusing with the ribs of the sacral vertebrae to form a synsacrum, suggesting this is the final stage of fusion in the development of the hindlimb girdle (Codorniu et al. 2006).

The supraneural plate of the pterosaur synsacrum is worthy of attention. This structure seems to develop late in ontogeny, although this is currently only—and by no means unambiguously—demonstrated in ornithocheiroid pterosaurs. The holotype of *Coloborhynchus piscator* (NSM-PV 19892) is osteologically immature, bearing a suite of unfused bones across its skeleton, including pelvic bones and a sacrum lacking a supraneural plate (Kellner and Tomida 2000). NSM-PV 19892 was not a small animal, with an estimated wingspan of 5 m (Kellner and Tomida 2000); a value almost comparable to RGM 400 801, the holotype of the 5.9 m span *Coloborhynchus spielbergi* (Veldmeijer 2003). The latter, however, has a supraneural plate and a generally more robust pelvic construction, suggesting that fusion of the supraneural region and complete ossification occurs in the final stages of growth. This agrees with other pterosaur specimens with supraneural plates: they only seem to occur in osteologically mature individuals (see, for examples, Young 1964; Bennett

2001; Fastnacht 2005). We suggest, therefore, that overall size does not influence pelvic morphology as much as degree of ossification (Fig. 3). The possession of “mature” pelvic anatomy in small ornithocheiroids such as the 2 m wingspan *Nyctosaurus* (see Williston 1903) further supports this observation. We also note that supraneural plates are only present in clades that also possess notaria, following the phylogeny of Lü et al. (2010), which allows isolated pelvic material with supraneural plates to be allocated to notaria-bearing clades. This suggests that the phylogenetic importance given to notaria (e.g., Young 1964; Kellner 2003; Unwin 2003) can be extended to the supraneural plate with the caveat that, like notaria, they can only be detected in osteologically mature individuals.

Sexual dimorphism in pterosaur pelves has been noted in at least *Pteranodon* and *Darwinopterus*, with both genera demonstrating relatively broad pelvic canals in putative females (Bennett 1992; Lü et al. 2011). Fortunately, these distinctions are relatively subtle and do not significantly alter other aspects of pelvic morphology, especially in lateral view. Accordingly, while we are mindful of ontogenetic effects on pterosaur pelves and restrict our overview to osteologically mature specimens as much as possible, we are less concerned about the effects of sexual dimorphism.

Results

Pterosaur pelvic morphology: general remarks

Pterosaur pelves, like those of all archosauriforms, comprise three pairs of ossified elements (ilium, pubis, and ischium) united dorsally by a variable number of sacral vertebrae (Fig. 1). Uniquely, the pterosaur pelvis possesses prepubes, a pair of bones that articulate anteroventrally with the pubes. Their pelves are generally longer than tall, and possess imperforate acetabulae incorporating all three pelvic bones, and broad ischiopubic plates. The pubis occupies only the anterior portion of the ischiopubic plate and is more laterally prominent than the ischium. The obturator foramen, a small opening in the ischiopubic plate, is situated ventrally to the acetabulum and variably positioned anteriorly or posteriorly to the acetabular margins. Some pelves are fused along their ventral margins to form a sealed pelvic canal that, in anterior or posterior view, gives the pelvic girdle a U- or V-shaped profile (Fig. 1D, E) (Bennett 1990, 2001). Other pelves appear to remain unfused along their ventral margins; a feature that has been suggested as exclusive to females (Lü et al. 2011). Other putative females, however, possess fused ventral pelvic margins while retaining relatively broad pelvic canals (Bennett 1992).

The ilium possesses a preacetabular process that projects anteriorly and is typically much longer than the postacetabular process. In lateral view, this process is a parallel-sided rod, but is somewhat spatulate in dorsal profile (Fig. 1A). The postacetabular process projects posteriorly and dorsally

in the majority of pterosaurs and shows considerable variation in height and complexity between taxa. The prepubic bones articulate with the anteroventral margin of the pubes via relatively narrow articular surfaces. These meet to form a “belly-spanning” cradle at their broader, distal margins. The distal regions of prepubic bones assume bifid, quadrangular or fan-shaped morphologies. While bifid morphologies may be restricted to certain clades, the latter seem ubiquitous across Pterosauria and show fairly continuous variation between the two morphotypes. We refrain from discussing prepubes further here, but suggest that morphometric or shape analysis of their variation may reveal some taxonomic utility.

The sacral vertebrae between each set of pelvic bones fuse to form a continuous sacrum comprising at least three, but more typically four or more vertebrae in all pterosaurs. As with other archosaurs, the precise number varies with age as the sacrum incorporates posterior dorsal vertebrae and, in some cases, anterior caudal vertebrae (Bennett 2001; Unwin 2005). The absolute sacral count of adult pterosaurs may have taxonomic significance, but too few well-preserved postcervical axial skeletons are known to evaluate this at present. Moreover, because sacral vertebral count is so variable through ontogeny, and the pterosaur record is biased in favour of immature individuals (e.g., Bennett 1995), we do not discuss it further here. Many pterosaurs retain separate sacral neural spines, but in others the dorsal portions of the neural spines fuse in such a way that they delimit elliptical fenestrae (Fig. 1B). This fusion seems to accompany ossifications of supraneural ligaments that pass over the dorsal margins of the neural spines, as suggested by the long extensions of bony fibres along their lengths (Fig. 1B; also Bennett 2001: fig. 102; Fastnacht 2005: 275). In some cases this plate is expanded slightly laterally.

Systematic variation

Dimorphodontidae.—The pelvis of the most basal pterosaur as recovered by Lü et al. (2010), *Preondactylus buffarini*, is poorly preserved (Wild 1984), so *Dimorphodon macronyx* and *Peteinosaurus zambellii* are the most basal pterosaurs with well-preserved pelvises (Fig. 4A, B; Wild 1978; Unwin 1988; Dalla Vecchia 2003). Only the ischiopubic plate of *Peteinosaurus* is known, revealing an angular, convex anterior edge, tapering posterior extension and a partial, large acetabulum (visible in MCSNB 3496; see Wild 1978 and Dalla Vecchia 2003). The pelvis of *Dimorphodon* is more completely known and bears several distinctive features. The ischiopubic plate is fully fused, with a convex anterior margin (Unwin 1988), a tapering, rounded posterior projection and a proportionally large acetabulum. The preacetabular process is distinctively short, barely projecting beyond the anteriormost extension of the pubis and it is subequal in size to the postacetabular process. Each iliac process (measured from the anterior and posterior margins of the ischiopubic plate) occupies approximately one third of the iliac length. Consequently, the total height of the *Dimorphodon* pelvis

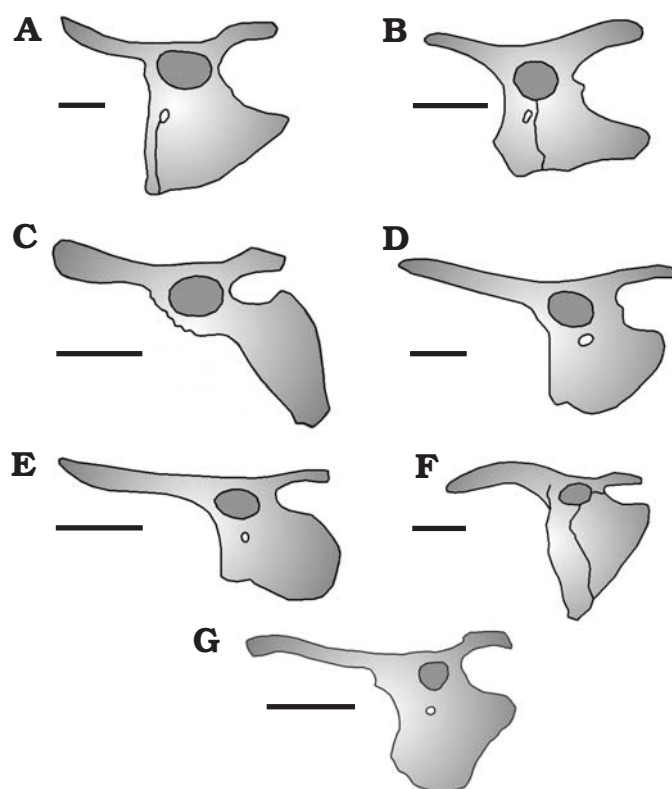


Fig. 4. Pelvises of non-pterodactyloid pterosaurs. **A.** *Dimorphodon macronyx* (composite of several specimens). **B.** *Peteinosaurus zambellii* (BSP 1994151). **C.** *Campylognathoides liassicus* (CM 11424). **D.** *Dorygnathus banthensis* (MBR 1905.15). **E.** *Rhamphorhynchus muensteri* (BSP 1955/28). **F.** *Darwinopterus robustodens* (41HIII-0309A). **G.** *Darwinopterus linglongtaensis* (IVPP V16049). Scale bars 10 mm. For sources, see Appendix 1.

is almost equal to its length, a condition not seen in other pterosaurs.

Anurognathidae.—Despite recent advances in our understanding of anurognathid anatomy (Dalla Vecchia 2002; Bennett 2007), the anurognathid pelvis remains poorly known and all examples are preserved in relatively uninformative dorsal views. The pelvic remains of *Dendrorhynchoides curvidentatus* reveal a long, laterally narrow preacetabular process, similar to that reported by Bennett (2007) for *Anurognathus ammoni* (Fig. 2A). The preacetabular process extends to the midpoint of the 3rd presacral vertebra, but the postacetabular process is unknown. The ischia are broad plates that converge with each other posteriorly and although little remains of the pubes, the ischia and the pubes are mostly unfused, a feature reflecting the immaturity of the best-known *Anurognathus* specimen (see Bennett 2007: casts at SMNS 81928a, b).

“Campylognathoidids”.—The taxonomy of “campylognathoidid” pterosaurs, here considered to comprise *Eudimorphodon*, *Caviramus* (= *Raeticodactylus*), *Austriadactylus*, *Campylognathoides*, and *Carniadactylus* is somewhat controversial (for different opinions on the phylogenetic arrangement of these taxa, see Dalla Vecchia 2009; Lü et al.

2010; Wang et al. 2009; Andres et al. 2010). We consider them together here because of their Triassic–Lower Jurassic age, heterodont dentition, dorsoventrally inflated mandibular tips and similar skull shapes, but we stress the controversial nature of this group.

Our understanding of “campylognathoidid” pelves (Fig. 4C) is disproportionate to the quality and completeness of many “campylognathoidid” specimens: to our knowledge, only one complete pelvis is known but difficult to interpret, and their pelves preserved in lateral aspect are invariably incomplete or partially obscured by other bones. The best-known pelves of this group occur in two specimens of *Campylognathoides* (BSP 1985 I 87; CM 11424). The latter specimen is complete, but is somewhat broken and many parts are obscured (Mike Habib, personal communication 2011) and have formed the focus of several investigations into pterosaur pelvic morphology (Wellnhofer 1974; Padian 1983a; Wellnhofer and Vahldiek 1986). Unfortunately, the pelvic bones are displayed in ventral and dorsal aspect, limiting their taxonomic value. What can be seen of the pelves in *Eudimorphodon*, *Carniadactylus*, and *Campylognathoides* suggests the preacetabular processes of some may be short (Wellnhofer 1974, 2003; Wild 1978, 1993; Wellnhofer and Vahldiek 1986; Padian 2008; Dalla Vecchia 2009), being only 40% of the total iliac length (measured from the anterior border of the pubis) in *Eudimorphodon ranzii* (MCSNB 2888) and *Campylognathoides liasicus* (CM 11424).

Rhamphorhynchidae.—Although the pelves of two rhamphorhynchine rhamphorhynchids, *Rhamphorhynchus muensteri* and *Dorygnathus banthensis*, are well known (Fig. 4D, E) Wellnhofer 1975; Bennett 1995; Padian 2008), those of other rhamphorhynchids—including all scaphognathines—are not. The pelves of *Rhamphorhynchus* and *Dorygnathus* are similar, and the suggestion that these as the most derived and most basal rhamphorhynchines, respectively (Padian 2008; Lü et al. 2010; Andres et al. 2010), suggests their pelvic morphology is probably common to all rhamphorhynchines. The preacetabular processes are long, occupying 50–60% of the iliac length, and are slightly dorsally expanded at their terminations. The postacetabular processes are short and directed posteriorly. The ischia have rounded posteroventral margins and extend beyond the distal ends of both the postacetabular processes and the pubes. The acetabulum is large and positioned proximal to the anterior margin of the pubis. The development of *Rhamphorhynchus* pelves through ontogeny is known in some detail and demonstrates that the basic characteristics of rhamphorhynchine pelves are consistent throughout growth, although the formation of a complete ischiopubic plate occurs later in ontogeny (Bennett 1995).

Wukongopteridae.—The anatomy of this newly discovered pterosaur group is already well known, including that of their pelves (Fig. 4F, G). There are six described wukongopterid species in four genera (Wang et al. 2010; Lü et al. 2011), although it has been claimed (Lü et al. 2011) that they are all conspecific. We note that many of the features used to sepa-

rate these taxa pertain to features of the skull that are known to be strongly influenced by ontogeny (e.g., shape of the lacrimal, crest morphology), taphonomy and preservational style, or require detailed morphometrics to demonstrate their validity (e.g., rounding of occiput). The following discussion assumes all named taxa are valid.

The pelvis of *Darwinopterus modularis* is known in forms with both closed and open pelvic canals (ZMNH M8782 and M8802, respectively; Lü et al. 2010; Lü and Fucha 2011). The preacetabular process of this species, as well as that of *Darwinopterus linglongtaensis* (IVPP V16049), is long and curves slightly dorsally. By contrast, the preacetabular processes of *Wukongopterus* (IVPP V15113) and *D. robustodens* (4IHIII-0309A) are short, being less than half the iliac length, compared to approximately 50% in the other *Darwinopterus* species (Wang et al. 2009; Lü et al. 2011). *D. robustodens* also has a unique preacetabular morphology among pterosaurs, being not only relatively robust, but arcing dorsally so that its termination points anteroventrally. Note that we only cautiously interpret this morphology, however, given some of the apparent diagenetic distortion that seems to have plastically re-modelled some bones of the *D. robustodens* holotype (e.g., the sinuous right tibiotarsus), and the obstruction of the right femur of the preacetabular process. The same configuration cannot be seen in *Wukongopterus*, however, as the pelvis is known only in dorsal aspect. In all *Darwinopterus* species, the postacetabular process rises only slightly above the preacetabular process. The anterior and posterior margins of the ischiopubic plate in *D. linglongtaensis* are strongly concave, whereas those of *D. robustodens* are slightly convex. The anterior regions of the *D. linglongtaensis* and *D. robustodens* ischiopubic plates form a very deep anterior region.

Ornithocheiroidea.—The distinctive pelves of ornithocheiroids are well known (Fig. 5) and were among the first to be analysed in detail (e.g., Williston 1897, 1903; Eaton 1910). The pelves of different ornithocheiroid genera vary somewhat, but much of this variation may be ontogenetic. Recently, several excellently preserved, three-dimensional ornithocheiroid pelves have been recovered from the concretions of the Early Cretaceous Santana Formation of Brazil and described in detail (Wellnhofer 1988, 1991b; Kellner and Tomida 2000; Veldmeijer 2003). Crushed pelves are also known from a number of ornithocheiroids (*Arthurdactylus*, Frey and Martill 1994; *Nyctosaurus*, Williston 1903; Bennett 2003) and particularly from the giant ornithocheiroid *Pteranodon* (Eaton 1910; Bennett 2001).

The sacrum of osteologically mature ornithocheiroids bears a well-developed supraneural plate. The ornithocheiroid preacetabular process is of variable length but generally forms half or more of the iliac length. It is always dorsally deflected to produce a broad angle between it and the anterior margin of the pubis. The extent of this angle is variable between species and difficult to quantify in taxa with curved preacetabular processes, but it consistently

considerably exceeds 90° , much greater than in most other pterosaurs. The postacetabular process extends posteriorly and is generally raised somewhat dorsally from the ilium. The postacetabular process of *Pteranodon* is unusual in growing particularly high and extending medially to fuse with the adjacent sacral neural spines (as in FHSM VP 2062). The postacetabular process does not project as far posteriorly as the ischium.

The large angle between the pubis and preacetabular process is accentuated by posterior deflection of the pubis. This is so pronounced that the ventral pubic region is always below or behind the acetabulum. The anterior margin of the pubis may be concave or straight. The ischia are also rotated posteriorly and are particularly long and narrow, extending well beyond the posterior margin of the postacetabular process. Many specimens have pelves with unfused pubes and ischia with large openings between these bones (see, for instance, AMNH 22555, Wellnhofer 1991b; NSM-PV 19892, Kellner and Tomida 2000). The unfused scapulocoracoids and skull bones of these remains suggest they represent immature individuals, indicating that only the oldest ornithocheiroids have completely fused, imperforate pelves. A complete, trapezium-shaped ischiopubic plate forms in osteologically mature

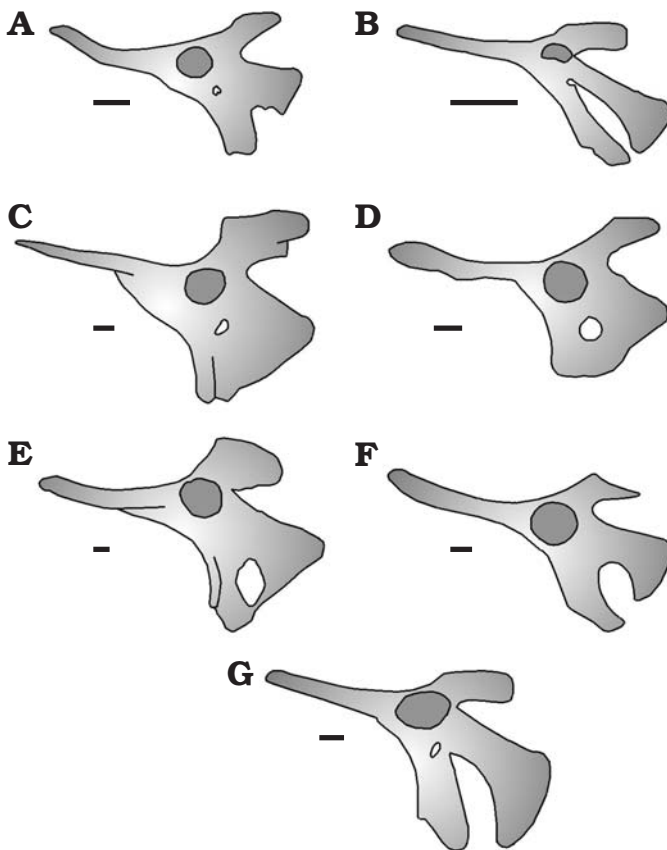


Fig. 5. Pelves of ornithocheiroid pterodactyloids. **A.** “The Queensland pterosaur” (QMF12982). **B.** Ornithocheiridae indet. (ZINPH 8E-G/43). **C.** *Pteranodon* sp. (composite of several specimens). **D.** *Nyctosaurus gracilis* (YMP 1178). **E.** *Coloborhynchus spielbergi* (RGM 410880). **F.** *Arthurdactylus conandoylei* (SMNK PAL 1132). **G.** *Anhanguera santanae* (AMNH 22555). Scale bars 10 mm. For sources, see Appendix 1.

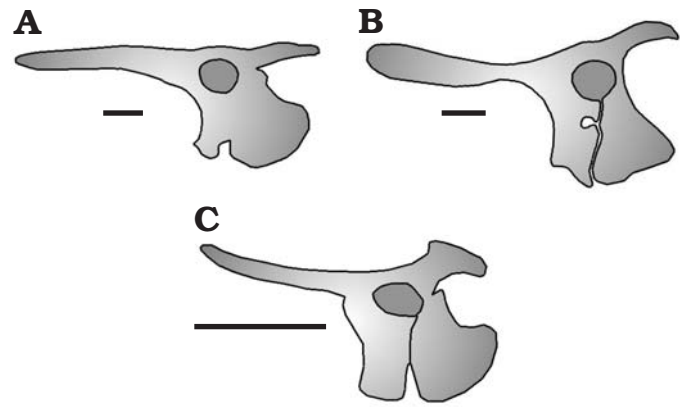


Fig. 6. Pelves of ctenochasmatoid pterodactyloids. **A.** “*Pterodactylus*” *longicollum* (JME-SOS 2428). **B.** *Cycnorhamphus suevicus* (MNH CNJ-71). **C.** *Pterodactylus anitquus* (BSP AS I 1739). Scale bars 10 mm. For sources, see Appendix 1.

individuals. The pubic plates are consistently fused along their ventral margins in *Pteranodon* and some ornithocheiroids (Bennett 1992, 2001; Veldmeijer 2003), but are open ventrally in others (Bennett 1990; Kellner and Tomida 2000). The pelvis of large *Pteranodon* specimens (e.g., “UNC 4” of Bennett 2001) is of further note for the fusion of a sternal rib and transverse process in the region between the preacetabular process and anterior margin of the pubis, which is seen in lateral aspect.

Ctenochasmatoidea.—Ctenochasmatoid pelves are known largely from the Late Jurassic Solnhofen Limestone and related deposits in Germany, despite the widespread occurrence of this group (Barrett et al. 2008). Unfortunately, the majority of these specimens represent immature individuals (Bennett 1996), suggesting only tentative analysis of their pelvic form can be performed (see discussion of ontogeny, above). Their pelves are typified by those of *Pterodactylus antiquus* (BSPG AS I 739), “*P.*” *kochi* (BSPG 1883 XVI 1, 1937 I 18a; SMNS R 404), “*P.*” *longicollum* (JME-SOS 2428), *Cycnorhamphus suevicus* (MNH CNJ-71; Fabre 1976) and *Ctenochasma gracile* (BSPG 1935 I 24) (Fig. 6). In all cases, the preacetabular process is long, assumes a roughly 90° angle with the pubis and may show slight dorsal deflection along its length. The postacetabular process is low and projects posteriorly as far as the posterior margin of the ischium with minimal dorsal deflection. Some specimens (BSPG AS I 739, 1883 XVI 1) have incompletely formed ischiopubic plates, but a near-adult specimen of *Cycnorhamphus* (MNH CNJ-71) shows completely fused pubes and ischia. The acetabulum is located halfway between the anterior and posterior margins of the ischiopubic plate (Wellnhofer 1970, 1978).

Dsungaripteroidea.—The pelves of dsungaripteroid pterosaurs are known from species covering a broad size range, from the ca. 1 m span “*Germanodactylus*” *rhamphastinus* to 3 m span *Dsungaripterus* (Fig. 7). Probably the best dsungaripteroid pelvic material belongs to DFMMh/FV 500, a generically indeterminate, mid-sized Jurassic dsungaripteroid

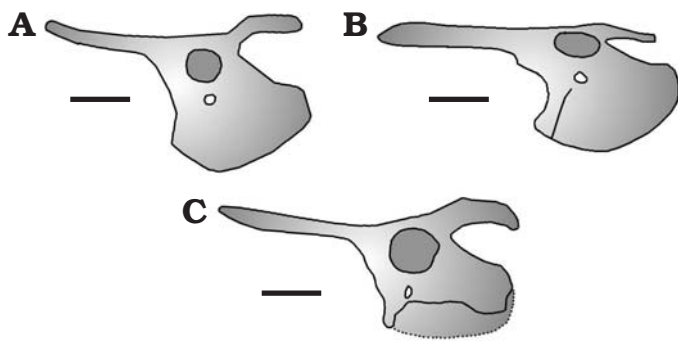


Fig. 7. Pelves of dsungaripteroid pterodactyloids. A. *Herbstosaurus pigmaeus* (CTES-PZ-1711). B. *Germanodactylus rhamphastinus* (BSP AS I 745). C. Dsungaripteroidea indet. (DFMMh/FV 500). Scale bars 10 mm. For sources, see Appendix 1.

described by Fastnacht (2005). Unfortunately, the ventral portion of this otherwise excellently preserved specimen remains obscured and, aside from the lateral splaying of the pelvic bones betraying an unfused pelvic canal, no details of this region are known. “*Germanodactylus*” *rhamphastinus* (BSPG AS I 745) reveals the entirety of the ventral pelvic region, although its usefulness for diagnosing the dsungaripteroid pelvis is questionable given its controversial affinities (but see discussion below).

Dsungaripteroid pelves have long preacetabular processes occupying around 60% of the iliac length. These processes may be slightly dorsally deflected towards their distal ends, but are relatively straight in “*G.*” *rhamphastinus*. The postacetabular process is short and somewhat elevated. The broken preacetabular process of an incomplete *Dsungaripterus weii* pelvis (IVPP V-2776) indicates that these processes may be raised comparably high from the main iliac body. Supraneural plates are present in both *Dsungaripterus* and DFMMh/FV 500. The ischiopubic plate of “*G.*” *rhamphastinus* has a very rounded posteroventral margin where the ischium projects more ventrally than the pubis. The anterior pubic margin is strongly concave, creating an anteriorly deflected distal pubis. The ischium projects beyond the posterior margin of the postacetabular process in “*G.*” *rhamphastinus*, but does not appear to do so in DFMMh/FV 500.

Azhdarchoidea.—Azhdarchoid pterosaurs are known from many complete, well preserved specimens (Barrett et al. 2008) but the pelvis is poorly documented. Pelves from *Zhejiangopterus*, *Shenzhoupterus*, *Sinopterus*, and *Huaxiapterus* are crushed and difficult to interpret (Cai and Wei 1994; Lü and Yuan 2005; Lü et al. 2008), while other azhdarchoid specimens provide little or no pelvic material. A three-dimensionally preserved pelvis of *Tupuxuara leonardii* is known (IMCF 1052; Kellner and Hasegawa 1993), but still awaits description, but a similarly preserved pelvis of an immature *Tapejara wellnhoferi* (SMNK PAL 1137) was recently described in detail by Eck et al. (2011). Some excellently preserved azhdarchoid pelves are known from very incomplete skeletons or isolated pelvic material that, because of their supraneural plates (and in one case, an associated notarium)

can be referred to the notarium-bearing Neoazhdarchia (Fig. 8; AMNH 22569, Bennett 1990; MN 6588-V, Sayão and Kellner 2006). Support for this assignment stems from the lack of supraneural plates in the tapejarids *Nemicolopterus* (probably a juvenile *Sinopterus*; unpublished data) and *Tapejara* (Wang et al. 2008; Eck et al. 2011). While this may be accredited to the immaturity of all specimens of these pterosaurs, adult remains of the tapejarid *Sinopterus* also seem to lack notaria and supraneural plates (e.g., Lü et al. 2006b), suggesting this group never attained neural spine fusion in their trunk region.

Azhdarchoid pelves show straight preacetabular processes that extend anterodorsally, nearly perpendicular to the anterior margin of the pubes. The postacetabular processes are large and complex, extending dorsally as high as the anteriormost projection of the preacetabular process and bearing a distinct “hatchet” shape. The pubes are large, with a relatively great distance between their straight anterior margin and the acetabulum. The ischia are broad and project posteriorly at least as far as the posterior extension of the postacetabular process. The ischiopubic plate is large and imperforate, with the obturator foramen located anteroventrally of the acetabulum. The neural spines of neoazhdarchian sacral vertebrae are fused in their dorsal region via a series of ossified tendons, forming a supraneural plate along the length of the sacrum. Some of this morphology has also been described from the crushed pelvis of the neoazhdarchian *Zhejiangopterus* (Cai and Wei 1994) and can be seen in the pelvis of *Tupuxuara leonardii* (DMM and MPW personal observations).

Discussion

Congruence of pelvic morphotypes with pterosaur phylogeny.—With so few pelvic characters incorporated in pterosaur phylogenies, assessing the variation and distribution of pelvic morphology across recent pterosaur phylogenies provides an interesting, if only qualitative, assessment of congruence. Of the competing cladograms, we found that the phylogeny of Lü et al. (2010) provides the best agreement between pelvic morphotypes and tree topology. The

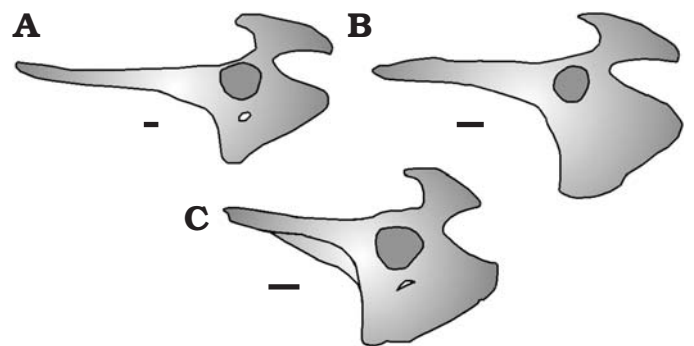


Fig. 8. Pelves of neoazhdarchian pterosaurs. A. Neoazhdarchia indet. (AMNH 22569). B. Neoazhdarchia indet. (MN 6588-V). C. Neoazhdarchia indet. (EH2). Scale bars 10 mm. For sources, see Appendix 1.

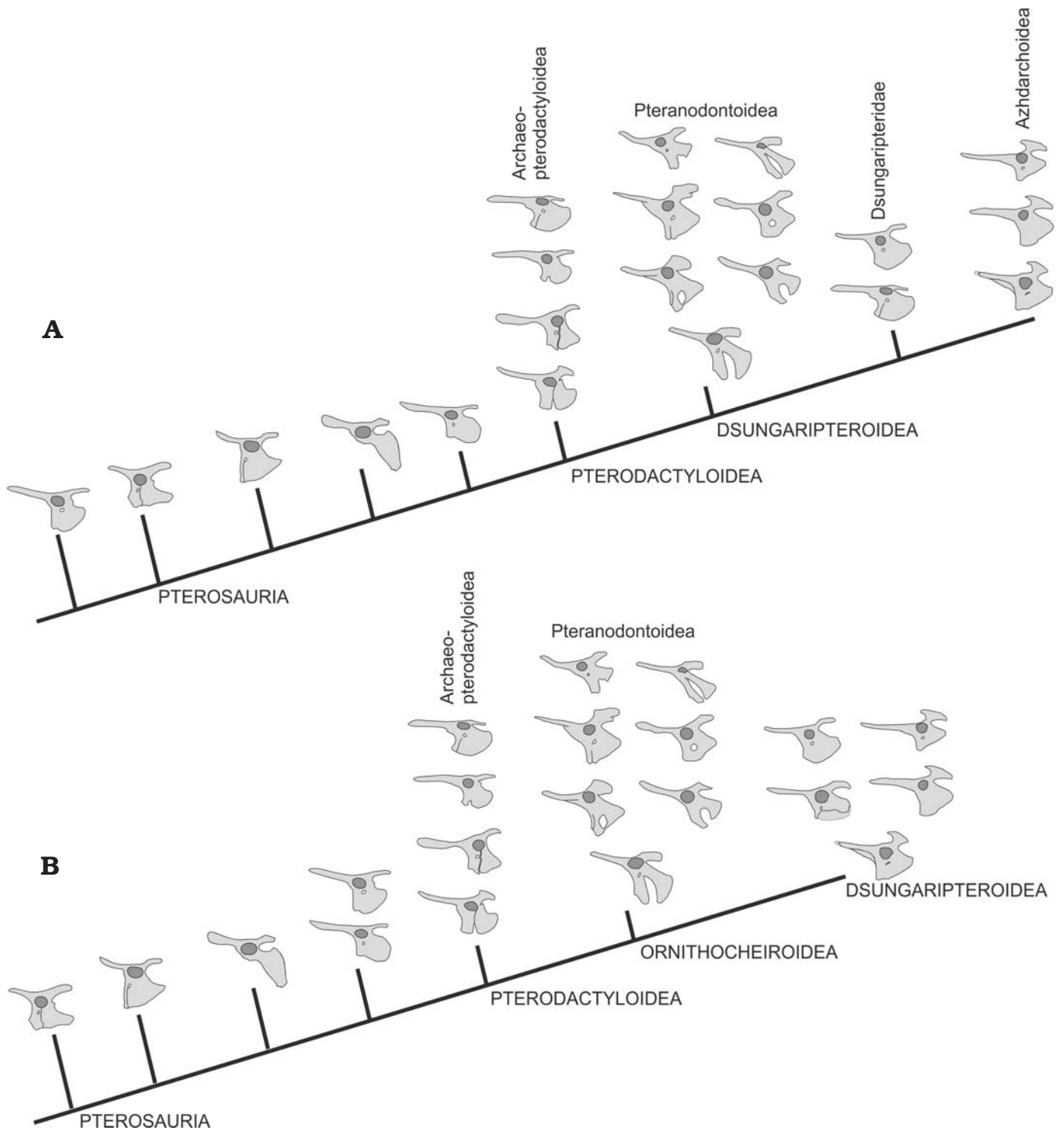


Fig. 9. Plots of pterosaur pelvis on the tree topology of Wang et al. (2009) and a composite cladogram of the “Andres dataset”, including separate pterodactyloid (Andres and Ji 2008) and non-pterodactyloid (Andres et al. 2010) phylogenies.

pelvic morphologies identified here are not shared between different clades (Fig. 2), suggesting that each type agrees with the basic taxonomic interpretations of this model. Least distinction in form is found between the pelvises of rhamphorhynchids, ctenochasmatooids, and dsungaripteroids, suggesting they possess relatively unspecialised pelvises compared

to other clades. Their pelvises do display some consistent differences, however, allowing them to be distinguished when well preserved.

Congruence is poorer when pterosaur pelvises are mapped to other analyses (Fig. 9). The “ornithocheiroid” pelvic morphotype is distributed across the Dsungaripteroidae of Wang

et al. (2009), although the pelvis of this clade fall within the unnamed Pteranodontoidea + *Nyctosaurus* clade of Andres and Ji (2008). “*Germanodactylus*” *rhamphastinus*, suggested to possess a dsungaripteroid-type pelvis here, does not pair with the same taxa according to Wang et al. (2009) or Andres and Ji (2008), but instead plots among their Archaeopterodactyloidea. Other “ctenochasmatoïd” pelvic morphs fall within Archaeopterodactyloidea. This is unsurprising considering that the content of these clades is virtually identical (Unwin 2003). Less agreement is seen with the “neoazhdarchian” pelvic morphology (i.e., an azhdarchoid pelvis with a supraneural plate), which is split widely across non-pteranodontoid ornithocheiroids in the topology of Andres and Ji (2008) or Azhdarchoidea in the Wang et al. (2009) scheme. Assuming that the “azhdarchoid” pelvis is restricted to a clade Azhdarchoidea, this might shed light on the content of Tapejaridae, an azhdarchoid clade considered to contain taxa with notaria (and, perhaps by extension, supraneural plates) by some (Kellner 2003, 2004; Wang et al. 2009) but not by others (Unwin 2003; Lü et al. 2006c, 2010). Greater consensus is seen, however, with the pelvises of *Dimorphodon* and *Peteinosaurus*, which are closely related to rather basal pterosaurs and the finding of a “rhamphorhynchine” pelvic morph in some phylogenies (Dalla Vecchia 2009; Andres et al. 2010). This does not apply to the tree of Wang et al. (2009), however, where “dimorphodontid” and “rhamphorhynchine” pelvises are rather widely dispersed across non-pterodactyloid pterosaurs.

It may be supposed that so little congruence is found between pelvic morphology and tree topology because the pterosaur pelvis was prone to convergence. While this is possible, and certainly suggested in some phylogenies, it is more parsimonious to assume that the agreement in pterosaur pelvic form and the tree topology of Lü et al. (2010) provides some support for this phylogenetic interpretation. This joins other suggestions that the Unwin’s dataset (outlined in most detail by Unwin [2003], but seen in its most recent guise in Lü et al. 2010) is comparatively robust and contains lower levels of homoplasy than other recent analyses (Andres 2007; Unwin and Lü 2010). The following discussions may prove helpful for the future identification of pelvic apomorphies.

Diagnosing pterosaur pelvises.—Not all pterosaur pelvises are sufficiently well known to ascertain apomorphies for lower taxonomic levels. This is certainly the case for the pelvises of anurognathids, “campylognathoidids”, and scaphognathines. For most other groups, however, a relatively complete, osteologically mature pelvis in lateral view can be readily identified.

The pelvis of *Dimorphodon* is among the most easily recognised of all pterosaur pelvises, and its similarity to *Peteinosaurus*, and what is known of the pelvises of “campylognathoidids” and *Preondactylus*, suggests that other early pterosaurs may have borne similar pelvises. If so, they are characterised by relatively small pelvises with especially short preacetabular processes equal in length to their postacetabular processes. Each of these processes occupies less than

40% of the total iliac length. Their acetabula, by contrast, are proportionally large. The obturator foramen is situated anteroventrally to the acetabulum rather than posteroventrally, and the posterior margin of the ischium forms a relatively long, tapered posterior extension.

Rhamphorhynchid pelvises are distinguished from those of other non-pterodactyloids by long preacetabular processes occupying at least 50% of the iliac length, and extension of the ischia below the ventral margin of the pubis. The angle between the ventral margin of the postacetabular process and the posterodorsal margin of the ischium is smaller (30–40°) than in other non-pterodactyloid pterosaurs. These pelvises can be difficult to differentiate from most other non-ornithocheiroid monofenestratans but may be distinguished by the close proximity of the acetabulum to the anterior margin of the pubis. Wukongopterid pelvises are similar to those of rhamphorhynchids, but can be differentiated by the relatively great depth of the anteroventral portions of the ischiopubic plate and, in some genera, by the brevity of the preacetabular process.

Ornithocheiroid pelvises are markedly different from those of other pterosaurs. They are distinguished by ilia with long, dorsally curving pre- and postacetabular processes, and an angle between the preacetabular process and pubis consistently above 90°. Their ischiopubic plates are narrow and posteriorly deflected so that the ventral region of the pubis lies below or behind the acetabulum, and the ischia terminate well beyond the postacetabular processes. It seems that the ischiopubic plate retains a large ischiopubic foramen in all but the oldest individuals. Supraneural plates form in mature specimens, a feature otherwise known only from dsungaripteroids and some azhdarchoids. Although the “hatchet-shaped” postacetabular process of *Pteranodon* is similar in lateral aspect to that of azhdarchoids, it can be distinguished by the partial fusion of this process to the supraneural plate in *Pteranodon*, as it remains entirely separate in azhdarchoids.

Ctenochasmatoïd pelvises have long preacetabular processes with only slight, if any, dorsal curvature. Their postacetabular processes show variable morphology, but are not elevated much above the rest of the ilia. The pubes and ischia of many ctenochasmatoïds have an obvious ventral partition, but this is likely to reflect the osteologically immature nature of most ctenochasmatoïd specimens. In any case, this division is generally smaller than that of ornithocheiroids, and their ischiopubic plates are, on average, more complete. The pubis and ischium are of similar proportions, but the pubis is almost rectangular and directed ventrally, while the ischium is positioned more posteroventrally and forms a broad angle between its posterodorsal margin and the ventral margin of the postacetabular process.

Dsungaripteroid pelvises can be difficult to differentiate from those of ctenochasmatoïds, but they do seem to differ in bearing more massive, rounded ischiopubic plates that form a smaller angle (< 20°) between the ventral margin of the postacetabular process and the posterodorsal margin of the ischium. The postacetabular processes may also be some-

what elevated compared to those of ctenochasmatooids. More definitive differentiation of dsungaripteroid pelvises can be made in mature individuals however, by their development of supraneural plates. To date, no fusion of the axial column has been reported in any ctenochasmatooids, making this a clear distinguishing feature.

The pelvises of azhdarchoids are quite distinctive by bearing long, anteriorly directed pre- and postacetabular processes, with prominent anterodorsal and posteroventral extensions forming a characteristic hook-shape in the latter. Bennett (2001) illustrated a similar morphology for the postacetabular process of *Pteranodon*, but it differs from those of azhdarchoids by being confluent with the supraneural plate: the azhdarchoid postacetabular process is entirely independent of the axial region. There is a shallow angle (ca. 30°) between the posterodorsal border of the ischium and the ventral border of the postacetabular process, and the fused pubis and ischium form a posteroventrally expanded ischiopubic plate. The description of a well-preserved juvenile *Tapejara* pelvis suggests that tapejarid pelvises were similarly constructed to those of neoazhdarchians (Eck et al. 2011), but the absence of a supraneural plate from all members of this clade suggests that, within Azhdarchoidea, the supraneural plate is probably restricted to neoazhdarchians.

The functional evolution of the pterosaur pelvis

The morphological variation among pterosaur pelvises presumably reflects variable pelvic function in different clades. Perhaps the most obvious implications concern locomotion, and especially terrestrial posture and gait, because there is no evidence that the pterosaur pelvis and hindlimb powered their flight (e.g., large areas for flight muscle attachment on the femur, particularly robust hindlimb bones), although there may have been a modest role in flight control. The impact of pterosaur pelvic morphology on posture (i.e., sprawling or erect) has been discussed previously (e.g., Wellnhofer 1974, 1988; Unwin 1988; Bennett 1990; Fastnacht 2005), but has principally been considered in terms of bipedal vs. quadrupedal locomotion. These discussions, combined with a wealth of ichnological and biomechanical evidence, indicate that all pterosaurs were primarily plantigrade quadrupeds when walking and running (e.g., Wellnhofer 1988; Unwin 1997; Clark et al. 1998; Mazin et al. 2003; Fastnacht 2005; Wilkinson 2008). A detailed overview of pterosaur pelvic function is beyond the scope of this paper. Note that we follow hypotheses that all pterosaurs, including the earliest forms, held their legs in an erect stance (Padian 1983a; Bennett 1990, 1997, 2001). Recent analysis of some non-pterodactyloid pectoral girdles and humeri suggests that their forelimbs may also have been capable of movement in the parasagittal plane (Witton, unpublished material) and therefore, we assume that most pterosaurs were capable of efficient terrestrial postures.

General considerations.—Pelvic and hindlimb morphology suggests that pterosaurs were well adapted for subcur-

sorial locomotion (e.g., Padian 1983a). The proportions of the *Dimorphodon* pelvis and hindlimbs are comparable with those of erect-limbed ornithomirans like *Scleromochlus* (Benton 1999) and dinosauromorphs (Sereno and Arcucci 1994; Fehner 2009) rather than sprawling or semi-sprawling archosaurs. Particular attention is drawn to the long iliac processes common to erect-limbed forms that engage in cursoriality, as these features also occur in all pterosaurs. Pterosaurs also share relatively small pelvises with cursors and, in addition, typically have shorter femora than distal leg bones (tibia + pes); a feature that serves to shorten the lever arm of the hindlimb muscles to increase the rotational speed of the legs during terrestrial locomotion (Hildebrand 1995). Additional cursorial features of pterosaurs are reduction in the height of neural spines around the pelvis, fusion of the sacrum, reinforcement of proximal limb musculature and reduction of distal musculature, hinge-like limb joints incapable of rotation and (in most taxa) the tight arrangement of the metapodials (Coombs 1978; Padian 1983a; Sereno and Arcucci 1994; Fehner 2009). Accordingly, we consider that, like Recent subcursorial animals such as most carnivorans and rodents (Coombs 1978), pterosaurs were capable of bursts of speed. Against this notion is that the uropatagia stretching between the hindlimbs of non-pterodactyloids might have impeded efficient terrestrial locomotion (Unwin 2005), but this ignores the possible use of asymmetrical gaits in these forms. It is not uncommon for many animals, and particularly those moving at speed, to move their forelimbs or hindlimbs in parallel, synchronised fashion in bounding gaits (Hildebrand 1995). Of particular relevance here are bats, as some species (e.g., *Desmodus rotundus*) can “hop” at high speed (2 ms⁻¹) despite possessing extensive uropatagia (Riskin and Hermanson 2005). The mechanically strong limbs of pterosaurs seem well suited to highly-stressed locomotion (including the hindlimbs, which only appear atrophied when compared to their oversized forelimbs: see Padian 1983a; Bennett 1997; Habib 2008; Witton and Habib 2010). Some pterosaur hindlimbs (those of “campylognathoidids”, rhamphorhynchines, and derived ornithocheiroids) show signs of losing some cursorial features such as their short femora and apparent reduction in proximal hindlimb musculature, but, given the generally derived anatomy of these forms, this probably reflects secondary reduction of terrestrial capabilities.

Lengthening of the preacetabular process.—Pterosaurs seem to have developed and maintained very long preacetabular processes early in their evolutionary history. There are many possible reasons for this. The broadening of the attachment site for epaxial musculature may reflect stiffening and strengthening of the torso, a trait that could be interpreted as a precursor to the development of supraneural plates over the pectoral and pelvic girdles in many forms. Mike Habib (personal communication 2011) also notes that this feature could reflect expanded anchoring for forelimb extensors/medial rotators, because the thoracodorsal aponeurosis connects

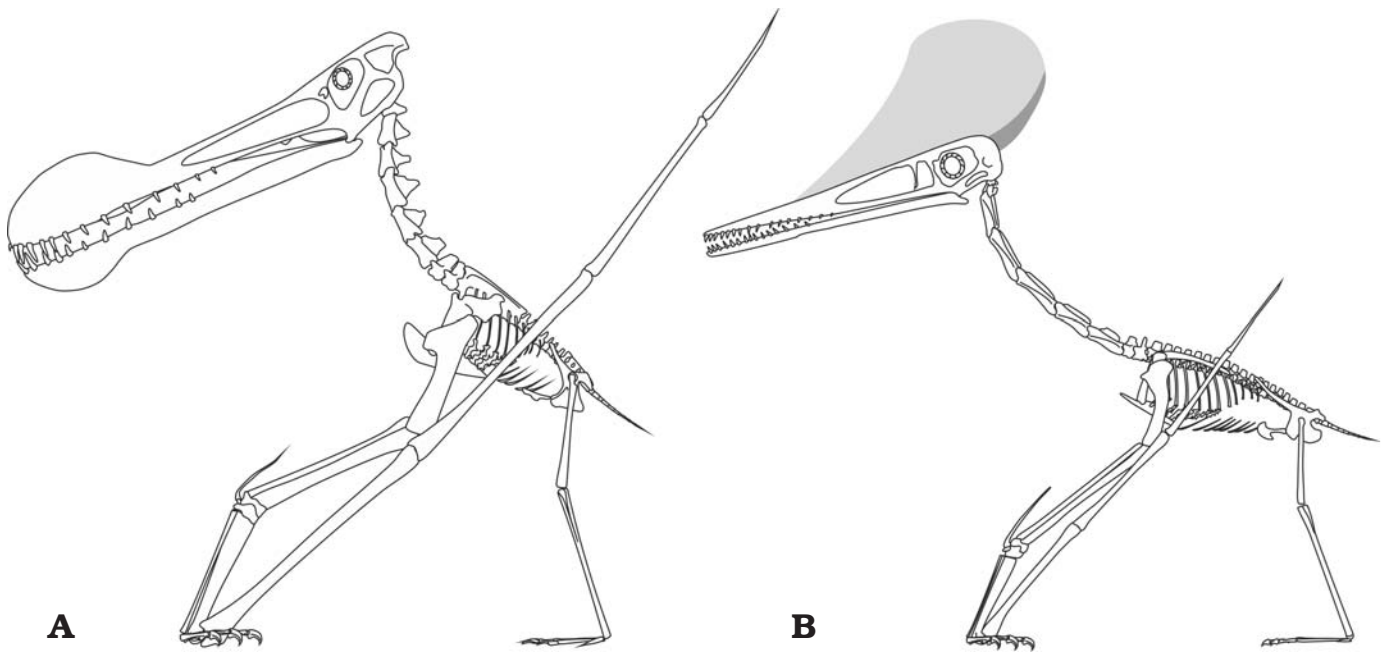


Fig. 10. Stance comparisons in ornithocheiroid (A) and non-ornithocheiroid pterodactyls (B). Note that, to assume the posture suggested by pterodactyl tracks, the long ornithocheiroid forelimb necessitates an erect stance that requires rotation of the ischiopubic plate to ensure suitable anchorage for the hindlimb musculature.

to the epaxial muscle sheath and preacetabular processes in most vertebrates.

A further alternative is that the elongate preacetabular process provides larger attachment sites or greater lengths for the hindlimb extensor muscles, thereby increasing their strength or endurance. The pterosaur hindlimb muscle reconstruction of Fastnacht (2005) is in agreement with this hypothesis, suggesting that the preacetabular process anchored the femoral extensors *M. iliotibialis* and *M. ilirotrochantericus*. We note some complications with this hypothesis, however: the hindlimb structure of pterosaurs with long preacetabular processes varies considerably from taxa with comparatively short, gracile hindlimbs (Rhamphorhynchinae; most ornithocheiroids), to large-footed forms with moderate limb lengths (Ctenochasmatoidea) and extremely long-legged terrestrial foragers (Azhdarchidae). The condition of the preacetabular process does not seem to change relative to hindlimb morphology, which may suggest its development is largely independent of hindlimb mechanics.

Several other arguments are worthy of consideration here. *Preondactylus* and *Dimorphodon* appear to have carried their relatively long hindlimbs with little difficulty despite having short preacetabular processes and hindlimbs that were equal to, or longer than, the forelimbs (excluding the wing finger). The long preacetabular processes of birds and mammals have convergently expanded dorsally, providing broad lateral surfaces for muscle attachment, but those of pterosaurs are rather differently constructed, with a transversely expanded, shelf-like morphology. It is possible that this reflects a fundamental change in pterosaur hindlimb musculature early in their evolution, perhaps to increase

the mechanical efficiency of the hindlimb regardless of its function, but there may have been reasons other than hindlimb mechanics alone. A detailed myological reconstruction of the pterosaur pelvic region and hindlimb is required for fuller understanding.

Ornithocheiroid pelves.—The pelves of ornithocheiroids have undergone greater changes than in any other pterosaur group, presumably reflecting distinct hindlimb mechanics in this clade. The dorsal inclination of the preacetabular process is their most distinctive pelvic feature and would have been detrimental to leverage of the limb extensors. Elevating the preacetabular process decreases the angles between the anterior hindlimb musculature and hindlimb, therefore lessening their mechanical advantage compared to an unelevated process (Fastnacht 2005).

Articulating the ornithocheiroid pelvis with the axial skeleton shows that the preacetabular process is not particularly dorsally deflected in relation to the body, however (e.g., Wellnhofer 1991b). Rather, the broad angle between this process and the pubis is formed by posterior displacement or rotation of the ischiopubic plate. This may have consequences for the habitual posture of grounded ornithocheiroids: if the torso was held entirely horizontally when walking (as per Wellnhofer 1988; Wilkinson 2008), hindlimb extensor and pronator muscles anchoring onto the pubis would be substantially shortened when the femur was extended beyond a vertical position. This would limit stride length considerably. If ornithocheiroids stood more erect (which seems likely given their disparately long forelimbs; see Chatterjee and Templin 2004), the posterior deflection of the ischiopubic plate aligns

the ischiopubic plate more evenly around the vertical femur, which may optimise muscle leverage in this region (Fig. 10). Such an orientation seems to permit relatively greater stride length and, therefore, increased terrestrial efficiency. Of course, the shortness of ornithocheiroid hindlimbs would have limited their overall stride length, and their terrestrial locomotion may have been rather inefficient compared to other pterosaurs. This is not surprising: if ornithocheiroids were the pelagic, seabird-like forms reconstructed by most authors (e.g., Bramwell and Whitfield 1974; Wellnhofer 1991a, b; Bennett 2001; Unwin 2005; Witton 2008), then their comparatively laboured terrestrial locomotion allies them with many living seabirds that are far poorer terrestrial locomotors than they are fliers.

Azhdarchoid pelves.—The pelves of azhdarchoids are defined by an atypically large ischiopubic plate and a large, hooked postacetabular process. These may indicate generally larger hindlimb musculature, a finding that corroborates observations that some neoazhdarchians (azhdarchids) were proficient on the ground (Witton and Naish 2008). The development of their large, complex postacetabular process is of particular note, as it may represent a unique solution to increasing hindlimb retractor power among archosauriforms. Most archosauriforms use their robust tails to anchor a powerful, femur-retracting *M. caudofemoralis*, but the slender pterosaur tail was unable to support such powerful musculature (Persons 2010). Instead, azhdarchoids appear to have increased the size and leverage of *M. flexor tibialis* and *M. iliofemoralis* musculature, and may have given them larger, more superficially mammalian-like haunches, than reptilian.

Conclusions

This preliminary review of the pterosaur pelvis suggests that there is considerable scope for more detailed research into their taxonomic utility and function. This mirrors recent findings that pterosaur pectoral girdles also have greater morphological diversity than previously realised and warrant greater phylogenetic and mechanical attention (Frey et al. 2003; Bennett 2003). While the lack of well-preserved pelves of named pterosaur specimens is a handicap to their potential phylogenetic use, the pelves of enough taxa are known to include some pelvic characters in future phylogenetic work. Using pelvic characters may aid in the resolution of some controversies over pterosaur taxonomy.

Acknowledgements

We have had helpful discussions with Darren Naish (University of Southampton, Southampton, UK), Steve Vidovic (University of Portsmouth, Portsmouth, UK), Dave Unwin (University of Leicester, Leicester, UK), Dino Frey and Ross Elgin (Staatliches Museum für Naturkunde, Karlsruhe, Germany), and Lorna Steel (Natural History Museum, London, UK). We especially thank referees Mike Habib

(University of Southern California, Los Angeles, USA) and David Hone (Queen Mary University of London, London, UK) for their extremely helpful and encouraging comments, and Michael Benton (University of Bristol, Bristol, UK) for a sterling editorial job.

References

- Andres, B. 2007. Pterosaur systematics. In: D. Hone (ed.), *Flugsaurier: The Wellnhofer Pterosaur Meeting, Munich. Abstract Volume*, 7. Bavarian State Collection for Palaeontology, Munich.
- Andres, B. and Ji, Q. 2008. A new pterosaur from the Liaoning Province of China, the phylogeny of Pterodactyloidea, and convergence in their cervical vertebrae. *Palaeontology* 51: 453–469.
- Andres, B., Clark, J.M., and Xu, X. 2010. A new rhamphorhynchid pterosaur from the Upper Jurassic of Xinjiang, and the phylogenetic relationships of basal pterosaurs. *Journal of Vertebrate Paleontology* 30: 163–187.
- Averianov, A.O. 2004. New data on Cretaceous flying reptiles (Pterosauria) from Russia, Kazakhstan, and Kyrgyzstan. *Paleontological Journal* 38: 426–436.
- Barrett, P.M., Butler, R.J., Edwards, N.P., and Milner, A.R. 2008. Pterosaur distribution in time and space: an atlas. *Zitteliana* B 28: 61–107.
- Bennett, S.C. 1990. A pterodactyloid pterosaur from the Santana Formation of Brazil: implications for terrestrial locomotion. *Journal of Vertebrate Paleontology* 10: 80–85.
- Bennett, S.C. 1992. Sexual dimorphism of *Pteranodon* and other pterosaurs, with comments on cranial crests. *Journal of Vertebrate Paleontology* 12: 422–434.
- Bennett, S.C. 1993. The ontogeny of *Pteranodon* and other pterosaurs. *Paleobiology* 19: 92–106.
- Bennett, S.C. 1995. A statistical study of *Rhamphorhynchus* from the Solnhofen Limestone of Germany: Year-classes of a single large species. *Journal of Paleontology* 69: 569–580.
- Bennett, S.C. 1996. Year-classes of pterosaurs from the Solnhofen Limestone of Germany: Taxonomic and systematic implications. *Journal of Vertebrate Paleontology* 16: 432–444.
- Bennett, S.C. 1997. The arboreal leaping theory of the origin of pterosaur flight. *Historical Biology* 12: 265–290.
- Bennett, S.C. 2001. The osteology and functional morphology of the Late Cretaceous pterosaur *Pteranodon*. *Palaeontographica A* 260: 1–153.
- Bennett, S.C. 2003. New crested specimens of the Late Cretaceous pterosaur *Nyctosaurus*. *Palaontologische Zeitschrift* 77: 61–75.
- Bennett, S.C. 2007. A second specimen of the pterosaur *Anurognathus ammoni*. *Palaontologische Zeitschrift* 81: 376–398.
- Benton, M.J. 1999. *Scleromochlus taylori* and the origin of dinosaurs and pterosaurs. *Philosophical Transactions of the Royal Society, London B* 354: 1423–1446.
- Bramwell, C.D. and Whitfield, G.R. 1974. Biomechanics of *Pteranodon*. *Philosophical Transactions of the Royal Society of London B* 267: 503–581.
- Butler, R.J., Brusatte, S.L., Andres, B., and Benson, R.B.J. 2011. How do geological sampling biases affect studies of morphological evolution in deep time? a case study of pterosaur (Reptilia: Archosauria) disparity. *Evolution* 66: 147–162.
- Cai, W. and Wei, F. 1994. *Zhejiangopterus linhaiensis* (Pterosauria) from the Upper Cretaceous of Linhai, Zhejiang, China. *Vertebrata Palasiatica* 32: 181–194.
- Chatterjee, S. and Templin, R.J. 2004. Posture, locomotion and palaeoecology of pterosaurs. *Geological Society of America Special Publication* 376: 1–64.
- Clark, J.M., Hopson, J.A., Hernández, R., Fatsovsky, D.E., and Montellano, M. 1998. Foot posture in a primitive pterosaur. *Nature* 391: 886–889.
- Codorniu, L. and Chiappe, M. 2004. Early pterosaurs (Pterodactyloidea: Pterodactyloidea) from the Lower Cretaceous of central Argentina. *Canadian Journal of Earth Sciences* 41: 9–18.

- Codorniu, L., Gasparini, Z., and Paulina-Carabajal, A. 2006. A late Jurassic pterosaur (Reptilia, Pterodactyloidea) from northwestern Patagonia, Argentina. *Journal of South American Earth Sciences* 20: 383–389.
- Coombs, W.P. 1978. Theoretical aspects of cursorial adaptations in dinosaurs. *Quarterly Review of Biology* 53: 393–418.
- Dalla Vecchia, F.M. 2002. Observations on the non-pterodactyloid pterosaur *Jeholopterus ningchengensis* from the Early Cretaceous of northeastern China. *Natura Nascosta* 24: 8–27.
- Dalla Vecchia, F.M. 2003. A review of the Triassic pterosaur fossil record. *Rivista del Museo Civico di Scienze Naturali "E. Caffi" Bergamo* 22: 13–29.
- Dalla Vecchia, F.M. 2009. Anatomy and systematics of the pterosaur *Carniadactylus* gen. n. *rosenfeldi* (Dalla Vecchia, 1995). *Rivista Italiana di Paleontologia e Stratigrafia* 115: 159–188.
- Dong, D. 1982. A new pterosaur (*Huanhepterus quingyangensis* gen. et. sp. nov.) from Ordos, China. *Vertebrata Palasiatica* 20: 115–121.
- Eaton, G.F. 1910. Osteology of *Pteranodon*. *Memoirs of the Connecticut Academy of Arts and Sciences* 2: 1–38.
- Eck, K., Elgin, R.A., and Frey, E. 2011. On the osteology of *Tapejara wellnhoferi* Kellner 1989 and the first occurrence of a multiple specimen assemblage from the Santana Formation, Araripe Basin, NE-Brazil. *Swiss Journal of Palaeontology* 130: 277–296.
- Fabre, J.A. 1976. Un nouveau Pterodactylidae du Gisement de Canjuers (Var) *Gallodactylus canjuersensis* nov. gen., nov. sp. *Annales de Paleontologie (Vertébrés)* 62: 35–70.
- Fastnacht, M. 2005. The first dsungaripterid pterosaur from the Kimmeridgian of Germany and the biomechanics of pterosaur long bones. *Acta Palaeontologica Polonica* 50: 273–288.
- Fechner, R. 2009. *Morphofunctional Evolution of the Pelvic Girdle and Hindlimb of Dinosauromorpha on the Lineage to Sauropoda*. 197 pp. Unpublished Ph.D. dissertation, Fakultät für Geowissenschaften, Ludwig-Maximilians-Universität, Munich.
- Frey, E. and Martill, D.M. 1994. A new pterosaur from the Crato Formation (Lower Cretaceous, Aptian) of Brazil. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 194: 421–441.
- Frey, E., Tischlinger, H., Buchy, M.-C., and Martill, D.M. 2003. New specimens of pterosauria (Reptilia) with soft parts with implications for pterosaurian anatomy and locomotion. In: E. Buffetaut and J.M. Mazin (eds.), *Evolution and Palaeobiology of Pterosaurs*. *Geological Society Special Publication* 217: 233–266.
- Frey, E., Buchy, M.-C., Stinnesbeck, W., Gonzalez, A., and di Stefano, A. 2006. *Muzquizopteryx coahuilensis* n. g., n. sp., a nyctosaurid pterosaur with soft tissue preservation from the Coniacian (Late Cretaceous) of northeast Mexico (Coahuila). *Oryctos* 6: 19–30.
- Habib, M.B. 2008. Comparative evidence for quadrupedal launch in pterosaurs. *Zitteliana B* 28: 161–168.
- Hildebrand, M. 1995. *Analysis of Vertebrate Structure, Fourth Edition*. 657 pp. John Wiley and Sons Inc., New York.
- Hogg, D.A. 1982. Fusions occurring in the postcranial skeleton of the domestic fowl. *Journal of Anatomy* 135: 501–512.
- Ji, S. and Ji, Q. 1998. A new species of pterosaur from Liaoning, *Dendrorhynchus curvidentatus*, gen. et sp. nov. *Jiangsu Geology* 22: 199–206.
- Kellner, A.W.A. 2003. Pterosaur phylogeny and comments on the evolutionary history of the group. In: E. Buffetaut and J.-M. Mazin (eds.), *Evolution and Palaeobiology of Pterosaurs*. *Geological Society Special Publication* 217: 105–137.
- Kellner, A.W.A. 2004. New information on the Tapejaridae (Pterosauria, Pterodactyloidea) and discussion of the relationships of this clade. *Ameghiniana* 41: 521–534.
- Kellner, A.W.A. and Hasegawa, Y. 1993. Postcranial skeleton of *Tupuxurara* (Pterosauria, Pterodactyloidea, Tapejaridae) from the Lower Cretaceous of Brazil. *Journal of Vertebrate Paleontology* 13: 44A.
- Kellner, A.W.A. and Tomida, Y. 2000. Description of a new species of *Anhangueridae* (Pterodactyloidea) with comments on the pterosaur fauna from the Santana Formation (Aptian–Albian), Northeastern Brazil. *National Science Museum Monographs* 17: 1–135.
- Lü, J. 2009. A new non-pterodactyloid pterosaur from Qinglong County, Hebei Province, China. *Acta Geologica Sinica* 83: 189–199.
- Lü, J. and Fucha, X. 2011. A new pterosaur (Pterosauria) from the middle Jurassic Tiaojishan Formation of western Liaoning, China. *Global Geology* 13: 113–118.
- Lü, J. and Yuan, C. 2005. New tapejarid pterosaur from Western Liaoning, China. *Acta Geologica Sinica* 79: 453–458.
- Lü, J., Gao, C. Meng, Q., Liu, J., and Ji, Q. 2006a. On the systematic position of *Eosipterus yangi* Ji et Ji. 1997 among pterodactyloids. *Acta Geologica Sinica* 80: 643–646.
- Lü, J., Jin, X., Unwin, D.M., Zhao, L., Azuma, Y., and Ji, Q. 2006c. A new species of *Huaxiapterus* (Pterosauria: Pterodactyloidea) from the Lower Cretaceous of Western Liaoning, China with comments on the systematics of tapejarid pterosaurs. *Acta Geologica Sinica* 80: 315–326.
- Lü, J., Liu, J., Wang, X., Gao, C., Meng, Q., and Ji, Q. 2006b. New material of pterosaur *Sinopterus* (Reptilia: Pterosauria) from the Early Cretaceous Jiufotang Formation, Western Liaoning, China. *Acta Geologica Sinica* 80: 783–789.
- Lü, J., Unwin, D.M., Deeming, D.C., Jin, X., Liu, Y., and Ji, Q. 2011. An egg-adult association, gender, and reproduction in pterosaurs. *Science* 331: 321–324.
- Lü, J., Unwin, D.M., Jin, X., Liu, Y., and Ji, Q. 2010. Evidence for modular evolution in a long-tailed pterosaur with a pterodactyloid skull. *Proceedings of the Royal Society B* 277: 383–389.
- Lü, J., Unwin, D.M., Xu, L., and Zhang, X. 2008. A new azhdarchoid pterosaur from the Lower Cretaceous of China and its implications for pterosaur phylogeny and evolution. *Naturwissenschaften* 95: 891–897.
- Mazin, J.-M., Billon-Bruyat, J., Hantzpergue, P., and Lafaurie, G. 2003. Ichnological evidence for quadrupedal locomotion in pterodactyloid pterosaurs: trackways from the late Jurassic of Crayssac. In: E. Buffetaut and J.-M. Mazin (eds.), *Evolution and Palaeobiology of Pterosaurs*. *Geological Society Special Publication* 217: 283–296.
- Molnar, R.E. 1987. A pterosaur pelvis from western Queensland, Australia. *Alcheringa* 11: 87–94.
- Padian, K. 1983a. A functional analysis of flying and walking in pterosaurs. *Palaeobiology* 9: 218–239.
- Padian, K. 1983b. Osteology and functional morphology of *Dimorphodon macronyx* (Buckland) (Pterosauria: Rhamphorhynchoidea) based on new material in the Yale Peabody Museum. *Postilla* 189: 1–44.
- Padian, K. 2008. The Early Jurassic pterosaur *Dorygnathus banthensis* (Theodori, 1830). *Special Papers in Palaeontology* 80: 1–64.
- Persons, W.S., IV. 2010. Convergent evolution of prezygapophysis/chevron rods in the tails of pterosaurs and dromaeosaurs and the parallel pattern of caudal muscle reduction in pterosaurs and birds. *Acta Geologica Sinica* 31: 54.
- Riskin, D.K. and Hermanson, J.W. 2005. Independent evolution of running in vampire bats. *Nature* 434: 292.
- Sayão, J.M. and Kellner, A.W.A. 2006. Nova esqueleto parcial de pterossaur (Pterodactyloidea, Tapejaridae) do Membro Crato (Aptiano), Formação Santana, Bacia do Araripe, Nordeste do Brasil. *Estudos Geológicos* 16: 16–40.
- Serenó, P.C. and Arcucci, A.B. 1994. Dinosaurian precursors from the Middle Triassic of Argentina: *Marasuchus lilloensis*, gen. nov. *Journal of Vertebrate Paleontology* 14: 53–73.
- Unwin, D.M. 1988. New remains of the pterosaur *Dimorphodon* (Pterosauria: Rhamphorhynchoidea) and the terrestrial ability of early pterosaurs. *Modern Geology* 13: 57–68.
- Unwin, D.M. 1996. The fossil record of middle Jurassic pterosaurs. In: M. Morales (ed.), *The Continental Jurassic*. *Museum of Northern Arizona Bulletin* 60: 291–304.
- Unwin, D.M. 1997. Pterosaur tracks and the terrestrial ability of pterosaurs. *Lethaia* 29: 373–386.
- Unwin, D.M. 2003. On the phylogeny and evolutionary history of pterosaurs. In: E. Buffetaut and J.-M. Mazin (eds.), *Evolution and Palaeobiology of Pterosaurs*. *Geological Society, London, Special Publications* 217: 139–190.

- Unwin, D.M. 2005. *The Pterosaurs from Deep Time*. 347 pp. Pi Press, New York.
- Unwin, D.M. and Lü, J. 2010. *Darwinopterus* and its implications for pterosaur phylogeny. *Acta Geoscientica Sinica* 31: 68–69.
- Veldmeijer, A.J. 2003. Description of *Coloborhynchus spielbergi* sp. nov. (Pterodactyloidea) from the Albian (Lower Cretaceous) of Brazil. *Scripta Geologica* 125: 35–139.
- Wang, X., Kellner, A.W.A., Zhou, Z., and Campos, D.A. 2008. Discovery of a rare arboreal forest-dwelling flying reptile (Pterosauria, Pterodactyloidea) from China. *Proceedings of the National Academy of Sciences USA* 105: 1983–1987.
- Wang, X., Kellner, A.W.A., Jiang, S., and Meng, X. 2009. An unusual long-tailed pterosaur with elongated neck from western Liaoning of China. *Anais da Academia Brasileira de Ciências* 81: 793–812.
- Wang, X., Kellner, A.W.A., Jiang, S., Cheng, X., Meng, X., and Rodrigues, T. 2010. New long-tailed pterosaurs (Wukongopteridae) from western Liaoning, China. *Anais da Academia Brasileira de Ciências* 82: 1045–1062.
- Wellnhofer, P. 1970. Die Pterodactyloidea (Pterosauria) der Oberjura-Plattenkalke Süddeutschlands, *Abhandlung der Bayerischen Akademie der Wissenschaften, Neue Folge* 141: 1–133.
- Wellnhofer, P. 1974. *Campylognathoides liasicus* (Quenstedt), an upper Liassic pterosaur from Holzmaden—the Pittsburgh specimen. *Annals of the Carnegie Museum* 45: 5–34.
- Wellnhofer, P. 1975. Die Rhamphorhynchoidea (Pterosauria) der Oberjura-Plattenkalke Süddeutschlands. *Palaeontographica A* 148: 1–33, 132–186, 149.
- Wellnhofer, P. 1978. *Handbuch der Paläoherpetologie*. 19. Pterosauria. 82 pp. Gustav Fischer, Stuttgart.
- Wellnhofer, P. 1988. Terrestrial locomotion in pterosaurs. *Historical Biology* 1: 3–16.
- Wellnhofer, P. 1991a. *The Illustrated Encyclopedia of Pterosaurs*. 192 pp. Salamander Books Ltd., London.
- Wellnhofer, P. 1991b. Weitere Pterosaurierfunde aus der Santana-Formation (Apt) der Chapada do Araripe, Brasilien. *Palaeontographica A* 215: 43–101.
- Wellnhofer, P. 2003. A Late Triassic pterosaur from the Northern Calcareous Alps (Tyrol, Austria). In: E. Buffetaut and J.M. Mazin (eds.) 2003. Evolution and Palaeobiology of Pterosaurs. *Geological Society, London, Special Publications* 217: 5–22.
- Wellnhofer, P. and Vahldiek, B.-W. 1986. Ein Flugsaurier-Rest aus dem Posidonienschiefer (Unter-Toarcium) von Schandelah bei Braunschweig. *Paläontologische Zeitschrift* 60: 329–340.
- Wild, R. 1975. Ein Flugsaurier-Rest aus dem Lias Epsilon (Toarcium) von Erzingen (Schwäbischer Jura). *Stuttgarter Beiträge Naturkunde B* 17: 1–16.
- Wild, R. 1978. Die Flugsaurier (Reptilia, Pterosauria) aus der Oberen Trias von Cene bei Bergamo, Italien. *Bolletino Società Paleontologica Italiana* 17: 176–256.
- Wild, R. 1984. A new pterosaur (Reptilia, Pterosauria) from the Upper Triassic (Norian) of Friuli, Italy. *Gortania-Atti Museo Friulano del Storia Naturale* 5: 45–62.
- Wild, R. 1993. A juvenile specimen of *Eudimorphodon ranzii* Zambelli (Reptilia, Pterosauria) from the upper Triassic (Norian) of Bergamo. *Rivista del Museo civico di Scienze Naturali di Bergamo “E. Caffi”* 16: 91–115.
- Williston, S.W. 1897. Restoration of *Ornithostoma* (Pteranodon). *Kansas University Quarterly* 6: 35–51.
- Williston, S.W. 1903. On the osteology of *Nyctosarus* (*Nyctodactylus*). *Field Columbian Museum Publications, Geological Series* 2: 125–163.
- Wilkinson, M.T. 2008. Three-dimensional geometry of a pterosaur wing skeleton, and its implications for aerial and terrestrial locomotion. *Zoological Journal of the Linnean Society* 154: 27–69.
- Witton, M.P. 2008. A new approach to determining pterosaur body mass and its implications for pterosaur flight. *Zitteliana B* 28: 143–159.
- Witton, M.P. and Habib, M. 2010. On the size and flight diversity of giant pterosaurs, the use of birds as pterosaur analogues and comments on pterosaur flightlessness. *PLoS One* 5: e13982.
- Witton, M.P. and Naish, D. 2008. A reappraisal of azhdarchid pterosaur functional morphology and paleoecology. *PLoS One* 3 (5): e2271.
- Young, C.C. 1964. On a new pterosaurian from Sinkiang, China. *Vertebrate Palasiatica* 8: 221–225.

Appendix 1

Pterosaur specimens considered in this study.

Higher clade	Taxon	Specimen number	References
Dimorphodontidae?	<i>Peteinosaurus zambellii</i>	BSP1994151	Wellnhofer 2003; Wild 1978
Dimorphodontidae	<i>Dimorphodon macronyx</i>	BMNH 41212, YPM350	Padian 1983b; Unwin 1988
Anurognathidae	<i>Anurognathus ammoni</i>	private specimen	Bennett 2007
	<i>Dendrorhynchoides curvidentatus</i>	GMV2128	Ji and Ji 1988
"Campylognathoidid"	<i>Campylognathoides liasicus</i>	CM11424	Wellnhofer 1974
	<i>Carnidactylus rosenfeldi</i>	MFSN 1797	Dalla Vecchia 2009
	<i>Eudimorphodon ranzii</i>	MFSN 2888, 3496	Wild 1978
Rhamphorhynchidae	<i>Dorygnathus banthensis</i>	A/III 493, MBR 1905.15	Wild 1975; Padian 2008
	<i>Rhamphorhynchus muensteri</i>	V432, BSP 1955/28, 1907 I 37	Wellnhofer 1975
Wukongopteridae	<i>Wukongopterus lüi</i>	IVPP V15113	Wang et al. 2009
	<i>Darwinopterus linglongtaensis</i>	IVPP V16049	Wang et al. 2010
	<i>Darwinopterus robustodens</i>	41HIII-0309A	Lü et al. 2011
	<i>Darwinopterus modularis</i>	ZMNH M8782, M8802	Lü et al. 2009, 2011
Ornithocheiroidea	<i>Anhanguera santanae</i>	AMNH 22555	Wellnhofer 1988
	<i>Coloborhynchus piscator</i>	NSM-PV 19892	Kellner and Tomida 2000
	<i>Coloborhynchus spielbergi</i>	RGM 401 880	Veldmeijer 2003
	<i>Arthurdactylus conandoylei</i>	SMNK 1132 PAL	Frey and Martill 1994
	"The Queensland Pterosaur"	QMF12982	Molnar 1987
	<i>Ornithocheiridae</i> indet.	ZINPH 8E-G/43	Averianov 2004
	<i>Pteranodon</i> sp.	UNC 4, YPM 1175, KUVP 993, FHSM VP 2062	Bennett 2001; Williston 1897
	<i>Nyctosaurus</i> sp.	"KJ2"	Bennett 2003
	<i>Nyctosaurus gracilis</i>	YPM 1178	Williston 1903
	<i>Muzquizopteryx coahuilensis</i>	UNAM IGM 8621	Frey et al. 2006
Ctenochasmatoidea	<i>Cynorhamphus suevicus</i>	MNH CNJ-71	Fabre 1976
	<i>Eosipterus yangi</i>	D2514	Lü et al. 2006a
	" <i>Pterodactylus</i> " <i>longicollum</i>	JME-SOS 2428	Wellnhofer 1970
	<i>Pterodactylus antiquus</i>	BSP AS I 1739	Wellnhofer 1970
	<i>Pterodaustro guinazui</i>	MHIN-UNSL-GEO-V 241	Codorniu and Chiappe 2004
	<i>Huanhepterus quingyangensis</i>	IVPPV9070	Dong 1982
Dsungaripteroidea	" <i>Germanodactylus</i> " <i>rhamphastinus</i>	BSP AS I 745	Wellnhofer 1970
	Dsungaripteroidea indet.	DFMMh/FV 500	Fastnacht 2005
	<i>Dsungaripterus weii</i>	IVPP V-2777	Young 1964
Dsungaripteroidea?	<i>Herbstosaurus pigmaeus</i>	CTES-PZ-1711	Unwin 1996
Dsungaripteridae	Dsungaripteroidea indet.	MOZ 3625P	Codorniu et al. 2006
Azhdarchoidea	<i>Nemicolopterus crypticus</i>	IVPP V-142377	Wang et al. 2008
	<i>Huaxiapterus jii</i>	GMN-03-11-001	Lü and Yuan 2005
	<i>Sinopterus dongi</i>	D2525	Lü et al. 2006b
	<i>Tupuxuara leonardii</i>	IMCF 1052	MPW and DMM personal observation
	<i>Zhejiangopterus linhaiensis</i>	ZMNH M1323 and M1325	Cai and Wei 1994
	Neoazhdarchia indet.	MN 6588-V	Sayão and Kellner 2006
	Neoazhdarchia indet.	AMNH 22569	Bennett 1990
	Neoazhdarchia indet.	"EH2"	ESH personal observation