



## Functional morphology of *Quetzalcoatlus* Lawson 1975 (Pterodactyloidea: Azhdarchoidea)

Kevin Padian, James R. Cunningham, Wann Langston JR. & John Conway

To cite this article: Kevin Padian, James R. Cunningham, Wann Langston JR. & John Conway (2021) Functional morphology of *Quetzalcoatlus* Lawson 1975 (Pterodactyloidea: Azhdarchoidea), Journal of Vertebrate Paleontology, 41:sup1, 218-251, DOI: [10.1080/02724634.2020.1780247](https://doi.org/10.1080/02724634.2020.1780247)

To link to this article: <https://doi.org/10.1080/02724634.2020.1780247>



© 2021 Kevin Padian, James R. Cunningham, Wann Langston Jr., and John Conway.



Published online: 07 Dec 2021.



Submit your article to this journal [↗](#)



View related articles [↗](#)



View Crossmark data [↗](#)

## FUNCTIONAL MORPHOLOGY OF *QUETZALCOATLUS* LAWSON 1975 (PTERODACTYLOIDEA: AZHDARCHOIDEA)

KEVIN PADIAN,<sup>\*1</sup> JAMES R. CUNNINGHAM,<sup>2</sup> WANN LANGSTON JR.,<sup>3,†</sup> and JOHN CONWAY<sup>4</sup>

<sup>1</sup>Museum of Paleontology and Department of Integrative Biology, University of California, Berkeley, California 94720-3200, U.S.A.,  
kpadian@berkeley.edu;

<sup>2</sup>Cunningham Engineering Associates, Collierville, Tennessee 38017, U.S.A.;

<sup>3</sup>Texas Vertebrate Paleontology Collections, University of Texas, Austin, Texas, U.S.A.;

<sup>4</sup>Johnconway.co, London, U.K.

**ABSTRACT**—We reconstruct the proportions and possible motions of the skeleton of the giant azhdarchid pterosaur *Quetzalcoatlus*. The neck had substantial dorsoventral mobility, and the head and the neck could swing left and right through an arc of ca. 180°. In flight, it is most plausible that the hind limbs were drawn up bird-like, with the knee anterior to the acetabulum. In this position, an attachment of the wing membrane to the hind limb would have been useless. A straight-legged posterior extension of the hind limb, such as rotation of the hind limb into a fully ‘bat-like’ pose, was likely prevented by soft tissues of the hip joint. Given these difficulties, the traditional ‘broad-winged’ bat-like restoration is unrealistic. On the ground, *Quetzalcoatlus*, like other ornithomirans, had an erect stance and a parasagittal gait. Terrestrial locomotion was powered almost entirely by the hind limbs. The pace length would have been limited to the length of the glenoacetabular distance, except that *Quetzalcoatlus* (like other pterodactyloids) had a unique gait in which the forelimb was elevated out of the way of the hind limb from step to step. If the humerus were retracted 80° and adducted nearly to the body wall, the elbow and wrist may have been able to extend to effect a quadrupedal launch with assistance from the hind limbs, assuming sufficient long bone strength and sufficient extensor musculature at these forelimb joints. A bipedal launch using the hind limbs alone also appears plausible: despite the animal’s great size, the hind limb to torso length ratio is the greatest for all known pterosaurs.

Citation for this article: Padian, K., J. R. Cunningham, W. Langston, and J. Conway. 2021. Functional morphology of *Quetzalcoatlus* Lawson 1975 (Pterodactyloidea: Azhdarchoidea); pp. 218–251 in K. Padian and M. A. Brown. The Late Cretaceous pterosaur *Quetzalcoatlus* Lawson 1975 (Pterodactyloidea: Azhdarchoidea). Society of Vertebrate Paleontology Memoir 19. Journal of Vertebrate Paleontology 41(2, Supplement). DOI: 10.1080/02724634.2020.1780247.

### INTRODUCTION

During the 1970s and 1980s, a series of bones of several individuals representing a new lineage of azhdarchoid pterosaur was excavated from the Upper Cretaceous Javelina Formation of Texas by ‘crews from The University of Texas at Austin’ (Lawson, 1975; Langston, 1981; Kellner and Langston, 1996; Brown et al., 2021; Lehman, 2021; Andres and Langston, 2021). Two size ‘morphs’ were identified. The larger, known from remnants of a single wing and several referred specimens, represented the largest pterosaur and the largest flying creature discovered up to that time; its wingspan was estimated at 35–40 feet (ca. 11–12 m) (Lawson, 1975; Langston, 1981). The smaller was estimated to have proportions about half the size of the larger, which was dubbed *Quetzalcoatlus northropi*. The ‘smaller morph’ has been informally called ‘*Q. sp.*’ to reflect uncertainty about its taxonomic status, but is officially named *Quetzalcoatlus lawsoni* in Andres and Langston (2021).

In 2000, de Ricqlès and colleagues reported on thin-sections of long bones taken from both ‘morphs.’ They were unable to analyze the sample from the larger specimen because the microstructure in the sample provided had been destroyed by fungus taphonomically. The smaller specimen suggested an animal not close to terminating active growth. The outer cortex was well vascularized, and there was no indication of an ‘external fundamental system’ (EFS) indicating the cessation of growth (Woodward et al., 2013). This suggested the possibility that the smaller ‘morph’ was a juvenile of the larger one, although the possibility remained that it was of a different taxon not represented by adults in the available sample of the smaller size range, or by juveniles of the giant morph. Andres and Langston (2021) diagnose these two ‘morphs’ as different lineages and identify a third in the collection, *Wellnhopterus brevirostris*, from the Javelina and Black Peaks formations.

For this and other reasons, it seems unproductive to talk about two size ‘morphs.’ The hundreds of bones from a variety of individuals that constitute the sample of the ‘smaller morph’ represent a range of sizes, most of which from the Amaral Site are consistent with wingspans in the range of 4–5 m, but some from nearby overbank deposits are much smaller and a few from the stream channel deposits are larger (B. Andres, pers. comm.). The ‘large morph’ (*Q. northropi* holotype) is represented by only a single partial wing that is twice the size of the average ‘small morph’ and an isolated proximal ulna, plus some other nonoverlapping elements from nearby channel deposits (Andres and Langston, 2021). Although there is a large gap in size between this single giant outlier and the larger sample of

\*Corresponding author.

†Deceased 2013.

© 2021 Kevin Padian, James R. Cunningham, Wann Langston Jr., and John Conway.

This is an Open Access article distributed under the terms of the Creative Commons Attribution-NonCommercial-NoDerivatives License (<http://creativecommons.org/licenses/by-nc-nd/4.0/>), which permits non-commercial re-use, distribution, and reproduction in any medium, provided the original work is properly cited, and is not altered, transformed, or built upon in any way.

Color versions of one or more of the figures in the article can be found online at [www.tandfonline.com/ujvp](http://www.tandfonline.com/ujvp).

bones in the smaller size range, the sample cannot be regarded as ‘dimorphic’ in a biological sense, because there is only one partial large specimen with several other possibly referred elements, and because the smaller ones are mostly not fully grown. Andres and Langston (2021) determined autapomorphies for both ‘morphs’ and regard them as distinct taxa (*Q. northropi* for the holotype and large ‘morph,’ and *Q. lawsoni* for the smaller, better-represented ‘morph’), which we accept for the purposes of our study; however, our work is based entirely on the smaller ‘morph.’ It should be noted that the names *Quetzalcoatlus lawsoni* and *Wellnhopterus brevirostris* are used in this paper, but they are officially named in Andres and Langston (2021) and should be cited as such. Any names or nomenclatural acts in this paper are disclaimed for nomenclatural purposes (Article 8.3 of International Code of Zoological Nomenclature; International Commission on Zoological Nomenclature [ICZN], 1999).

Apart from a study of some skull remains of a relatively complete smaller specimen (TMM 41961-1: Kellner and Langston, 1996), and a new report on the stratigraphy and the taphonomy of the source beds (Lehman, 2021), no comprehensive morphological or functional study has been published on *Quetzalcoatlus* in the peer-reviewed literature since its initial announcement (Lawson, 1975), although there have been many comparative references to it in the context of other studies (e.g., Langston, 1981; Frey and Martill, 1996; Witton and Naish, 2008; Witton and Habib, 2010; Chatterjee and Templin, 2012), and it continues to generate interest in the popular literature.

Here, we undertake a study of the functional morphology of *Quetzalcoatlus*, mainly comprising feeding, flight, walking, and launching. A study of the functional morphology and flight capability was begun in 1981 by Langston and Padian, which grew into a collaboration with the late Dr. Paul MacCready and his crew at AeroVironment, Inc., to engineer a mechanical flying model called ‘QN’ (MacCready, 1985). Langston and Padian’s work was later suspended while both were occupied with various other projects, then the work was continued with a bioaerodynamic approach by Langston and Cunningham that was eventually suspended for other reasons. Some time after Wann Langston’s death in 2013, and at the invitation of the director and the staff of the collections [OR] UT, the remaining two of us (K.P., J.R.C.), with the addition of John Conway as coauthor and artist, agreed to redouble our efforts in tribute to Wann and to make our information and analyses available to the scientific community, so that *Quetzalcoatlus* can be integrated into the broader understanding of pterosaurian paleobiology.

No coauthored manuscripts or drafts by Wann Langston and colleagues survive, the result of hiatuses between collaborative efforts and the successive crashes of computers and the inability to recover lost information, so we redid the study completely. We benefited greatly from Wann’s identifications of bones, his measurements, his reconstructed models and casts, and his observations and inferences in correspondence to us, all of which we checked for accuracy.

**Institutional Abbreviations**—TMM, Texas Vertebrate Paleontology Collections, The University of Texas at Austin, Texas, U.S.A.

## MATERIALS AND METHODS

The aim of this study is to reconstruct the functional morphology of *Quetzalcoatlus*, in the air and on the ground. Although the giant specimen (*Q. northropi*) has attracted most attention, it is far too incomplete to provide much meaningful information, except as a supplemental extension to that provided by the smaller sample (named *Q. lawsoni* by Andres and Langston, 2021). The left humerus is its only complete bone apart from the distal syncarpal, although the ulna is reasonably complete. The smaller specimens, on which our study is almost completely

based, comprise over 300 skeletal elements (Andres and Langston, 2021) and represent at least a dozen individuals from the main Pterodactyl Ridge Sites (Brown et al., 2021; Lehman, 2021). Some of the individuals represented in the smaller specimens vary within about 10% of each other in size, but others are considerably smaller or larger (these are usually represented by only a few elements). A complete inventory of these materials is provided by Brown et al. (2021).

The bones are preserved in three dimensions but are sometimes distorted by crushing, breakage, and asymmetrical compression, although not nearly to the degree seen in *Pteranodon* and many other typical pterosaurs (Wellnhofer, 1978, 1991). In general, enough duplicate elements are preserved in these specimens, or in comparative taxa, for most anatomical details to be clarified. Wann Langston constructed models of many missing and incomplete elements by comparison and incorporation of differentially preserved specimens. He often constructed models of unpreserved bones from opposite sides of the body by restoring their better-preserved counterparts in clay with the aid of a mirror or combined well-preserved parts of several specimens to achieve a more complete restoration. We have checked his reconstructions of morphology and lengths, and these are reflected in this paper. In our study, we only inferred functional articulations from complete and relatively uncrushed specimens, correcting as necessary with recourse to comparative visual examination and models.

All specimen numbers discussed here have the prefix ‘TMM.’ This is the traditional prefix for the studied specimens, which are actually curated and housed at the Texas Vertebrate Paleontological Collections at University of Texas at Austin (Brown et al., 2021). To our knowledge, all specimens of *Quetzalcoatlus* in the public trust that have been legally collected from Big Bend National Park, Texas, are deposited at the University of Texas [OR] UT. The ‘WL’ prefix denotes Wann Langston’s field numbers of a single individual (see Brown et al., 2021).

We worked from the complete collection of skeletal elements at the University of Texas, manipulating specimens of each element in their respective articulations and correcting for distortion and lack of preservation. We reconstructed angles of articulation and ranges of motion by hand using protractors. Maximum extensions and flexions were estimated taking into account absent soft parts as far as possible. We assumed, as in most birds, that cartilaginous caps on bones were relatively thin, which accords with the tightness of articulation with which most articulated pterosaur skeletons are preserved. For example, figures in Wellnhofer (1970, 1975, 1978) of relatively undisturbed specimens show adjacent bones of the limbs tightly butted against each other, which speaks against thick epiphyseal cartilages, more similar to the condition in neognaths than to that in paleognaths or crocodiles (Holliday et al., 2010). The complex and well-preserved articular surfaces of adjacent *Quetzalcoatlus* bones conform to each other closely and allow relatively constrained estimates of motion (Hutchinson and Gatesy, 2006; Gatesy et al., 2009).

To exclude poses and ranges of motion (ROMs) that were impossible or improbable (Gatesy et al., 2009), we placed articulated series of bones in positions that would have allowed them to achieve primary skeletal functions. This included motions of the neck, execution of the flight stroke(s) by the forelimbs, terrestrial walking and leaping by the hind limbs, and terrestrial locomotion by the forelimbs in concert with the hind limbs. Traditionally, paleontologists have been limited in reconstructing ROM mainly by either the presence of bony stops or obvious disarticulation of the joint (Manafzadeh and Padian, 2018). The presence of layers of soft tissues tends to restrict ROM but sometimes can increase or change it (Hutson and Hutson, 2012). By articulating entire limbs or limb segments against the ground (for terrestrial

locomotion) or with respect to required movements of the forelimb stroke (for flight), we were able to assess ROMs of several joints performing a function simultaneously. We do not provide ROMs for every joint in the skeleton without kinematic context. Instead, we provide estimates of ROMs of individual joints in the context of how they moved during locomotion.

Wann Langston cast or modeled nearly every element in the skeleton, often combining the best-preserved surfaces of several specimens into a single reconstruction. We assessed the accuracy of these reconstructions against actual specimens when attempting to model skeletal kinematics. Estimates of mobility were confirmed by all of us. We recognize that different investigators may reconstruct different ranges of motion for these joints, and we leave room for other interpretations.

We caution readers that measurements of joint angles provided here are based on fossils of dry bones, missing all soft tissues. Reconstructions of mobility based on measurements of dry bones alone generally (but not always) suggest substantially more mobility than was available to or used by the living animal. Constraints added by cartilage, joint capsules, ligaments, tendons, muscles, and other soft tissues can be substantial (e.g., Hutson and Hutson, 2012; Arnold et al., 2014; Manafzadeh and Padian, 2018), but these constraints cannot be reliably reconstructed for most joints in the pterosaur skeleton. This is an occupational hazard of paleobiology, and so when we discuss degrees and directions of articulations and motion, we try to stress that these are maximum estimates; the actual ranges of motion were almost certainly smaller: an apparent ability to perform a function mechanically does not imply that the animal actually performed it.

#### RECONSTRUCTION OF THE PROPORTIONS OF THE SKELETON

Here, we list the available material that allows us to restore the joint articulations and the proportions of *Quetzalcoatlus*. Although many reconstructions and restorations of the skeleton of *Quetzalcoatlus* have been illustrated in various publications, there has never been a justification for the proportions of the bones used in any illustration. This is understandable because Wann Langston's projected description of the material was never completed, although Wann's restorations were based on his careful comparisons of associated bones. Below we provide measurements of several skeletons of available material of *Quetzalcoatlus* in which there are well-preserved elements that overlap with those of other specimens (Table 1). These measurements have been rounded to the nearest centimeter, because as Wann (pers. comm.) noted, sometimes corresponding elements in the same skeleton varied by a few centimeters. Crushing and distortion play a role here, but a minor one in most cases.

Three of the six specimens in Table 1 have associated skull and mandibular material. The occipital region of the skull is unknown (but may not have been much different from that of the related *Hatzegopteryx*; Witton and Naish, 2008), and although there is some indication of a dorsal crest on the midline of the skull (Kellner and Langston, 1996), it is not clear whether a crest protruded behind the mandible and (or) the occipital region (Fig. 1). Because the skull length is uncertain, we prefer to use the more conservative estimates of mandible length, which vary from 94 to 96 cm (Kellner and Langston, 1996), an insignificant difference for animals of this size range.

Cervicals 1, 2, 8, and 9 are relatively short and mostly not well preserved. The first two constitute the atlantoaxis (Andres and Langston, 2020), which, as Wann Langston restored it from TMM 41954-39, would have been about 4 cm long; however, when articulated with the 3rd cervical, its effective length reduces to 2 cm. Allowing for variation, cervical 3 (CV3) is 16–19 cm long, CV4 is 25–26 cm long, CV6 is 35–38 cm long, and CV7 is poorly known but about 25 cm long. In CVs 3–6, the

TABLE 1. Postcranial lengths (cm) for specimens of *Q. lawsoni* in which several overlapping elements are preserved.

Element	TMM 41961	TMM 42422	TMM 41544	TMM 42138-1	Model
Scapula/coracoid	Sc 16 (L, R)	Sc 15, Cor 13	Sc 17, Cor 18	Sc 17, Cor 11	Sc 15–18, Cor 13–16
Humerus		L 24, R 25		23	23–25
Radius		L 36			36–39
Ulna		L 36		39	36–39
MC IV	~47				46–47
Wph1	58 (–2)	60 (–2)	56.5 (–2.5)	39+ (incl.)	56–60 (–2)
Wph2	~30	30		28	28–30
Wph3	18	16			16–18
Wph4	1.5	~5 (+ ≤3)			3–5
Femur	~33	~32 (+ ≤4)			33–38
Tibia	55	L 57, R 60			55–60
MT + d3					15 + 13 (est.)

The 'Model' column represents the range of measurements used in our reconstructions. L = left, R = right (for specimens in which both were preserved); for the first wing phalanx, the additional number in parentheses is the length of the medial process. **Abbreviations:** Cor, coracoid; d3, digit III; MC, metacarpal; MT, metatarsal; Sc, scapula; Wph, wing phalanx.

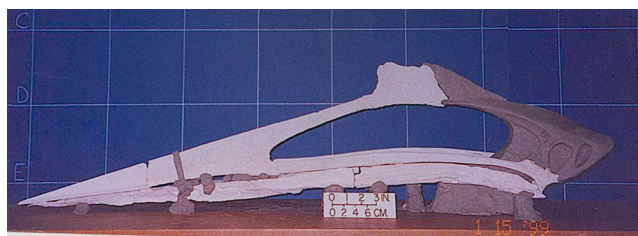


FIGURE 1. Wann Langston's reconstruction of the skull of *Quetzalcoatlus lawsoni*, based on the initial reconstruction by Kellner and Langston (1996), later amended by the Romanian material of *Hatzegopteryx*. There is no evidence of a crest in *Quetzalcoatlus*.

effective length in articulation is reduced by about 2 cm per vertebra, because the prezygapophyses overlap the posterior ball of the centrum of the vertebra anterior to it, fitting into a recess of about 2 cm. In other words, the posterior projection of the central ball is absorbed by its overlap with the anteriorly extending prezygapophyses by about 2 cm. With CV7, this discrepancy increases to 5 cm posteriorly (TMM 42180-3), showing that CV7 could flex dorsally to a considerable extent against CV8 but could not flex ventrally at all.

The restoration of the dorsal vertebral column is based on the notarium preserved at least in part in several specimens (Andres and Langston, 2021). Other dorsal material is poorly known but based on comparative materials from other pterodactyls. Wann Langston created a model in which the notarium comprised five or six vertebrae, followed by four free dorsal vertebrae and a synsacrum of eight vertebrae, of which the last five possessed sacral ribs. Some of this restoration was conjectural, but fairly accurate based on comparative material, and the total length of the restored dorsal column was 46 cm. In our restoration (Table 2), the notarium comprises only four vertebrae, as does the sacrum, and there are six or seven free dorsals between them (to total 27 or 28 precaudal vertebrae, as in other pterosaurs; Table 2).

We describe below how the scapulocoracoid articulated with the notarium and the sternum, and its resulting orientation. The length of the scapula, measured from its distal tip (articulation

TABLE 2. Vertebral counts in various pterosaurs.

Pterosaur	Cervicals		Dorsals		Sacrals	
	CVs	DCVs	NOT	FDVs	SDVs	SVs
<i>Rhamphorhynchus</i>	8	0	0	15	0	3–4
<i>Pterodactylus</i>	7	0	0	14–15	0	3–4
<i>Pteranodon</i>	7	2	6	3	3	6
<i>Quetzalcoatlus</i> (WL)	7	2	6	4	3	5
<i>Quetzalcoatlus</i> (this paper)	7	2	4	7?	3	4

*Rhamphorhynchus* and *Pterodactylus* from Wellnhofer (1978); *Pteranodon* from Bennett (2001a). The doubtful number of FDVs for our reconstruction of *Quetzalcoatlus* reflects the pattern of 27 precaudal vertebrae in Eupterodactyloidea; the actual number of FDVs is unknown. **Abbreviations:** CVs, normal cervicals; DCVs, dorsalized cervicals; FDVs, free dorsal vertebrae; NOT, notariums; SDVs, sacralized dorsal vertebrae; SVs, sacral vertebrae; WL, wing length.

with the notarium) to the center of the glenoid fossa, was 15–18 cm, and the corresponding measure for the coracoid (articulating with the sternum) was 13–16 cm. The distance between the distal ends of the scapula and the coracoid was 16–18 cm. The humerus was 23–25 cm long, the radius and the ulna were 36–39 cm (and possibly longer), and metacarpal (MC) IV was about 46–47 cm long, although the single nearly complete element is missing the proximal articular surface. Wann Langston restored a model of this bone at 53 cm, but we do not think that the available material warrants this length.

The first wing phalanx (Wph1) is 56–60 cm long, but 2 cm of that is represented by the anteroproximally oriented extensor tubercle. Wph2 is 28–30 cm long, a substantial drop in size compared with that of more basal pterosaurs, Wph3 is 16–18 cm long, and the very delicate Wph4 is 3–5 cm long.

In the hind limb, the femur was at least 33 cm and as great as 38 cm in length, and the corresponding tibia (or, more correctly, tibiofibulotarsus or TFT, because the tibia, the fibula, and the proximal tarsals are fused) ranged from 55 to 60 cm. We provide evidence below that the foot, as Wann Langston reconstructed it, was anomalously small for other pterodactyloids, and although no foot material is associated with other hind limb bones, we estimate that the metatarsus was about 15 cm long and the pedal digits I–IV of nearly the same lengths and approximately as long as the metatarsus.

In very rough figures, then, the skull as Kellner and Langston (1996) reconstructed it for the ‘small morph’ was about 100 cm long (modified later by Langston to about 109 cm in his model at the TVPC), and the neck about 135–140 cm (although the neck would not have been stretched straight in natural articulation; see Andres and Langston, 2021, for a more detailed discussion). The dorsal column was nearly another half-meter long, although, as noted, the distance between the glenoid and the acetabulum would have been only about 40 cm. Any cartilaginous discs between the vertebrae would have been very thin and would not have added substantially to these estimates.

Articulated against the notarium and the sternum, the glenoid fossa of the scapulocoracoid would have been positioned about 15 cm lateral to the body midline, which gives some idea of the size of the torso. (The lack of ribs, apart from indications of their attachment to the vertebrae and the sternum, prevents reconstruction of the ribcage.) Adding to this the lengths of the bones of the wing, including the syncarpals, suggests a total length of about 240 cm from the body midline (about 227 cm comprising wing bones alone). This would suggest a total straight-line wingspan of about 480 cm, but it should be recalled that the wing bones were not laid out straight end to end in flight, so a more realistic estimate, based on the natural ranges of motion discussed

earlier, would be 15–30 cm less for each wing, depending on the mode of flight. For example, in flapping flight, midway through the downstroke, the effective wingspan would be ca. 440–450 cm.

## FUNCTIONAL MORPHOLOGY OF THE SKULL AND AXIAL COLUMN

In Figure 2, we reconstruct the skeleton of *Quetzalcoatlus* positioned for soaring flight, with several alternative configurations that reflect both the range of motion that appears to have been possible at individual joints and the uncertainties of how they used certain joints. Some reconstructions of particular regions and joints have been proposed by authors in the past (e.g., Frey and Riess, 1981; Bennett, 2001; Wilkinson et al., 2006; Wilkinson, 2008) and shown incorrect by others (e.g., Bennett, 2007). This obviates further discussion here. Where other possibilities remain open, we try to test them in the context of the movements of the entire animal, as far as they can be determined.

The principal functional questions about *Quetzalcoatlus* concern its feeding and locomotion, both in the air and on the ground. We discuss individual areas of the skeleton in these contexts and then summarize the complete picture of the animal in relation to these questions. Much has been written about the functional morphology and related behaviors of pterosaurs; we do not provide an exhaustive review of the literature but rather let the evidence of these specimens speak for itself, noting various hypotheses that may be supported or weakened by this evidence.

### Skull and Jaws

Kellner and Langston (1996) reviewed the basic anatomy of the skull and jaw material of *Quetzalcoatlus* based on four of the smaller specimens (no skull or neck material is preserved of the large holotype specimen of *Q. northropi*, but there is an unassociated cervical). In their model, the skull terminated posteriorly just behind the jaw joint. However, after the discovery of *Hatzegopteryx* (Buffetaut et al., 2002), Wann modified his model to reflect a more expanded occipital region, although this material is not known in *Quetzalcoatlus* (see Andres and Langston, 2021), to a length of about 109 cm. Our reconstruction, based on consultation with Brian Andres (see Andres and Langston, 2021), depicts a somewhat smaller crest (Fig. 1), but we stress that the anatomy is unknown.

The snout and the lower jaw are highly attenuated and toothless; Kellner and Langston (1996) reported that the snout ends in a narrow point with a slight distal dorsoventrally flattened expansion, based on the morphology of the anterior mandible. They estimated that the jaw could have opened to nearly a 52° gape, but it is unlikely to have needed to do so in order to trap prey. The skull was very narrow (the distance between the mandibular condyles is reconstructed at about 13 cm for a jaw some 95 cm long), and large prey could not have been consumed, nor could the toothless, attenuated jaws have torn flesh or bitten larger prey items (whether animal or vegetable) into smaller pieces (W. Langston, pers. comm., compared the ends of the attenuated jaws to ‘chopsticks’). Although it may not be impossible that these animals could have fed on carrion (cf. Lawson, 1975), the internal organs of the prey would first have had to be laid open by other animals. *Quetzalcoatlus* had no teeth, and its highly attenuated, almost delicate beak is not hooked as in raptors, so it appears virtually impossible that it could have ripped and torn fragments of organ or muscle from a carcass. A distinction can be made with the feeding habits of extant storks that scavenge carcasses: storks have relatively shorter, stouter, and stronger beaks that are not as attenuated. Storks usually scavenge in the company of vultures, whom they follow after the latter have torn into a carcass with their powerful, hooked beaks. Storks can tear flesh from a carcass once it is opened,

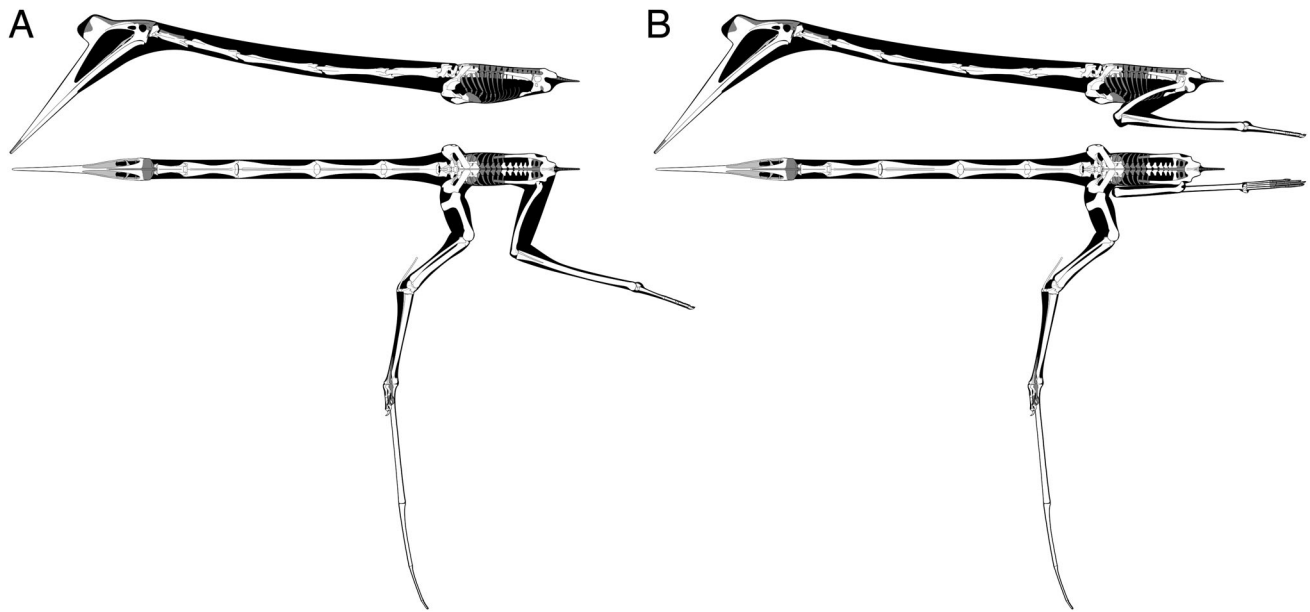


FIGURE 2. Two general models for the skeleton of pterosaurs in flight, in lateral (above) and dorsal (below) views. The main difference between models **A** and **B** is the position of the hind limbs: **A** characterizes the ‘bat-like’ and ‘aerodynamic tail’ models and **B** characterizes the ‘bird-like’ model. For explanation, see text.

but it is difficult for them to negotiate a thick-skinned carcass alone.

Several hypotheses of aquatic feeding for *Quetzalcoatlus* have been advanced over the years. Kellner and Langston (1996) discussed the possibility that *Quetzalcoatlus* was a fish eater. The potential gape of the jaws and the quadrate-articular joint, which as in other pterodactyloids facilitated a slight widening of the posterior mandibles as the jaws opened (Wellnhofer, 1978), suggested to them comparisons with birds that skim the surface of the waters in search of fishes and other near-surface prey. Their inference of a possible small gular pouch has not been substantiated by other lines of evidence, although not ruled out. Below we show that the neck vertebrae hypothetically appear to have been able to accommodate the motions needed for skim-feeding over water, although we do not support this idea for other reasons. First, it is important to delineate several kinds of water-feeding from the air. In skimming, the bird places the tip of its lower jaw in the water and flaps vigorously (with shallow amplitude) to combat drag as it plows along (see [www.youtube.com/watch?v=HJuT8jEZOIk](http://www.youtube.com/watch?v=HJuT8jEZOIk)). *Quetzalcoatlus* was far too large to flap with great frequency, based on size-related data for living birds and bats (Pennycuik, 1990; Norberg and Norberg, 2012). Dip-feeding, such as swallows and kingfishers do ([www.youtube.com/watch?v=ZIUodTbEDY](http://www.youtube.com/watch?v=ZIUodTbEDY)), is characterized by very rapid flight and plucking prey almost at random from near-surface waters, a physical impossibility for a large pterosaur. Plunge-diving, such as cormorants and pelicans do ([www.youtube.com/watch?v=6XSQzeNip8M](http://www.youtube.com/watch?v=6XSQzeNip8M)), would likely have broken the neck of an animal such as *Quetzalcoatlus*. And gulls usually land on the water as they feed ([www.youtube.com/watch?v=KRkAXtrfHj0](http://www.youtube.com/watch?v=KRkAXtrfHj0)), which would have been cumbersome for an animal such as *Quetzalcoatlus*, even if it lived near deep fresh water (it was not oceanic).

In place of these possibilities, we hypothesize that the long, attenuated jaws of the animal, reminiscent of those of a heron or stork, were used to pluck fishes, small tetrapods, and invertebrates from a subaerial or subaqueous substrate, while prowling shallow waters or meadows. Its neck could not curve to the

extent of that of a heron or stork (see below), so it would have been incapable of sudden predatory strikes from a coiled position. However, it would have been capable of both quick dorsoventral and sweeping lateral strikes (see below), and the neck was mobile enough to facilitate predation by holding the head and the neck nearly vertically to help in swallowing prey. Wann Langston had arrived at these conclusions by 1980 (pers. comm.), and they were suggested independently by Witton and Naish (2008).

There is no evidence for kinesis between any of the preserved articulations of the skull bones described by Kellner and Langston (1996). They could not detect sutures between any but two or three bones, and even these were indistinct. Given that individuals of this size were apparently not skeletal adults (which would have been marked by the near cessation of longitudinal growth of the long bones; Ricqlès et al., 2000), it appears that skull fusion may have preceded skeletal maturity. The lack of cranial kinesis, if valid, and the generally strut-like construction of the skull bones, suggests that *Quetzalcoatlus* did not masticate hard objects such as large mollusks or seeds, or objects that were unpredictably variable in their hard to soft texture. These facts and the narrowness and toothlessness of the skull suggest that the animals ingested small or soft prey, or slightly larger prey with a high aspect ratio such as fishes and small tetrapods that could have been reoriented in the mouth and swallowed without much processing, as herons and egrets do. The apparent ability of the neck and the head to be raised and oriented perpendicular to the ground and far above it (see below) suggests that the animals could have used gravity to assist swallowing.

The question of the orientation of the skull in flight is open. Witmer et al. (2003) described different orientations of the semicircular canals in the ears of pterodactyloids and basal pterosaurs. They correctly inferred that the differences reflect postures of the head on the neck. In basal pterosaurs, the neck entered the skull in a relatively posterior position, whereas in pterodactyloids the occipital condyles were more ventrally positioned (Wellnhofer, 1978). There remains the question of whether the orientation of these canals more closely reflected

flying behavior or terrestrial locomotion, both of which may have differed between pterodactyloids and basal pterosaurs, but this question is beyond the scope of the present work.

### Movements of the Neck

No material of the occipital region of the skull is preserved, and the posterior end of the skull is in general so incomplete and crushed that the orientation and mobility of the occipital condyle cannot be restored. The occipital condyle and therefore the atlas-axis were normally oriented approximately horizontally in basal pterosaurs; they were oriented at about 45–60° to the horizontal in pterodactyloids (Wellnhofer, 1970; Bennett, 2001a; Witton and Naish, 2008), and we assume that as in other pterosaurs the craniocervical joint in *Quetzalcoatlus* was a subovoid ball-and-socket joint that allowed some rotation, especially dorsoventrally.

Here, we provide estimates of ROM based on manipulation of contiguous cervical vertebrae. We caution, again, that ROMs that appear possible from manipulation of ‘dry bones’ may not have been realized by the animal (Hutson and Hutson, 2012). Kambic et al. (2017) usefully showed that ROMs in the wild turkey neck in three directions (dorsoventral, lateral, and rotational) vary regionally, although this is not reflected in vertebral morphology. They also showed that the zygapophyses allow more movement than traditionally estimated from bones alone, which may have implications for the reconstructions of ROM in fossil taxa, including *Quetzalcoatlus*. Here, we restrict our reconstructions to measurements that appear possible from simple manipulation of the vertebrae.

Wann Langston assembled and photographed a cervical series (minus the contribution of cartilage, which is likely to have been quite thin) in what he reconstructed as maximum ventral, dorsal, and lateral deflection on a rectilinear grid background, from which the approximate degrees of motion available at each cervical joint were determined (Fig. 3), and we have checked and re-analyzed this information. As Wann acknowledged, the cervical series was not from a single individual, although the bones appear to have been from individuals of similar size, so although imprecise, our estimates of motion do not appear unreasonable (see Table 3). As with other joints, we manipulated these bones until bony stops prevented further movement or articular surfaces separated from each other. In these respects, our estimates could err on the side of more or less movement than realistically possible (Taylor and Wedel, 2013), but given the generally tight fit of articulation, we expect that the error is not great. Figure 4 summarizes the reconstructed lateral movement possible for the

TABLE 3. Estimated dorsoventral flexion at the cervical joints of *Q. lawsoni*, estimated from manipulations of the bones and their casts alone.

Cervical vertebral joint	Maximum dorsal flexion	Maximum ventral flexion
2nd–3rd	5°	35°
3rd–4th	10°	15°
4th–5th	45°	20°
5th–6th	Indeterminate (est. 25°)	Indeterminate
6th–7th	30°	Insignificant
7th–8th	Insignificant	Insignificant
8th–9th	Insignificant	Insignificant
9th–notarium	Insignificant	Insignificant

neck, as well as a reconstruction of how it might have elevated the neck and head to swallow small prey.

We begin with the root of the neck, where it emerges from the torso. In what we would call ‘normal’ articulated position, in which contiguous joint surfaces of centra and zygapophyses most extensively overlap, the cervical vertebral series does not form a straight dorsoventral line. We describe these respective contiguous orientations and then discuss the apparent ranges of movement at each joint.

The 8th and 9th cervicals (e.g., TMM 42422-8 and TMM 42422-7, respectively) were free. Manipulation of the 9th cervical (TMM 42422-7) against two different notaria (fused anterior dorsal vertebrae: TMM 41954-60 and TMM 42246-3, shows that the articulation between these two bones was normally level with the notarium. The 8th vertebra is larger and longer than the 9th and has a tall, long neural spine that broadly anchored the dorsal neck muscles. There seems to have been little movement possible between the 8th and 9th cervicals, or between the 9th and the notarium, although their articular surfaces are dorsally flattened ovoids (about three times broader than high) that might have allowed some dorsoventral accommodation but very little laterally. The bases of the 8th and 9th cervicals are offset by 20°, so that the 8th pitches upward in normal articulation. Relative to the 8th cervical, if in horizontal position, the 7th is normally offset 20° ventrally, the 6th is offset 25° dorsal to the 7th, and the 5th was estimated by Wann Langston as offset at 25° dorsal to the 6th (however, the articulations here are poorly preserved, so this was an estimate based on adjacent joints). If the 9th vertebra was oriented parallel to the horizontal (or the notarium with which it articulated), as it seems, the 8th would have faced slightly dorsally (about 20°) and the 7th would have been

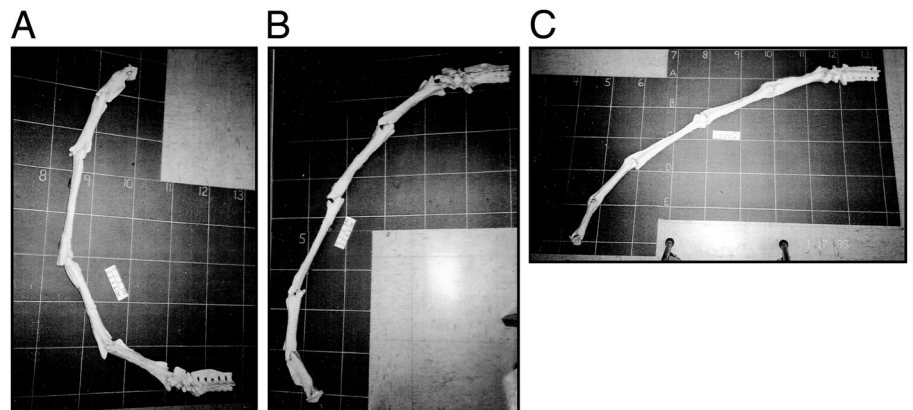


FIGURE 3. Photographs taken by Wann Langston of CVs 3–7 in **A**, dorsal, **B**, lateral, and **C**, ventral deflections, assembled from several specimens. Scale bars in inches and cm.

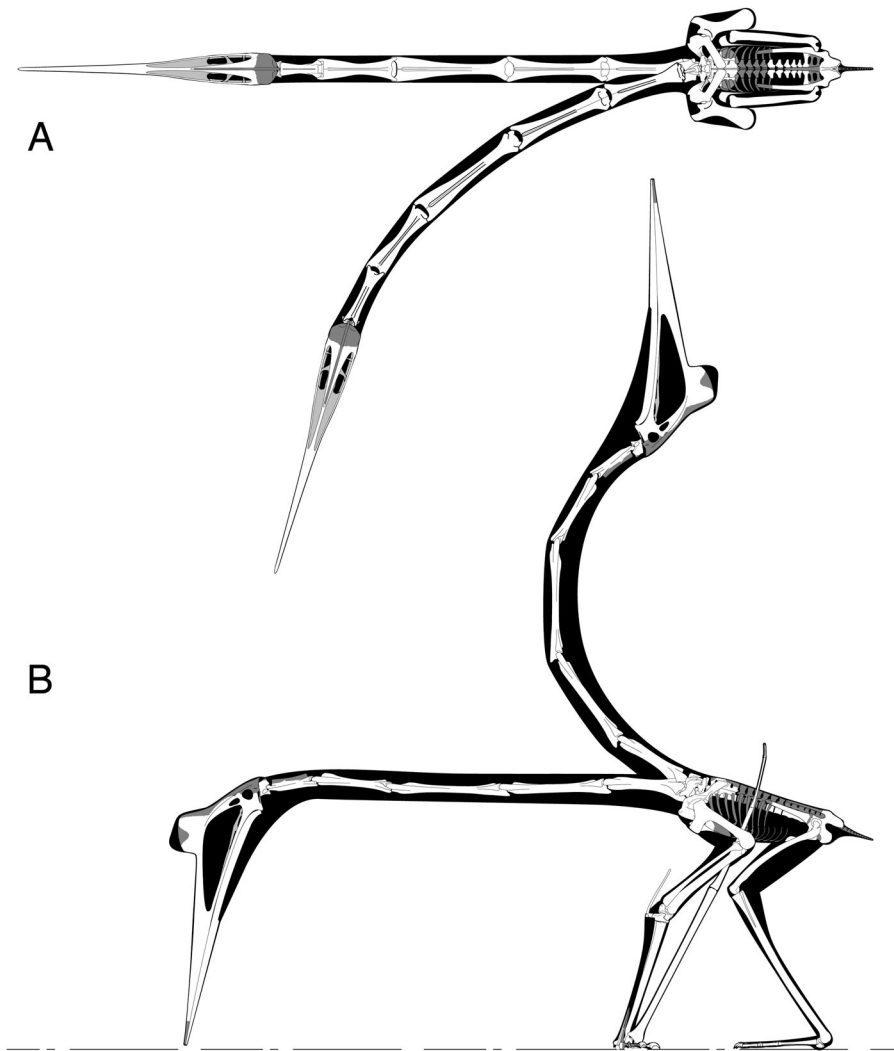


FIGURE 4. *Quetzalcoatlus* reconstructed on land. **A**, in dorsal view with reconstructed maximum lateral motions of the cervical vertebrae; **B**, in lateral view with the neck and skull elevated in the act of swallowing small prey. The neck and the head could be depressed far lower than ground level. For explanation, see text.

oriented about  $20^\circ$  ventral to that (i.e., horizontally), thereby canceling the orientation of the vertebra behind it. The dorsal offset of the 7th and 8th cervicals would have had the effect of mitigating the horizontal compressive load of the neck on the dorsal column by increasing the offset between the dorsal tendons and the cervical vertebrae.

It appears from articulation of the cervical column that in flight the neck was slightly bowed dorsoventrally in a mild 'S'-curve as shown in Figure 2. To accomplish this, the root of the neck was oriented slightly anterodorsally: then, moving cranially, the vertebrae inclined slightly ventrally and leveled out by the 6th vertebra. We hypothesize that when air struck the base of the neck where the vertebrae begin to curve upward, the airflow would have been divided along the left and right sides of the neck to create twin counter-rotating turbinal vortices on the dorsal side of the neck posterior to this point, with the top sides of the vortices rotating medially. This would have formed an area of low pressure above the neck vertebrae, creating lift on these regions of the neck that reduced the weight of the neck and head applied to the body. The best example of this mechanism among living birds is the swan (Fig. 5), which has a very long neck that is extended directly forward and also uses this mild 'S'-curve, although in the swan the inflection point in the neck

is slightly more anterior. A neck is not necessary for this mechanism. Dirigibles do this by the anterior canting upward of their fuselage: twin counter-rotating vortices resulting from forward velocity create lift atop the dirigible and help support its weight (Munk, 1979). We draw this upward-canting analogy to the dorsally directed posterior cervical vertebrae of *Quetzalcoatlus*.

The maximum dorsal and ventral ranges of motion possible at the joints between the 2nd cervical vertebrae and the notarium, as we have reconstructed them, are summarized in Table 3.

Lateral movement of the neck was limited from joint to joint, because the ball-and-socket joints of the centra were dorsoventrally compressed to produce an ovoid cross-section that delivered more dorsoventral than lateral movement. Lateral movement was also restricted by the zygapophyses. Based on Wann Langston's reconstructions (Fig. 3), which we reassessed for accuracy (and estimating the incomplete articulation between the 5th and 6th vertebrae), the lateral flexion of the neck from its base until the articulation between the 3rd and 2nd cervicals totaled about  $65\text{--}70^\circ$ . This implies that, even if the occipital condyle could only rotate  $20^\circ$  on the atlas-axis complex, the animal would have been capable of  $180^\circ$  mobility left to right between the skull and the torso. Given that, as in other pterosaurs (Witmer et al., 2003), and based on Wann



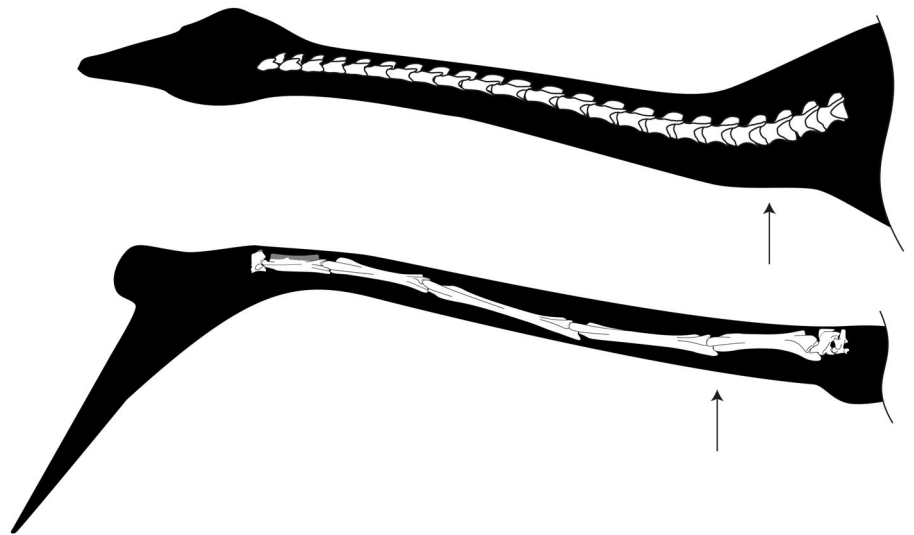


FIGURE 5. Swan in flight with slight dorsoventral 'S'-shaped curvature in the posterior cervical vertebrae (arrows). A similar configuration is proposed for *Quetzalcoatlus*; see text for explanation.

Langston's reconstruction of the available bones of the skull, its eyes were positioned so that it could see directly laterally as well as forward (stereoscopically); when it turned its neck and head, it would have had a 180° field of vision in both directions.

In the air during soaring flight, significant dorsal movement of the neck was not likely: elevation of the neck and head on the torso would be associated with a pitching up of the torso and a consequent slowing of speed, at worst possibly including a sudden stall. There are no compelling aerodynamic reasons to do this, because deceleration is possible without pitching the neck upward; only a sudden unexpected need to avoid an obstacle in flight might cause this motion.

Lateral movement of the neck is associated with yaw (an uncoordinated rotation of the animal to the left or right, not necessarily associated with a turn); a large, tall skull presents a surface on which considerable aerodynamic forces could build. If a lateral gust of wind were to strike the soaring animal, the head and neck could have been rotated in the opposite direction of the yaw (i.e., into the wind), so as to minimize the upset force. Bramwell and Whitfield (1974) hypothesized that to make a turn, *Pteranodon* had only to look in the direction in which it wanted to go, and drag on the skull and its crest would perform the turn. It seems more likely that those motions would have been initiated by differential movements of the wings and (or) by asymmetrical positioning of the hind limbs, as in birds and bats. In such a case, the animal could move the neck laterally but turn the head either medially or laterally to help maintain a coordinated turn.

As to ventral movement, at least hypothetically the neck and the mandible could have been lowered in order to pluck or skip-skim (low-altitude flight with the lower mandible intermittently dipped into the water for a few meters at a time) for fish near the surface of the water, although we think this habit unlikely for reasons discussed above. If it were feeding in flight or flying over the surface of water or land for another reason, it would have needed a safety mechanism for the head and the mandible in case of a sudden encounter with an obstacle on the surface. The mobility of the cervical articulations suggests that it would have been possible for the animal to recover, because the head can deflect downward more than perpendicular to the torso (i.e., about 20° posterior to the vertical); the stresses could be mitigated through the various cervical joints. The downward deflection of the neck also would have had the effect of sweeping the wings forward so as to move the center of lift forward, pitch

the animal up, and temporarily increase lift for altitude recovery. However, given that *Quetzalcoatlus* is found some 400 km from the nearest paleoseashore (Langston, 1981), nearshore trawling would seem to have been unlikely.

In soaring flight, if the neck and head yawed slightly, aerodynamic forces on the neck and head would tend to increase the degree of yaw, which the animal would have to counter actively by turning its head away from that direction of rotation. If the neck is elevated slightly, the counter-rotating vortices over the neck will tend to raise the head and neck, which pitches the animal upward, and the increased velocity of the air over the body (through lowered pressure above the neck and the torso) will cause the entire torso to gain elevation. Deceleration will also occur. If the neck is moderately lowered, the opposite effect occurs: the head, the neck, and the torso pitch downward, and the torso loses elevation.

### Structure and Movements of the Postcervical Axial Column

Virtually nothing is preserved of the postcervical vertebrae or of the pelvic girdle except two notarial regions and fragments of two others, a partly preserved right prepubis, a partly preserved spinal segment, and a nearly complete but partially crushed left pelvic girdle. The notaria provide important information about the articulation of the shoulder girdle and the orientation of the wing; however, pelvic remnants are too incomplete to facilitate an accurate reconstruction of the pelvis.

Bennett (2001a) reasoned that the elements recognized as the 8th and 9th cervicals in *Pteranodon* and some other pterodactyls are likely cervicalized dorsal vertebrae; that there are 12 other dorsals and six sacrals in *Pteranodon*, although more posterior dorsals can be incorporated into the sacrum and the notarium can have four to six vertebrae; and that this can vary individually and ontogenetically. That would provide a total of 18 dorsal and sacral vertebrae in one form or another. The regionalizations of vertebrae in several pterosaurs, including reconstructions for *Quetzalcoatlus*, are compared in Table 2.

In *Quetzalcoatlus*, the first four dorsal vertebrae are fused into a notarium (Fig. 6). The 9th cervical vertebra articulates freely with the notarium as noted above, but motion is limited. In TMM 41954-60, the neural arches are low and incomplete to some degree, so no information about the articulation of the scapula is preserved. However, in TMM 42246-3, the three posterior spines are better preserved. They connect with each other dorsally, forming

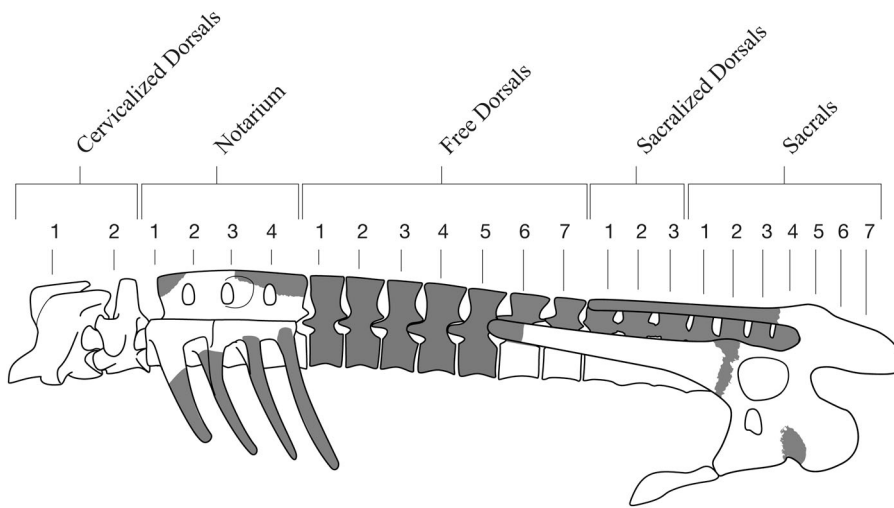


FIGURE 6. The dorsal vertebral column of *Quetzalcoatlus*, including the first two cervicalized dorsals, the notarium (four fused dorsals), the 7 free dorsals (by comparison with other pterodactyls), and the sacrum of seven vertebrae, including three sacralized dorsals. No caudal vertebrae are preserved.

rounded windows beneath the connections. On both lateral sides of the third neural spine is a long, nearly ellipsoidal depression that is angled ca. 25° anterodorsally. This corresponds in shape to the articular end of the scapula and also defines its orientation with respect to the sternum, which can be located in its natural position by articulating both scapulocoracoids in the notarial sockets and causing them to meet anteroventrally in close tandem at the junction of the articular ends of the coracoids.

Wann Langston reconstructed an articulated dorsal and pelvic region formed partly from casts of actual bones (including TMM 41954-57), partly from sculpted features taken from a composite of variably preserved specimens, and partly from sculptures of other pterosaurs that preserved bones that are not preserved in *Quetzalcoatlus* (Fig. 7). By his reconstruction, there would have been two more dorsals incorporated posteriorly into the fused notarium (which is not correct: there are only four), four free dorsals (which are not preserved), and eight sacral vertebrae (we can confirm only seven), of which the posterior five (we

can find evidence for only four) would have had sacral ribs and transverse processes fused to the ilium. This model was constructed partly by comparison with other large pterodactyls; some elements are not preserved in *Quetzalcoatlus*. Of course, the degree of fusion and the incorporation of vertebrae may have varied with size and ontogeny. No caudal vertebrae of *Quetzalcoatlus* are known.

Only one specimen representing a portion of the postnotarial axial column is preserved (TMM 41954-57). It includes the left pelvis, nearly complete, the last four presacral vertebrae (one free, three sacralized), and a displaced transverse process of a (likely the first) sacral vertebra (Fig. 8), plus a right prepubis (TMM 41954-58). The specimen has been crushed so that the anterior prong of the ilium has been displaced ventrally, and it now lies ventral to the level of the acetabulum, to which it would normally be horizontal and perhaps slightly deflected dorsally at its anterior end. Its natural position is now occupied by the displaced transverse process. The prong of the ilium would have



FIGURE 7. Inset, the scaffolding of Wann Langston's reconstruction of the postcranial skeleton of *Quetzalcoatlus*, held in place by strings, wooden support, and clay. This model allowed manipulation and release of skeletal elements, such as most of the dorsal vertebral column in this photo, taken in 2017; it is now disassembled. Wann Langston reconstructed bones by comparison among preserved elements in different specimens. Photo courtesy of Gary Staab. **B**, Wann Langston, ca. 1985, with a similar mount of the wing skeleton. Photo courtesy of Matthew Brown.

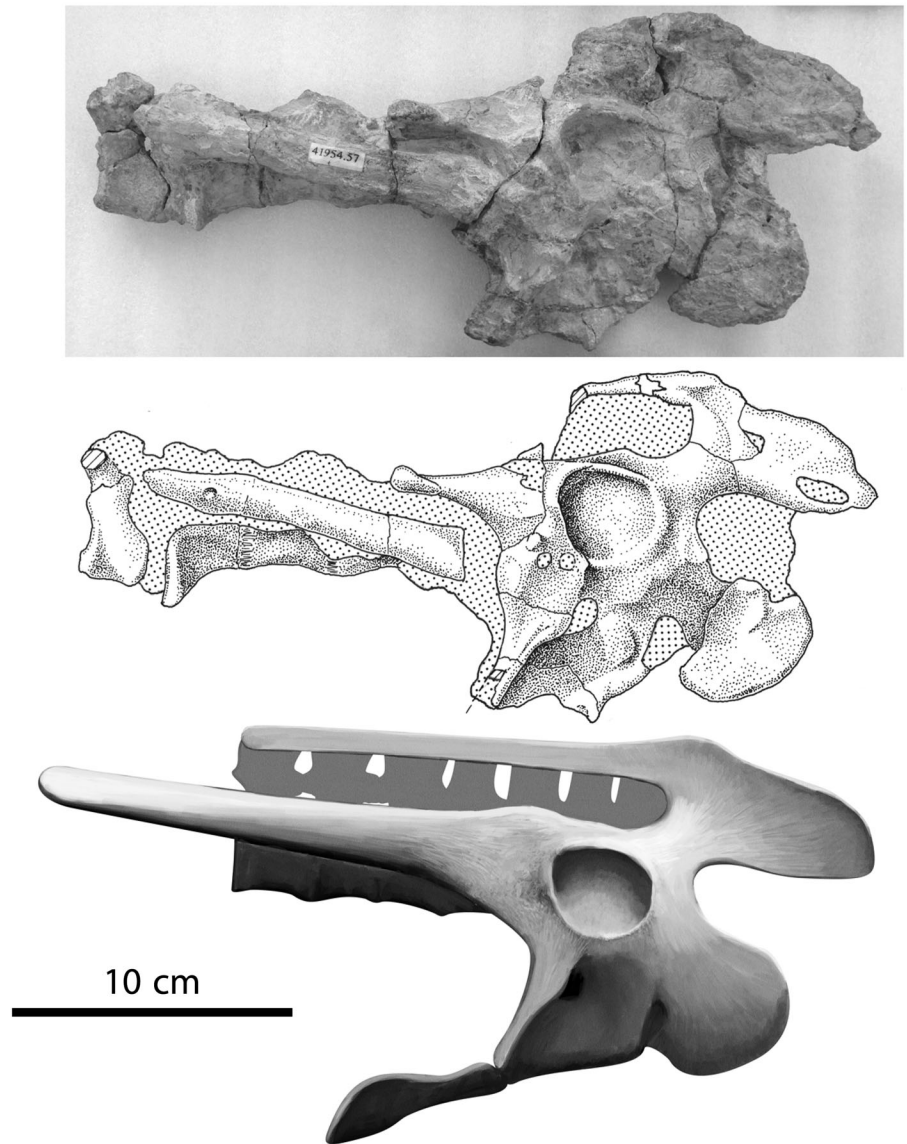


FIGURE 8. The pelvis of *Quetzalcoatlus* (TMM 41954-57). **A**, photograph in left lateral view; **B**, drawing of the same; **C**, reconstruction of the pelvis after Wann Langston's comparisons with other pterodactyloids.

extended anteriorly to the length of three vertebrae in front of the four basal sacral vertebrae. The neural spines are almost entirely obscured by matrix or abraded away, and there is no trace of a supraneural plate. The vertebrae are only clearly seen in ventral view, and these are limited to the last four presacrals, of which only the last two vertebrae are clearly fused to each other. The first and the second of these four (the last free dorsal and the first sacralized dorsal) are not fused to each other, and the contact between the first and second sacralized dorsals is obscured by a break with a thin separator of matrix. This fact suggests that the first and second sacralized dorsals were not fused, or at least not fused at this ontogenetic stage; unfortunately, the sacral ribs that could indicate fusion are not visible. The sacrals are obscured by matrix except for most of the right lateral edge of the transverse process of the first of the four sacrals.

Given the preceding considerations, movement in the postcervical column mainly would have taken place posterior to the notarial vertebrae and anterior to the sacrum, including the sacralized dorsal vertebrae. The heights of the dorsal centra, even allowing for lateral crushing, judging from the last free dorsal

associated with the pelvis of TMM 41954-57, are approximately twice their widths, and including the spine the height was about four times the width. This would suggest that lateral flexion may have been more possible than dorsoventral flexion, a mobility that is not desirable in the air but may have been useful on the ground. This is a very different situation from the saddle-shaped dorsosacral joint in the Jurassic pterodactyloid *Mesadactylus* (Jensen and Padian, 1989), which has a strongly procoelous, laterally ellipsoid anterior facet to the first sacral centrum that would have permitted considerable dorsoventral motion.

#### FUNCTIONAL MORPHOLOGY OF THE PECTORAL GIRDLE AND FORELIMB

##### Articulation and Mobility of the Shoulder Girdle

The motion of the pectoral girdle depends on understanding the rotation of the scapular end against the vertebral column, the articulation of the end of the coracoids against the sternum, and the structure and possible movement of the sternum (Fig. 9).

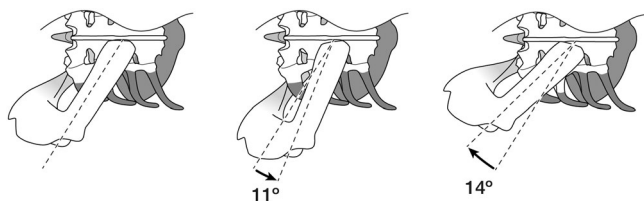


FIGURE 9. Reconstruction of the articulation of the left scapulocoracoid with the notarium and the sternum in dorsal view, showing anteroventral–posterodorsal rotation possible to ca. 25°. Hypothesized resting position is shown on the left.

**Articulation of the Scapula against the Notarium**—In one of the best-preserved specimens, TMM 42422-25, the articular end of the left scapula is a dorsally flattened, ventrally rounded ellipse. The long axis of the ellipse, if oriented parallel to the long axis of the scapular fovea (with the spinal column approximately horizontal in flight), situates the articulation of the coracoid with the sternum ca. 25° anterior to the articulation of the scapula with the notarium (see above).

**Articulation of the Coracoid against the Sternum**—The articular end of the coracoid is a ‘U’-shaped, concave-convex surface that fits snugly against the convex base of the cristospine. The bases of the left and right coracoids overlap the midline of the cristospine, and the right coracoid articulates in front of the left one. (This feature is common to several pterosaurs including *Campylognathoides*, *Rhamphorhynchus*, and *Pteranodon*, but the facets may be symmetrical in others: Wellnhofer, 1978; Padian, 2008b.) The axes of the articular surfaces on the sternum are not perpendicular to the sagittal plane but are oriented so that the proximal end is ca. 45° anterior to the distal end. In the same way, the longitudinal axes of the articular ends of the coracoid and the scapula are offset by 45°.

Specimen TMM 42180-12 preserves a good cristospine and much of the sternal plate. The cristospine is about 5 cm long, and it widens to nearly 3 cm posteriorly at its base. The sternal plate is about 6 cm long at the midline and about 5.25 cm at its widest preserved edge. On a similar specimen (TMM 42422-29), more poorly preserved, the plate widens to 7.5 cm. The sternal plate does not seem to have widened sharply at the base of the cristospine as reconstructed for *Pteranodon* but is tapered more as in *Nyctosaurus* (see Wellnhofer, 1978:abb. 8). This can be confirmed in dorsal view, where the edges of the plate are sharply defined. The sternal plate thins to 1–1.5 mm along its preserved posterolateral edges, and it seems unlikely that it would have been calcified much farther posteriorly. There appear to be articular prominences on the preserved edge of the left side of TMM 42422-29, suggesting the attachment points of up to four sternal ribs, but this is difficult to confirm. Both specimens preserve diagonal articular facets, oriented in tandem, for the coracoids on the dorsal side of the base of the cristospine; in both, the facet for the right coracoid is anterior to the left one, as in other pterosaurs (Wellnhofer, 1978; Padian, 2008a, 2008b). A third specimen, TMM 42138-1.5, is poorly preserved and provides little new information.

**Motions of the Scapula against the Notarium and of the Coracoid against the Sternum**—The effect of the orientations just described is that the scapula can rock fore and aft slightly against the notarium, and the coracoid can do the same against the sternum (we estimate about 10°, limited by the surrounding muscle and other tissue; this would increase the fore-aft excursion of the distal end of the humerus by 3.5 cm in a specimen of the size of TMM 42422-25). This possibility of motion would have been able to dampen accelerational forces at the wing root by distributing them more gradually to the axial column. It may also have

allowed a fore-and-aft muscular-powered displacement of the scapulocoracoid that would have enhanced wing sweep, downstroke lift and thrust production, and launch power. This may have had implications for breathing during flight, but any inferences on that subject would be speculative (particularly given the apparent limits of dorsoventral flexion at the dorsosacral joint discussed above; an accessory hepatic piston mechanism like that of crocodiles may have been plausible, but this question is outside our present scope). Conversely, if the sternum remained stationary, the glenoid would move fore and aft at an angle of about 25° anterodorsal and posteroventral to the horizontal, because the sternal articulation is ca. 25° anterior to the notarial articulation. Bennett (2001b) hypothesized three ranges of motion linking the notarium and the sternum through the scapulocoracoid, but we suspect that in *Quetzalcoatlus* the scapulocoracoid would have had less fore-aft mobility than Bennett reconstructed for *Pteranodon*, because the articulation with the notarium is not round but subrectangular, oriented anterodorsally–posteroventrally at ca. 25°.

The ‘swing’ or sweep rotation (the position of the wings relatively fore and aft of what would be ‘normal’ position, most relevant to fixed-wing soaring animals; Anderson, 1997) would be anterodorsal during the downstroke and posteroventral during the upstroke, because thrust production during the downstroke would cause forward rotation, whereas drag on the wings would cause posterior rotation during the upstroke (Rayner, 1979). This swing effect could also be enhanced or ameliorated by muscle power while soaring, flapping, or launching. Combined with an offsetting humerus sweep in the opposite direction, it allows pitch command authority without altering the sweep or angle of attack of the wing, which has a profound effect on flight stability. Retracting the scapulocoracoid while protracting the humerus by the same angular deflection increases pitch stability. This motion of the scapulocoracoid influences the position of every bone distal to the shoulder.

### Movements of the Wing Bones in Flight

Apart from some possibility of rotation during pitch at several joints (mainly the shoulder and carpometacarpal joints), plus the ability to flex and rotate passively to absorb the forces of flight, two of the major joints of the wing (elbow and metacarpophalangeal) are essentially hinge-like. The humerus is the most complex segment of the wing because it can both rotate in pitch and depress and elevate and can use combinations of these movements. And because it is anchored at the root of the wing, its motions automatically influence the positions of every other bone of the wing.

**The Shoulder Joint**—Based on the right limb of TMM 42138-1, the humerus could have rotated in the glenoid about 40°, elevated about 45°, and depressed about 25–35°, depending on the fore-to-aft position of the humerus in the glenoid (Fig. 10). The deltopectoral crest forms the camber line of the leading edge of the root of the wing. (The camber line is the curve that is halfway between the upper and lower surfaces of the airfoil.) We hypothesize that in soaring flight, in order to form and fall within the camber of the wing, the humerus would have been oriented with its distal end about 20° above the horizontal and the radius and the ulna would have been oriented with their distal ends ca. 15° below the horizontal. The angle between the humerus and the forearm in dorsal view would have been about 115° (Fig. 10). These estimates are subject to continuous slight variation in flight, according to gust conditions and adjustments for pitch and yaw.

The humerus has considerable mobility, as described above, but in lateral orientation it cannot be directed more than 3–5° anterior of the shoulder before hitting a hard stop. When it reaches this hard stop, the vertical mobility is limited to about

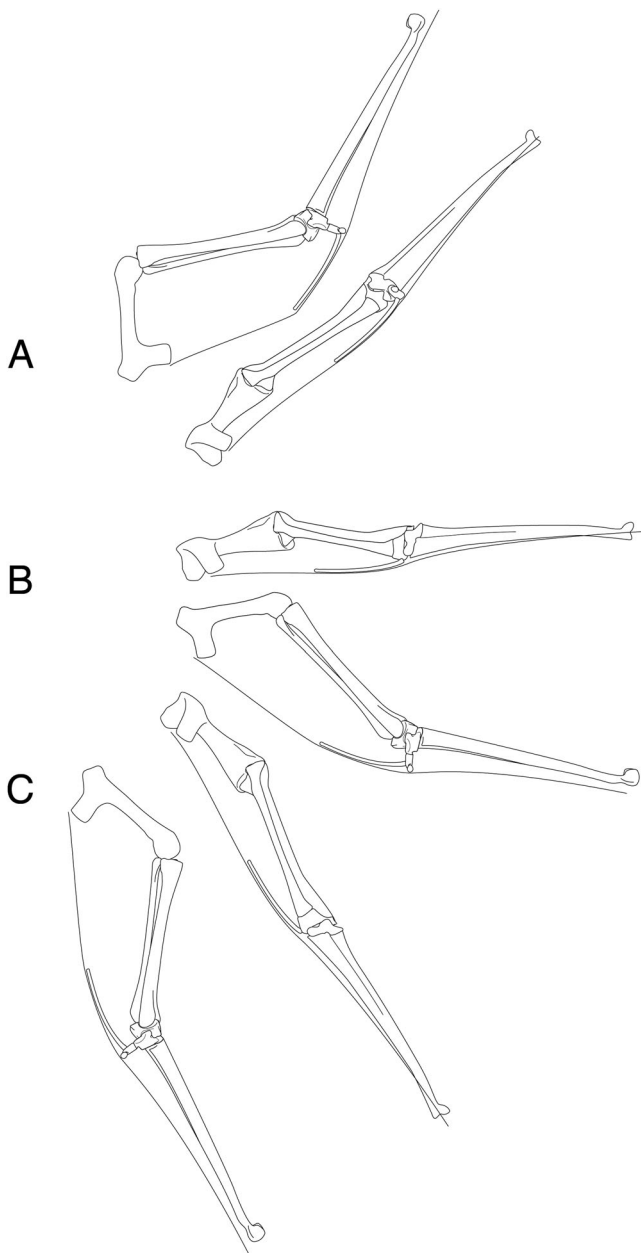


FIGURE 10. Illustrations of the inner wing (humerus to metacarpophalangeal joint). **A**, at the top of the upstroke in dorsal and anterior views; **B**, at the middle of the downstroke in anterior and dorsal views; **C**, at the bottom of the downstroke in anterior and dorsal views.

5° above the horizontal and about 10° below it. This poses certain limitations for the role of the shoulder joint in both flight and terrestrial progression, because when the humerus is fully rotated forward (pronated) in this position, the motion capable of protraction and retraction is no more than 40–45°. When the humerus is oriented approximately laterally, it can be elevated above the horizontal about 35°. As noted above, it would likely not be so elevated during flight, but during terrestrial progression or crouching before a quadrupedal liftoff, this mobility may have been useful. The humerus could not be retracted much past the vertical plane that runs through both glenoids in this position, or the posterior tuberosity would have encountered the musculature of the coracoids. In laterally oriented position, however, the

humerus could rotate forward, and this suggests its role in terrestrial progression.

**The Elbow and the Wrist**—The radius and the ulna are restricted from rotation against the humerus and the proximal syncarpal by the tight configuration of the joints at each end. The elbow is almost exclusively capable of flexion and extension. The maximum flexion of the elbow forms an angle of not more than 90° between the humerus and the forearm, and it can be extended to 160° (interior angle). When the elbow is flexed typically for flight, it forms a deflection angle of ca. 50° with the radius and the ulna (i.e., the angle between the humerus and the forearm anteriorly is 130°). This flexion has the effect of displacing the radius distally so that its distal end extends lateral to that of the ulna, offsetting the joint with the proximal syncarpal by ca. 50°. Because there is no required variation in the range of articulation between the two syncarpals (i.e., it is a direct pass-through of orientation unless an active motion between the syncarpals overrules it), the metacarpal is accordingly rotated posteriorly ca. 50° (Padian, 1983b). These are maximum estimates of motion that may not have been frequently actualized.

The effect of this linkage is as follows (Bramwell and Whitfield, 1974; Padian, 1983b). For every degree of flexion of the elbow (approximately), the metacarpus flexes posteriorly to the same degree. If the wing begins in an extended position and the elbow is flexed 15°, the carpometacarpal joint will flex correspondingly and so maintain its position with respect to the orientation of the leading edge of the wing. Therefore, this motion has the effect of shortening the wingspan without substantially distorting the wing planform. This allows the camber to increase as the spanwise tension is reduced and also produces lift even when the angle of attack of the wing is zero. The two effects combine to increase the lift coefficient. As long as the wing area is not substantially changed, the wing will at first rise when span is reduced. However, continued shortening of the wing will cause tension in the wing membrane to fall and eventually initiate flutter (a nonlinear effect) (Johnston, 1997).

Without this linkage, flexing the elbow would move the entire distal wing forward, causing an upward pitch, and extending the elbow would move the distal wing backward and cause downward pitch.

In pterosaurs, the proximal and distal rows of carpals are each fused into single syncarpals (the proximal [PS] and distal [DS] syncarpals), with the addition of a medial distal carpal, an associated sesamoid bone, and a pteroid bone (Figs. 11, 12; Wellnhofer, 1978; Bennett, 2001a). The linkage described above causes the proximal syncarpal (PS) to rotate posteriorly, parallel to the local camber line, without changing its dorsoventral orientation. This maintains the camber line and does not change the angle of attack of the wing, nor does it significantly change the center of lift. If the humerus is not moved while the elbow is flexed, the leading edge will be brought forward as the wing shortens, moving the center of lift forward. If the humerus is retracted as the elbow is flexed, the center of lift will not change, although the wing will shorten (Fig. 13).

The morphology of the articular surfaces explains why this motion is possible and virtually all other motions are not (Fig. 11). The distal articular surface of the ulna in flight comprises a vertically elongated, dorsally convex, comma-shaped condyle that fits snugly into a corresponding depression in the proximal side of the PS. On its ventral end is a rounded depression that receives a corresponding rounded prominence from the PS. The bones cannot rotate on this rounded surface (pronate or supinate) because the dorsal end of the ulna is bounded by bony borders on the anterior, dorsal, and posterodorsal sides of the PS. Therefore, this joint cannot actuate any change in pitch. The linkage described above is parallel to the camber line and is best described as a posterior flexing of this joint complex.

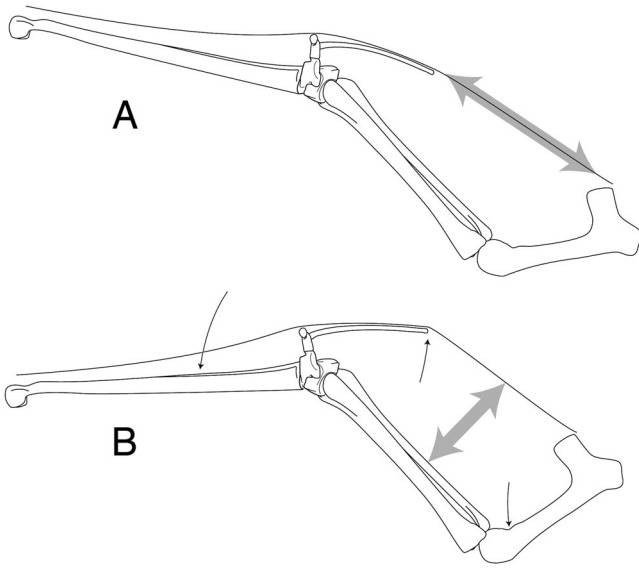


FIGURE 11. The wrist-sesamoid-pteroid complex, in two positions. **A**, typical soaring flight; **B**, during wing upstroke.

The joint of the radius with the PS is a vertically elongated, nearly ellipsoid concave-convex articulation that is slightly narrowed ventrally toward the edge of the PS. The convex surface of this joint on the PS has well-bounded edges that restrict all movement apart from the linkage described above.

**Articulations of the Wrist and the Metacarpus**—The faces of the PS and the DS (distal syncarpal) are complex, partly because they perform several functions and partly because they each represent the fusion of originally separate carpals. The morphology of these bones remained remarkably conservative since the first known pterosaurs (Padian, 1983a, 1983b; Padian and Wild, 1992; Padian, 2008a, 2008b). The distal face of the PS mainly comprises two nearly semiellipsoid concave surfaces, the longitudinal axes of which are offset by about 25°. The corresponding proximal surface of the DS comprises convex longitudinal ridges that match the depressions in the DS. Dorsal rotation (supination) of the DS against the PS is restricted by the dorsal prominence of the PS, which locks the DS by means of a ‘V’-shaped configuration.

Some authors have suggested that the intersyncarpal joint was fixed in pterosaurs (see Bennett, 2001b, and references therein). However, Bennett (2003) reports scarring in arthritic specimens of *Pteranodon*, which suggests that this joint is indeed mobile. The motion of the joint in *Quetzalcoatlus* is similar to that described by Wilkinson et al. (2006) for *Anhanguera*; retraction

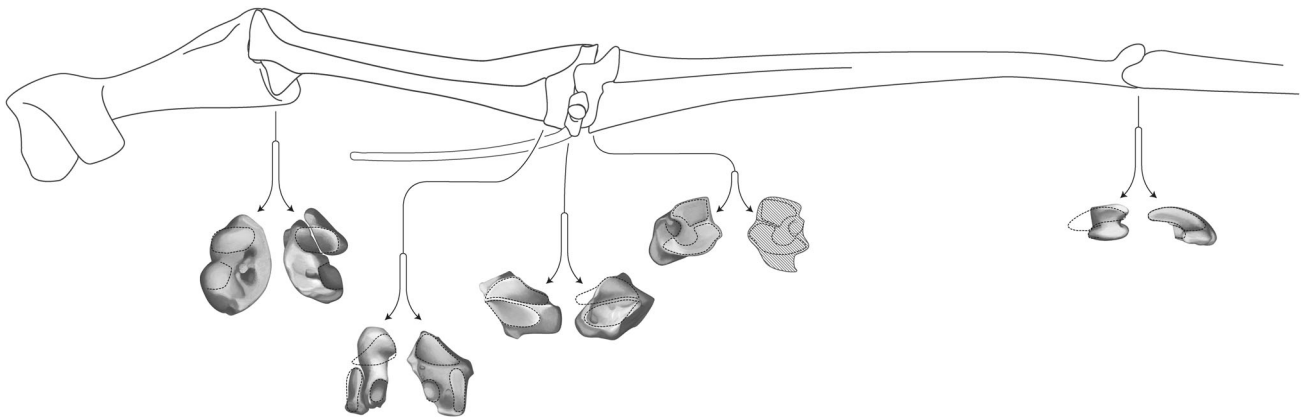


FIGURE 12. Articular surfaces of the wrist area, from the distal ends of the radius and the ulna to the proximal end of the wing metacarpal.

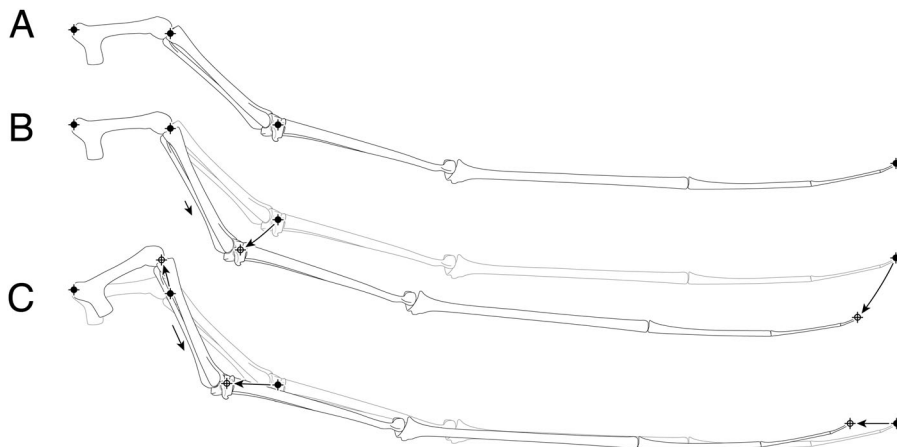


FIGURE 13. The functional linkage of flexion and extension of the elbow and wrist joint in dorsal views. **A**, the extended wing. **B**, flexion of the elbow with concomitant flexion of the wrist, showing fixed humerus and protraction of the wing's leading edge. **C**, the same but with retraction of the humerus as the elbow flexes, showing shortening of the wing.

also depresses the outer wing slightly, by shifting the distal syncarpal posteroventrally with a sliding corkscrew motion. Bennett (2001b) suggests that at least 25° of angulation was possible in *Pteranodon*, Unwin (1988a) suggests 30° for *Dimorphodon*, and Wilkinson et al. (2006) give 25° for *Anhanguera*. The intersyncarpal joint in *Quetzalcoatlus* appears to be capable of a larger degree of angulation than described for other pterosaurs and can be moved through an arc of 65–70° without disarticulating the joint. It is doubtful that such a large range of motion was needed in flight, and although such motion may have been useful in terrestrial locomotion or launch, it is not clear how much would be possible in life (Figs. 10–12, 14).

Such a large range of motion, even if substantially restricted by soft tissues, would suggest that this joint was actively controlled (Unwin, 1988a; Bennett, 2001b; Wilkinson et al., 2006). Partial retraction of the wing in flight would cause substantial anterior rotational force by moving the center of lift posteriorly, and we hypothesize that the highly buttressed structure of the intersyncarpal joint resisted torsion within the joint itself and passed this force onto the inner wing.

In normal soaring orientation, the axis of the articulation of the radius with the PS is sloped anteroventrally about 30°. The pronation has the effect of swinging the metacarpus fore and aft along the camber line (Figs. 10–12).

The articulation between the DS and the wing metacarpal (fourth metacarpal or MC IV) cannot be precisely reconstructed in *Quetzalcoatlus*. There is not a well-preserved proximal end of the metacarpus in the collection of Big Bend pterosaur material. Inferences of joint mobility must be inferred from the distal face of the DS and from comparative material of the MC IVs of other pterosaurs. The distal face of the DS has three major articular surfaces. Anteriorly and slightly dorsally is a round socket; posterior to this on the dorsal side is a depressed quadrangular flat surface separated from the round socket by a narrow strip of bone elevated above both these areas. This strip continues ventrally and broadens into a nearly semicircular flat surface that also stands out in relief from the previous two surfaces. In soaring flight position, the round socket would have occupied an anterodorsal position. In theory, the metacarpus could have rotated to some degree on the round prominence that articulated with the

round socket on the DS, but it could only have done so for 15–20° of pronation, being restricted from supination by the edge of the flat surface that is situated ventral to the others. However, these hypotheses appear to be contradicted by the complete fusion, or at least extremely tight appression, of the DS with MC IV in the holotype of *Q. northropi*. This fusion does not appear to be the result of pathology, injury, or postmortem taphonomy. It certainly suggests that the animal could fly with no mobility at this joint, and perhaps that it ordinarily had none. If so, it could be that the degree of motion that has traditionally been reconstructed at this joint (Bramwell and Whitfield, 1974; Bennett, 2001b) may have reflected a safety factor in soaring that reduced the outboard angle of attack in response to load stresses from gusting winds, and that also actively modulated the outboard angle of attack during flapping. Or it may have been related to terrestrial locomotion.

It has not been broadly appreciated that the distal 20% of the fourth (main) metacarpal shaft is bent ventrally relative to the more proximal part of the shaft by about 18–20°. This bend occurs at a point that maximizes the ventral rate of curvature in the leading edge of the wing at about 45% of the semispan. That is to say, this is the point of the leading edge, viewed anteriorly, at which maximum rate of ventral curvature occurs. This curvature, we hypothesize, minimizes washout in the outer wing (tailoring the spanwise lift distribution so as to reduce the risk of wing tip stall) by reducing the spanwise progression of passive pronation in the outer wing membrane caused by lift and torsion along the outer wing. If the membrane were rectangular and carrying a uniform load and were supported only at the ends, it would produce a catenary curve (a curve formed by how a chain, a rope, or a wire hangs between two points). The point of maximum spanwise curvature would occur at midspan, or 50% of the semispan. However, the pterosaur wing membrane is approximately triangular and is supported at the wing root and along the leading edge by the wing spar. Hence, the curve is not a catenary, although somewhat similar: the point of maximum inflection for a triangular membrane would occur medially at ca. 42% of the semispan if not flapping (Johnston, 1997). The stronger the flight stroke, the farther laterally the inflection point will move. In a *Quetzalcoatlus* in typical flight configuration,

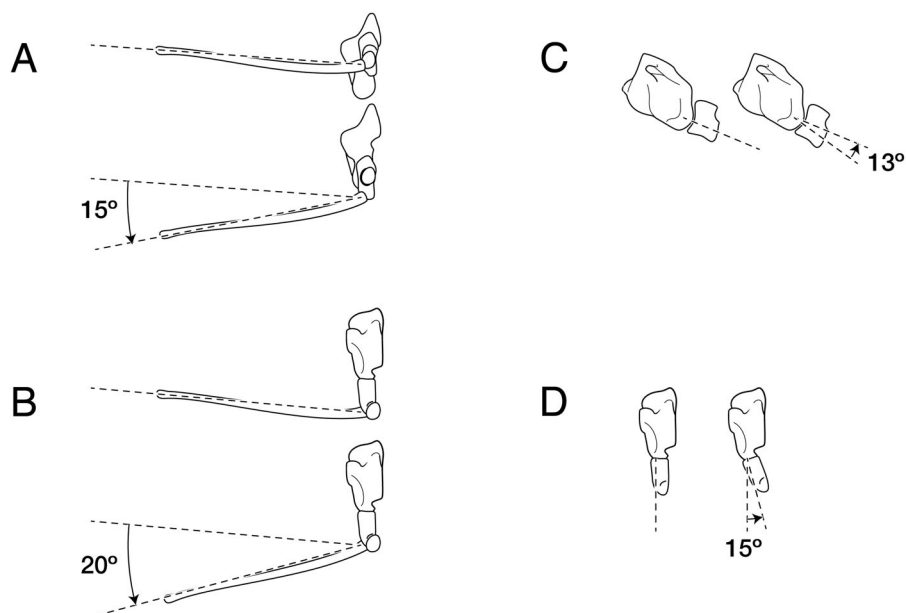


FIGURE 14. Reconstructed approximate ranges of motion of the medial distal carpal and pteroid. **A**, pteroid movement in anterior view. **B**, pteroid movement in dorsal view. **C**, medial carpal movement in proximal view. **D**, medial carpal movement in dorsal view.

the point of maximum inflection is at about 45% of the semispan. This metacarpal bend serves to orient the terrestrial position of the hand more vertically and also to keep the wing finger clear of the inner arm when the wing finger is folded.

The bone that we call the medial distal carpal has had several names, including lateral distal carpal, anterior distal carpal, and preaxial carpal (Figs. 10–14). It is clear that the bone articulates with the distal syncarpal, although only histological analysis might be able to determine whether, like the pteroid, it is distal carpal 1 or a neomorph (Unwin et al., 1996). Padian (1983b) preferred the term ‘medial distal carpal’ because in classic tetrapod anatomical position, the forearm is oriented more or less parasagittally, which places this carpal on the medial side of the wrist, and this term is useful for that reason. In flight, the carpal would be anterior and ventral to the rest of the wrist and wing. The term ‘preaxial carpal,’ on the other hand, conveys little of the anatomical context of the bone, and ‘anterior distal carpal’ is misleading because the orientation is not always anterior to the other carpals. Before its position and orientation were well known, ‘preaxial carpal’ was a reasonable neutral term for the bone, but on balance, ‘medial distal carpal’ seems preferable for the accuracy of its anatomical orientation.

We based our study primarily on three medial distal carpals (MDCs): TMM 41954-61 (right), TMM 41961-1.14 (right; poorly preserved), and TMM 42180-14.4 (left). The MDC articulates on the anteroventral surface of the DS by means of an ellipsoidal concave-convex joint (the MDC is concave). In flight, the dorsal margin of the MDC continues the anteroventral curvature of the dorsal edge of the DS to form the anterior border of the leading edge of the wing, as well as the origin of the camber line. It can be rocked slightly, perpendicular to its major axis, and pronated and supinated slightly against the DS. A fovea on its anterodorsal face, buttressed laterally by a slight ridge, supports a sesamoid that facilitates the action of *M. extensor carpi ulnaris* across the syncarpal joint (Bennett, 2007). The MDC can be moved medially to help swing the outer wing forward, and laterally to help it to swing backward (Figs. 14, 15). On the anteromedial face of the MDC, Bennett (2007:887) identified in *Pteranodon* and other pterosaurs “an indistinctly marked convex oval on the medial surface [his fig. 7], although in ... old individuals with prominent muscle attachment scars, the articular surface is surrounded by rugose bone that probably represents the margin of the joint capsule.” Examination of the *Quetzalcoatlus* material confirms his view. In TMM 42180-14.4, there is a partially circular remnant of a fovea with a raised margin of bone that may have housed the cartilage capsule supporting the base of the pteroid; in TMM 41954-61 and TMM 41961-1, this takes the form of a raised rugose surface, so it is perhaps more likely an attachment site for a tendon or muscle behind the base of the pteroid.

The bone that we term the ‘carpal sesamoid,’ named informally ‘sesamoid A’ by Langston in his curatorial notes, was simply named ‘sesamoid’ by Bennett (2007), among other authors. However, although there are no other known sesamoid bones in the pterosaur carpus, sesamoids have sometimes been found posterodorsal to the claws of pterosaurs such as *Eudimorphodon* (Wild, 1978) and *Dorygnathus* (Padian, 2008a), so we use here the specific term ‘carpal sesamoid’ to avoid any confusion. (In the TMM collections, several isolated bones are tentatively identified as ‘sesamoids’ on the basis of their shape and small size, but they are not associated with any other elements.)

The carpal sesamoid (CS) is roughly in the shape of an ovoid flattened on the dorsal side with rounded medial and lateral edges; the rounded side fits the shape of the fovea on the MDC in which it sits. It narrows posteriorly to a thin edge; anteriorly, it is thicker, and its anteroventral surface bears a depression that matches and extends the shape of the fovea. We hypothesize that this fovea and depression housed a ligament that held the two

bones together and resisted forces that would pull the CS medially. Those forces would have been generated by the tendon of the *M. extensor carpi ulnaris* as it passed over the flat anterodorsal face of the CS (Bennett, 2001b). Lateral forces would have been resisted by the lateral lip of the fovea on the MDC. The CS protrudes dorsomedially over the MDC and likely anchored a tendinous or muscular attachment to the proximal MC IV, which would have modulated pitch in the outer wing during the flapping cycle (Figs. 11, 14, 15).

**The Pteroid Bone**—The pteroid bone attaches to the carpal sesamoid (Bennett, 2007). Of the preserved specimens of *Quetzalcoatlus*, TMM 41954-21 is a left pteroid, and TMM 41954-22, the right pteroid, is more poorly preserved. TMM 41954-69 is still in the matrix, and its shaft is quite worn, as is its basal end.

The shaft of the pteroid is ‘D’-shaped in cross-section; the flat face is posterior in flight. This ‘D-spar’ construction is standard in aviation: it allows the leading edge spar to minimize the amount of material needed to resist both horizontal and vertical bending loads while still resisting twisting loads (Ong and Tsai, 1999). In *Quetzalcoatlus*, the curved front of the ‘D’ forms the leading edge of the wing. The flat posterior edge moves the neutral axis (the line of zero bending stress and strain) posteriorly within the cross-section, increasing tensile stresses on the anterior surface and reducing compressive stresses on the posterior surface.

The base of the pteroid is anteriorly almost bicondylar: two ridges of bone run dorsomedially and ventromedially to about 20% of its length, slightly past the beginning of the ‘D’-shaped cross-section of the bone. Posteriorly at the base of the pteroid is a broad surface that follows the enhanced basal curvature of the bone. This surface may have been the attachment point for muscles that retracted the pteroid and controlled its pitch, in opposition to muscles on the anterior side. In anterior view, the pteroid assumes a very slight ‘S’-curve: first dorsal, then ventral, then dorsal, roughly equivalent to dividing its length into thirds. This may have controlled the shape of the leading edge of the wing under varying load conditions.

Bennett (2007) established beyond reasonable doubt that the pteroid bone could not point anteriorly (contra Frey and Riess, 1981; Wilkinson et al., 2006; Wilkinson, 2008). The normal position of the pteroid would be toward the tip of the deltopectoral crest because both structures and the line between them form the leading edge of the medial portion of the wing. The pteroid could be protracted and retracted very slightly. Orientation of the presumed muscles at the anterior side would suggest a maximum of 20° protraction, although the medial end of the pteroid would have bent posteriorly, much like a wishbone or half of an English longbow, so the long axis of the bone would not have been directed nearly so far forward. Posteriorly, a retraction of 10–15° appears plausible. This forward motion would have assisted in inhibiting flutter when the wing was slightly retracted. However, it is not clear that simply because these motions appear possible, they were actuated. The pteroid likely could be pronated and supinated a few degrees to modulate the leading edge camber and pitch (Figs. 11, 14). (This motion would have maintained the aeroelastic number, which is essentially a function of the force needed to stretch a membrane and the membrane’s thickness, inversely proportional to the dynamic pressure and the wing chord length at the point of interest [Johnston, 1999]. The higher the number, the more aeroelastically competent it is, and the less subject to flutter.)

**Joints of the Wing Finger**—The metacarpophalangeal (MP) joint allowed more anteroposterior movement than any other joint in the wing (Fig. 15). Manipulations of the bones alone provide a maximum extension to 160° and a maximum flexion to 45° or less. Compared with basal pterosaurs, pterodactyls



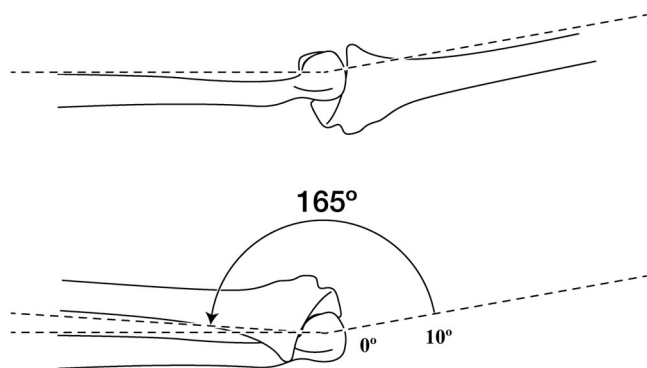


FIGURE 15. Range of motion at the metacarpophalangeal joint in dorsal view.

have a metacarpus that is greatly elongated. This allowed them to touch the ground with their fingers, which would not have been possible for non-pterodactyloids without having their acetabula situated substantially above the shoulder joint (Padian, 2008b). The fourth (main) metacarpal (MC IV) is flattened anteriorly and rounded posteriorly, and the long, thin metacarpals of the first three digits lie along this surface. Proximally, they seem to originate in grooves that surround a ridge that is connected to the rounded articular prominence on the proximal face of MC IV. (The proximal ends of the few preserved fourth metacarpals of the smaller specimens are not well preserved; the details are reconstructed from the corresponding region in the large specimen, in which the proximal end is fused to the distal syncarpal.) They terminate just proximal to the distal bicondylar facets of MC IV. The fingers of the first three digits were directed anteroventrally and likely extended against the anterodorsal surface just posterior to the leading edge of the wing during flight.

MC IV ends distally in a double condyle superficially similar to the distal end of an ornithodiran tibia. The difference is largely in the orientation of the condyles (Currie and Padian, 1983). The dorsal condyle of MC IV is positioned slightly posterior to the ventral condyle. In anterior view, the ventral condyle is initially parallel to the shaft. Posteriorly, it curves dorsally and continues to curve dorsally and medially until its terminus near the shaft. The sulcus between the condyles is about as wide as either condyle, which are subequal in that respect. The dorsal condyle is initially inclined dorsolaterally, and it continues this orientation dorsally until its medial termination. As a result, the offset of the two condyles increases posteriorly. This should have the effect of providing more freedom of movement, particularly in the dorsal direction, as the wing finger is retracted. However, because the articulating surface of Wph4 is dorsoventrally concave, the actual effect is first to depress the wing finger as it is retracted, then to begin to elevate it again as the angle between the two bones approaches 90°. By this point in retraction, the wing in flight would have lost competence, so we infer that the action of elevating the wing finger as the joint was flexed further had the effect of sweeping the distal wing finger dorsomedial to the inner wing when the animal was in quadrupedal motion on the ground. This would have protected it from damage by drawing the distal wing medially over the back. However, this final phase of dorsal flexion at the MP joint had no role in flight.

We base our study of the wing phalanges on TMM 42422, which has a complete series that is relatively uncrushed, supplemented by comparison with other specimens. *Quetzalcoatlus* is unusual in the degree to which its wing phalanges decrease in size distally. Table 4 provides length, proximal articular width, proximal shaft (nonarticular) width, distal shaft (nonarticular) width, and distal

TABLE 4. Measurements (in cm) of the wing phalanges in TMM 42422, *Q. lawsoni*.

Element	Length	Proximal articular width	Proximal shaft width	Distal shaft width	Distal articular width
Wph1	57.5	6	2.5	2.5	3
Wph2	30	3	3	1.3	1.5
Wph3	15.7	1.4	0.9	0.4	0.5
Wph4	4	0.5	0.3	0.2	0.3

articular width. Measurements of Wph1 exclude the proximal trochanter (extensor tendon process).

The ventral facet of the proximal Wph1 is anteroposteriorly shorter than the dorsal facet, and it is angled posterolaterally in extended soaring flight position, whereas the dorsal facet is angled posteriorly. The offset of these axes matches the offset of the axes of the distal end of the wing metacarpal. At the posteroventral end of the ventral facet is a trochanter that likely anchored the collateral ligaments that extended to the middle of the ventral surface of the rounded ventral trochanter of the distal wing metacarpal. The proximal end of the ventral facet, which extends medially more than the dorsal facet does, forms the ventral face of a prominent trochanter that forms the anterior border of both facets and represents the most medial extension of Wph1. This prominent trochanter slopes anterolaterally until, at the level anterior to the medial extent of the dorsal facet, it ends with a depression. In this depression is a pronounced groove that runs ventrolaterally. Lateral to it on the anterior edge of Wph1 is another, smaller trochanter. Somewhat lateral to this, on the anterior edge, is yet another small trochanter. Finally, on the posteromedial end of the dorsal facet is another pronounced trochanter. Each of these would have anchored tendons that flexed, extended, and helped to stabilize the MC IV/Wph1 joint.

Wph1 is slightly longer than the wing metacarpal, and it has a complex broadened proximal end, compared with those of the other wing phalanges. TMM 42242-2 is the best example. Its dorsal surface is rounded into a broad semiellipse. On the proximal end, a semielliptical sulcus on the dorsal side receives the dorsal condyle of the wing metacarpal and constitutes ca. 130° of possible posterior rotation given that the angle between the two bones was about 160° when maximally extended, and when maximally flexed the two bones likely formed an angle of ca. 45° or less (again, based on manipulating bones alone).

The Wph1/2 articulation was a spoon-shaped, ellipsoid, convex-concave joint in which the proximal and distal major axes are anteroposteriorly oriented and parallel to each other. We hypothesize that the morphology of this joint minimized anteroposterior movement and allowed minimal passive movement in the vertical plane.

The proximal end of Wph2 is more attenuated anteriorly than the distal end of Wph1, and there are enlarged anterior and posterior trochanters for the attachment of ligaments that minimized anteroposterior movement (Bennett, 2001b).

A unique T-bar-shaped cross-section in Wph2 and Wph3 supplement the usual interactions between load and deformation in the outer wing. As Johnston (1977:132) noted, "Because the triangular wing of pterosaurs is not elliptically loaded, the downwash varies along the span (nonelliptical loading), and the induced angle of attack at the tip can be significant, on the loose order of 20 to 30 degrees." This means that the wings can be pronated anteriorly by a similar amount near the tip in order to keep flow attached (to avoid stalling the tips) and thereby increase thrust production during flapping flight.

Upward gusts increase the bending moment in the spar and the tensile stress in the wing membrane. As in all thin membranes,

these loads must be carried parallel to the local plane of the membrane. Because the skeletal spar is located along the plane of the membrane, no couple is developed to transfer the pitching moment due to the lift forces into the spar. Therefore, pterosaurs used indirect techniques to accomplish this transfer. The most obvious (although not the only) transfer method combines the spanwise membrane tension with the downward camber in the aft portion of the airfoil and the trailing edge curvature to transfer some upward load into the spar at the wingtip and at the trailing edge wing root. This excess tension translated the wingtip posteriorly and dorsally, causing a nose-down twisting rotation in the skeletal spar and its support structures, thereby unloading the wing.

Azhdarchids, penalized by their relatively shorter outer wing, facilitated this spanwise pitching rotation by modifying the cross-section of Wph2 and Wph3 into a T-bar cross-section. As a result of moving selective portions of the bone wall perimeter closer to the centroid of the section, the T-bar section reduces resistance to twisting (for a given applied couple, it will twist more per unit length than a non-azhdarchoid pterosaur) while retaining essentially the original resistance to bending laterally or dorsally (Fig. 16).

Wph2 is arched dorsoventrally and the Wph2/3 joint is essentially similar to the Wph1/2 joint. The 'T'-shaped cross-section begins with Wph2 and continues until nearly the end of Wph3.

The articulation of the Wph3/4 joint is expanded and more circular in cross-section than the shafts and the more medial articulations; the rounded cross-section suggests that the aerodynamic loads become relatively lower and more uniform distally, while potential impact loads become more significant, which also explains why the distal wing phalanges are so progressively smaller and more flexible. The T-bar cross-sectional shape ends about 2–3 cm before the distal end of Wph3 and becomes more rounded, which is continued in Wph4.

## FUNCTIONAL MORPHOLOGY OF THE HIND LIMB

### The Pelvis

Only two specimens (TMM 41954-57 and TMM 41954-58) preserve pelvic material. The former portion comprises the left ilium, the ischium, and the pubis, plus a sacral rib, and at least four presacral dorsals, some of which may have been incorporated into

the pelvis (discussed above). The main sacral vertebrae are obscured by matrix. A small portion of the anterodorsal ridge that buttresses the acetabulum is also chipped away, and the end of the pubic peduncle is somewhat incomplete. The ventral border of the ischium is similarly fragmented.

New preparation of the pelvis reveals that this region in *Quetzalcoatlus* was more unusual than previously thought (Fig. 8). The anterior prong of the ilium extends anteriorly to the length of approximately three presacral vertebrae. The dorsal blade of the ilium is very short, and it is displaced posteriorly. It tapers anteriorly to reach only as far as the middle of the acetabulum. Its shape is of an inverted shallow triangle, connected by a stout peduncle to the rest of the pelvis. A deeply incised notch separates the lower border of the posterior iliac blade from the posterior blade of the ischium. The pubis has a stout, ventrally projecting anterior peduncle, as in all pterosaurs, and dorsally the posterior edge of this tubercle bears a ridge that curves dorsally, then posteriorly, then dorsally again, to approach the acetabulum and form the anterior border of the rather large obturator foramen. The acetabulum is not perforated, but it is not very shallow, and its anterior and dorsal borders are especially reinforced by pronounced ridges. Finally, a subovate prepubis, extending anteriorly, is connected by a narrow peduncle to the ventral end of the pubis. Although in pterosaurs, as in other amniotes (with the secondary exception of neornithine birds), these bones met and sutured along the ventral midline when the animals were fully grown, in this specimen the medial edge of the prepubis is rounded and the bone surface is complete. This suggests either that the bones approached each other but did not meet medially or that the specimen is immature and that eventually these bones would fuse at the midline, if they were not already connected by cartilage at that stage of growth.

### Movements of the Hind Limb

The terrestrial locomotion of pterosaurs has had several traditional interpretations (reviewed by Bennett, 2001b; Padian, 2008a, 2017). Some were based on interpretations of single joints of the pelvis and hind limb with poorly constrained biomechanical and phylogenetic comparisons. Some were based on trackways attributed to pterosaurs that may or may not actually pertain to them and that usually have not been ground-truthed to see whether the animals could have made them (Padian, 2003). Here, we begin with anatomy and functional morphology.

In considering terrestrial locomotion of pterosaurs, two principles should be kept in mind. First, basal pterosaurs walked differently from pterodactyloids, because the proportions of their forelimbs differ (largely the result of the longer metacarpus of pterodactyloids). In particular, pterodactyloids had forelimb segments medial to the wing finger that were long enough to reach the ground easily, enabling them to make quadrupedal tracks (Mazin et al., 1995, 2009). This was not the case for basal pterosaurs, which when placed in a quadrupedal pose would have found themselves with the hip joint substantially higher than the shoulder joint (Padian, 2008b:fig. 23). Several lines of evidence indicate that pterosaurs evolved from bipedal ancestors and were bipedal themselves (Padian, 2008c), only becoming facultatively quadrupedal with the evolution of pterodactyloids.

Second, although pterodactyloids, like all other tetrapods, required a locomotory strategy that integrated the gaits of the fore- and hind limbs, the motions of the two sets of limbs themselves can be treated as independent questions to some extent. First, we analyze the possible motions of the hind limb.

To begin with, in pterosaurs, generally all joints of the hind limbs are essentially hinges (but see below), with the exception of the hip, which in pterodactyloids has a configuration of the proximal femur eerily reminiscent of the human femoral head and in basal pterosaurs is more of an offset oblate spheroid

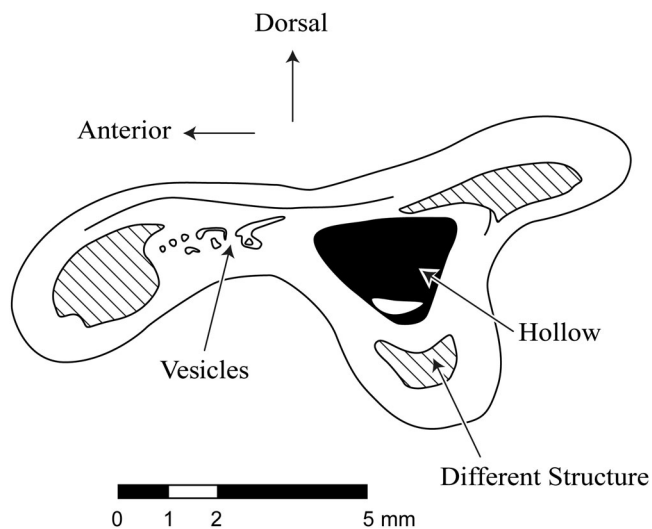


FIGURE 16. T-bar cross-sections of wing phalanges 2 and 3. For explanation, see text.

nearly identical to some basal dinosaur femora (Padian, 1983a, 1983b). This joint is the most problematic, so we will return to it after considering the other joints of the hind limb.

Padian (1983b) first drew attention to the detailed similarities of the hind limb joints of pterosaurs, birds, and other dinosaurs, and their dissimilarities to bats, for reasons outlined below. The knee, ankle, and joints of the feet are traditionally considered hinges, as noted above, which implies that their motions were restricted to a single plane of flexion and extension. However, it should not be assumed that these uniplanar mobilities were necessarily rigid. Kambic et al. (2014) used XROMM (X-ray reconstruction of moving morphology) analysis to show that the guinea fowl's hip, knee, and ankle joints, traditionally considered hinge joints that move in a parasagittal plane, can actually rotate to a substantial degree (up to  $68^\circ$  in the case of the ankle) when the animal is sidestepping and turning in a variety of situations. Given the similarity of pterosaur hind limb joints to those of birds, it is reasonable to assume the same flexibility, although it cannot be measured directly.

There is nothing unusual about the joints of the hind limb in *Quetzalcoatlus*, compared with other pterodactyloids. To begin with the knee, the distal end of the femur (Fig. 17) is very well preserved in TMM 41961-1 (although the femoral head is missing) and crushed dorsolaterally in TMM 41544-2, so remarks here are based on the former specimen.

The lateral and medial condyles are nearly equal in size, but the lateral one is slightly larger; the lateral trochanter is also larger than the medial one. This is also the case in terrestrial birds; the effect is to direct the shaft of the tibiotarsus slightly medially, counterbalancing the lateral splay of the distal end of the femur as its shaft clears the animal's abdomen (e.g., Kambic et al., 2014, and [www.xromm.org/projects/long-axis-rotation](http://www.xromm.org/projects/long-axis-rotation)). Three tendons run over the anterior surface of the knee: one between the two condyles and one each between the condyles and their associated trochanters. They ostensibly stabilized mediolateral movements of the knee and provided the actuation for its

extension. Unfortunately, the proximal surfaces of the available tibiae of *Quetzalcoatlus* provide few anatomical details, because they are crushed, incomplete, or abraded. It appears from preserved specimens that the proximal tibia is mediolaterally just slightly narrower than the distal end of the femur, the condyles of which overlap the tibia medially and laterally. If this preservation is accurate, it would reinforce the hypothesized stability at the joint.

The tibia is a long bone of high aspect ratio (over 20:1 length to midshaft width) that bows slightly anteriorly (perhaps  $5^\circ$  at midshaft, although with crushing and distortion this is difficult to assess). The best-preserved specimens in the *Quetzalcoatlus* series are TMM 42422-9 and TMM 42422-10, although other specimens provide useful features. The fibula is greatly reduced; it tapers along the proximal quarter of the tibial shaft before finally merging with it completely. Distally, as in all pterosaurs, the tibia expands slightly anteriorly and develops two condyles that form its distal end (Fig. 10). These condyles are composed mostly of the astragalus and the calcaneum; thus, the entire fused element should properly be called the tibiofibulotarsus (TFT).

The condyles of the distal TFT form a pulley-like shape. In lateral view, the intercondylar sulcus extends from about  $60^\circ$  anteriorly to  $280^\circ$  posteriorly along the perimeter of the distal TFT, but this range greatly exceeds the potential articular surface of the joint. Anteriorly, the two condyles begin to converge proximally, because the medial condyle is oriented with a slight dorso-medial inflection, whereas the lateral condyle is parallel to the long axis of the shaft. The situation is similar in *Pteranodon*, and Bennett (2001b) provided a careful description of features of the TFT that are not as well preserved in *Quetzalcoatlus*.

The distal tarsals are preserved in articulation through matrix in TMM 42138-2, although the posterior corner of the (right) medial distal tarsal (MDT) appears to be incomplete (Fig. 10). This part of the MDT is complete in TMM 41954-64, a pair of left distal tarsals preserved in articulation but separated. Other

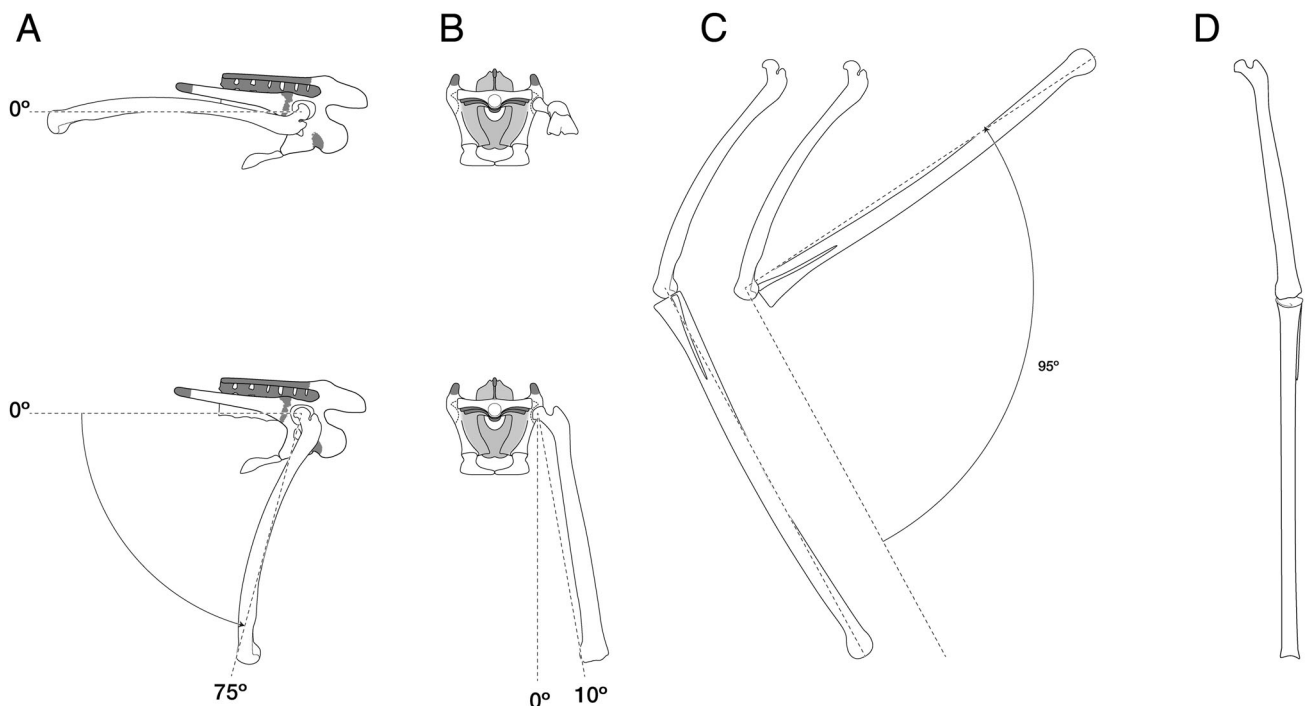


FIGURE 17. A, anterior and B, lateral views of the hip joint, showing how the neck and head of the femur extend medially, dorsally, and posteriorly into the acetabulum. C, lateral and D, anterior views of the knee joint.

preserved distal tarsals include an unnumbered right lateral distal tarsal, with its lateral side still attached to matrix, and TMM 41954-8, a left lateral distal tarsal associated with four metatarsals.

Padian (1983a, 1983b) described articulated distal tarsals of *Dimorphodon* and showed how they fit in the ankle assembly to contribute to a parasagittal gait. Within pterodactyls, distal tarsals have been described in *Pteranodon* (Bennett, 2001b:figs. 112, 113) and in *Tapejara* (Kellner, 2004). The configuration of the tarsals in TMM 42138-2, which are tightly articulated in their natural position through a thin band of matrix, provides an unambiguous orientation of the two tarsals. Figure 18 shows what are unquestionably the proximal faces of these two agglutinated elements, because they bear shallow depressions for reception of the distal condyles of the TFT. The anteroposterior ellipsoid shape implies that the tarsus rotated anteroposteriorly, that is to say, in the parasagittal plane, against the TFT. The tarsal element on the right in Figure 18 is the lateral distal tarsal (LDT), on the basis of several distinct features. First, its lateral face houses a diagonal groove that runs anteroventrally for reception of the proximal end of metatarsal (MT) V, which would have been directed posterolaterally and ventrally. Kellner (2004:29) described the same feature in *Tapejara*: “The articulation with metatarsal 5 is well marked and situated on the lateral surface of this bone, facing ventrolaterally.” This facet corresponds to the one in *Dimorphodon* that faces posterolaterally and ventrally for reception of MT V (Padian, 1983b:fig.

17). Second, as Padian (1983a:26) noted for *Dimorphodon*, “[a] tuberos posterior process of the lateral tarsal partly overlaps the posterior face of the medial tarsal, and may have been the site for tendinous attachments of muscles that extended the foot.” In the two complete sets of distal tarsals in *Quetzalcoatlus* (TMM 42138-2 and TMM 41954-64), the posterior end of the LDT partly overlaps the posterior end of the MDT in the same way as in *Dimorphodon*. Moreover, this tuberos posterior process of the LDT in *Quetzalcoatlus* bears a deep groove running ventrolaterally, which likely housed a tendon that attached to the proximal metatarsus and retracted it. This feature appears to corroborate Padian’s (1983a) suggestion for *Dimorphodon* noted above. Finally, a similar groove on the posteromediodistal face of the LDT is for the reception of the fourth metatarsal (see Padian, 2017, for further details and comparisons among ornithodirans).

Correspondingly, TMM 41954-28 is an isolated right lateral distal tarsal. The unnumbered TMM distal tarsal is a right lateral one; its lateral side remains attached to matrix. The distal tarsal associated with four metatarsals in TMM 41954-8 is a left one; its anteroventral face contacts the proximal end of one of the outer metatarsals, which are preserved in ventral view. This articulation is rotated about 90° out of position, but it identifies the adjacent metatarsal as the first one, and II, III, and IV as the progressively lateral metatarsals of the left foot in ventral view. In proximal view, the ends of the first four metatarsals are somewhat flattened mediolaterally and also canted so that in articulation they overlap each other anteromedially: that is to say, each one’s anterior face tends to slant medially over the surface of the metatarsal medial to it.

As for material of the fifth metatarsal associated with the rest of the foot, there remain representatives in TMM 42138-2.2 and TMM 42180-14.9, and an incomplete piece associated with TMM 41954-64. Its proximal end comprises a double-pulley joint, reminiscent of the distal ends of MC IV and the tibiotarsus. It articulates with the deep facet on the lateral side of the LDT, and it swivels in a proximal-anterior to distal-posterior plane. Its function remains unknown. Traditionally, the fifth pedal digit was claimed to anchor the brachiopatagium to the hind limb, but there is not only no evidence for this in any pterosaur, there is substantial evidence against it (Padian, 1983b; Padian and Rayner, 1993). Moreover, a salient feature of the transition from basal pterosaurs to pterodactyls was the utter reduction of the fifth digit, formerly possessing two greatly elongated and modified phalanges, to the stub of a metatarsal. Yet the depth of the articular facet on the LDT remains, deeper than in any other group of ornithodirans (Padian, 2017).

When the ankle is assembled, the mediolateral width of the distal tarsals is not great enough to accommodate the articulation of more than three metatarsals distally. Because we know where MT V articulated, we know that MT IV must have been adjacent to it, and so it is likely that only MTs II–IV contacted the distal tarsals (see Padian, 2017). Padian (1983a) found that this was the case in *Dimorphodon* as well, and for most pterosaurs illustrated by Wellnhofer (1978) that are not distorted or disarticulated, the same configuration is obtained: as in most ornithodirans, MT I does not directly contact a distal tarsal.

Appressed in this way, there would have been little or no rotation of the proximal ends of the metatarsals against each other. They seem to have flexed parasagittally as a unit. No other motions appear to have been important, but the articular surfaces of the distal tarsals that receive the proximal faces of the metatarsals are not distinct, and it is likely that here there was the possibility of some passive movement that absorbed ground reaction forces and other torsional forces (note Kambic et al.’s [2014] discussion above).

Historically, some authors have hypothesized that pterosaurs could spread their metatarsals mediolaterally, perhaps

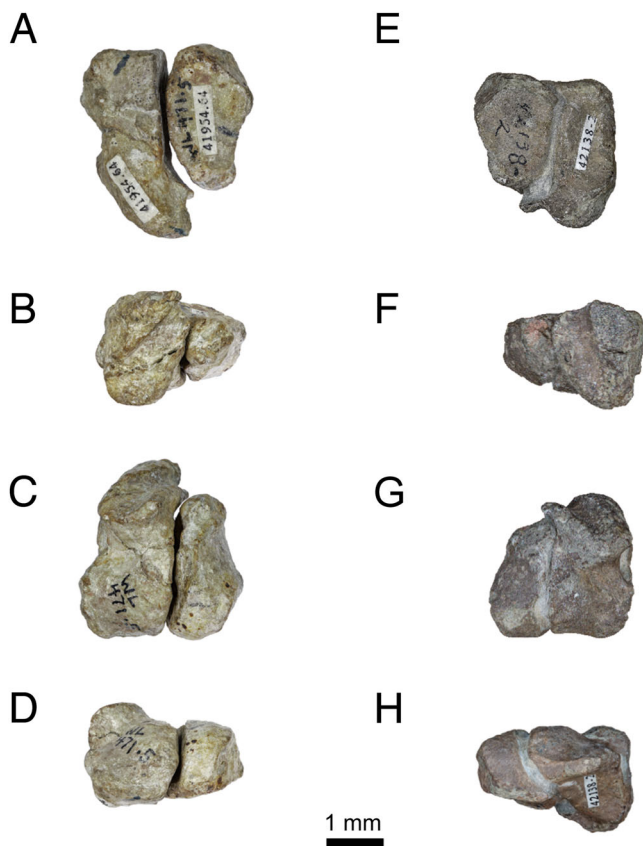


FIGURE 18. *Quetzalcoatlus* tarsals. A–D, TMM 41954.64, left distal tarsals in A, proximal, B, posterior, C, distal, and D, anterior views. E–H, TMM 42138-2, right distal tarsals in E, proximal, F, posterior, G, distal, and H, anterior views. The figures in the series are successively oriented as if the upper part of the previous photo were rotating away from view. Photos by D. Strauss, University of California Museum of Paleontology.

incorporating a web that hypothetically also encompassed the pedal digits. There is no evidence of which we are aware that any tetrapod can actively splay its metatarsals to any significant degree, because although musculature exists lateral and medial to the individual metatarsals, it is not sufficient to actuate this motion, which would have been further restrained by ligaments and other soft tissues, including the binding of the metatarsus by the skin. Therefore, when metatarsals are observed splayed (or found that way in fossils), they are either fixed that way or are passively spread by ground or water reaction forces. In fossils, splayed metatarsals can only result from postmortem taphonomic processes. *Dimorphodon* has beveled medial and lateral edges to its metatarsals, indicating their close appression (Padian, 1983a). Even if this is not the case for some other pterosaurs, an anatomical justification that they could therefore splay their metatarsals would rely on extraordinary evidence, which has never been produced.

The distal ends of the metatarsals are rounded, implying considerable flexion and extension of the phalanges against them (contra the interpretation of Clark et al., 1998, for *Dimorphodon*). Although some isolated and incomplete pedal phalanges are preserved in *Quetzalcoatlus*, the material is not sufficient to reconstruct the entire foot. Generally in larger pterodactyls (e.g., *Pteranodon*: Bennett, 2001b), the longest pedal digits are approximately the length of the longest metatarsals, and in the absence of better evidence we will presume this condition for *Quetzalcoatlus*.

With this understanding of the joints at and distal to the knee, the position and mobility of the femur in the acetabulum can be considered. The parasagittal plane of the knee articulation should be vertical, or possibly tilted ventromedially by a few degrees, allowing the tibiotarsus to angle slightly medially along its shaft. In this position, the natural curve in the femoral shaft is oriented dorsoventrally, which is how it is arranged in birds and other theropods (Padian, 1986). The neck proceeds as a narrow constriction from the shaft and ends in an expanded, rounded femoral head that, relative to the femoral shaft, extends dorsally, posteriorly, and medially to enter the acetabulum in normal position (Fig. 19). In terrestrial locomotion, the femoral shaft likely diverged from the parasagittal axis about

15° laterally in order to clear the abdomen, as in birds. However, it is difficult to reconstruct this anatomical region with respect to the pelvis because they are not completely preserved, and the only available example (TMM 41954-57) is flattened. As a result, the pelvis cannot be reconstructed in three dimensions with confidence. However, the acetabulum is roughly a shallow circular depression, deeper anteriorly and dorsally and shallower posteroventrally, and the pronounced antero-dorsal ridge suggests greater buttressing in this region against compressive forces. Such compressive forces would arise from combinations of gravity, inertia, and active and passive soft tissue forces depending on the behavior used. The volume of soft tissues surrounding joints, as well as the functions of tendons and ligaments, tends greatly to restrict motions that appear possible merely from manipulating dry (and often distorted and incomplete) fossil bones (Firbas and Zweimüller, 1971; Hewitt et al., 2001, 2002; Hertel and Campbell, 2007; Martin et al., 2008; Hutson and Hutson, 2012; Arnold et al., 2014; Manafzadeh and Padian, 2018).

Given the bird-like features of the entire hind limb, which not only bear anatomical resemblance but speak to functional similarity, it appears reasonable to begin with the kinds of postures and degrees of movements found in birds. Kambic et al. (2014) present photos of guinea fowl in which the shaft of the femur is oriented between 10° and nearly 60° below the horizontal during normal locomotion. This appears to be a reasonable range for *Quetzalcoatlus*, judging by manipulation of casts of the bones. When squatting or crouching before a leap, it may have been possible to bring the shaft to the horizontal or even slightly above, at least passively as in the kiwi (Abourachid and Renous, 2000). Given the phylogenetic bracket of joint capsule configuration seen in birds and crocodiles (Tsai and Holliday, 2015; Manafzadeh and Padian, 2018), it is also unlikely that the femur could have been flexed and extended much beyond a range of 70°, based on comparison with ratites (Abourachid and Renous, 2000:fig. 7), because ligaments that hold the femur in the acetabulum would have prevented this. The vertical positioning of the femur in *Anhanguera* by Costa et al. (2014) would have been extremely unlikely for several reasons, including that (1) the knee joint is hyperextended in this position; (2) a limb

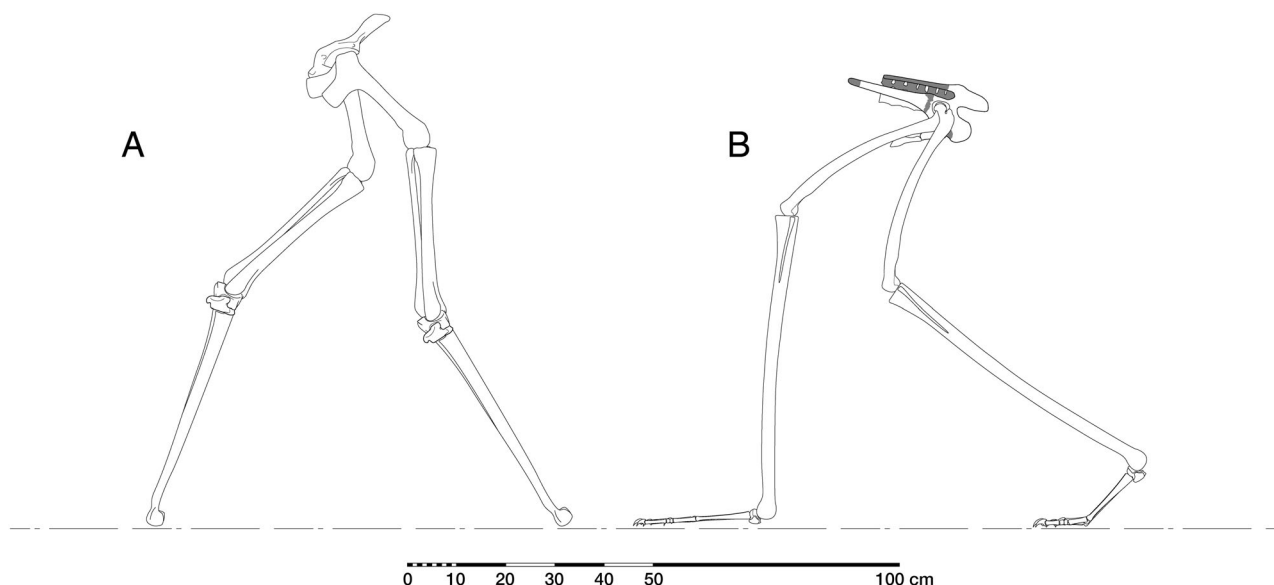


FIGURE 19. Reconstruction of **A**, the shoulder girdle and the forelimb and **B**, the pelvis and the hind limb, showing the estimated range of motion in lateral view during walking.

in columnar stance does not have a bowed femur; and (3) for reasons noted above, it is unlikely that the hip joint could have flexed and extended more than about 70° (see also Bertram and Biewener, 1992). If the hypothesis of these authors about *Anhanguera's* walking ability were feasible, one might posit a range of flexion and extension of the femur of up to 90°. If this locomotory hypothesis were accepted, then during flight the femur would have been limited to the same orientation, which would have been detrimental to any kind of flight by creating unrealistic drag.

In summary, this is what can be said about the movements of the pterosaurian hind limb. The knee joint is a 'hinge' in traditional parlance (but see Kambic et al., 2014), as is the TFT/distal tarsal joint. The tarsometatarsal joint is also mainly hinge-like, but not a tight morphological fit like the DS–MC IV articulation. The 'hinge-like' inference is sustained more from the oblique gathering of the proximal metatarsal ends than from the features of the distal faces of the distal tarsals, which are not well defined. The metatarsophalangeal joints are typical of those of birds and other dinosaurs, so we infer that they were mainly parasagittal (dorsoventral) in their motion. Given the essentially hinge-like motion of all these joints, it is clear that the hip joint provided the basis for most of the potential variation in excursion of the limb. The offset head of the femur extends upward, backward, and inward toward the acetabulum. The neck is starkly offset from the shaft in *Quetzalcoatlus* and other pterodactyloids. Its curvature speaks to its subhorizontal orientation (Abourachid and Renous, 2000).

#### RECONSTRUCTION OF THE WING PLAN FORM

It should be appreciated that we know literally nothing about the shape of the pterodactyloid wing. As far as we are aware, not a single specimen of pterodactyloid is preserved with wings outstretched so that the membrane can be reconstructed on the basis of evidence as opposed to conjecture (pace Elgin et al., 2011), in contrast to several good specimens of *Rhamphorhynchus* (Padian and Rayner, 1993). The *Rhamphorhynchus* specimens clearly show a gull-like wing outline, exceedingly narrow behind the elbow (perhaps less than 50% the length of the humerus) and continuing toward

the body wall. These specimens also show that the foot and ankle were completely free of the wing, so even if the trailing edge plunged posteriorly as it approached the body wall the lower leg (at least) was not involved. This indicates that the long, jointed fifth metatarsal also had no role in the manipulation of the main wing. If such a role is postulated for pterodactyloids, it needs to be explained (1) why the main wing would need such expansion beyond the basal pterosaur condition and (2) why the fifth metatarsal would be reduced and not enlarged (like the allegedly analogous bat calcar; Padian, 1983b) to take on a greater role.

Although there are many possible configurations of the pterodactyloid wing, and a great many that have been hypothesized (Elgin et al., 2011:fig. 2), here we consider only four (Fig. 20). Two are not viable, as far as we can tell, and we disagree among us about the viability of the other two, but we think it is an advantage to be able to compare the pros and cons of the evidence.

#### Four Models of Pterosaur Wingplan

**The 'Straight-legged' Model**—In this model (Fig. 20A), the hind limbs are extended directly posteriorly, so that the femur, the tibia, and the foot are nearly horizontal. The femur is retracted in the hip socket from a subhorizontal position facing anteriorly and slightly ventrally to a subhorizontal position facing posteriorly and slightly ventrally (most of these are based on reconstructions by Wellnhofer, 1978, and other publications). This requires an extension of the hip joint of about 150°, which is far more than observed in ornithodirans (see above). The femur is rotated and moderately abducted in this model (in fact in all the model illustrations of Elgin et al., 2011:fig. 2a–d, although incorrectly so for traditional 'bat-like' and 'bird-like' models).

In this position, if the wing membrane is connected to the ankle or knee, the aspect ratio of the wing membrane is very low and its area is larger than for any other type of reconstruction (especially with an ankle attachment). The area can also vary with the shape of the trailing edge (connecting straight from wingtip to ankle, or curved resulting in less area: models 1, 2, 8, and 9 of Elgin et al., 2011). As a result, the wing loading is lower for this model than for any other, and we think unrealistically so: it would seem

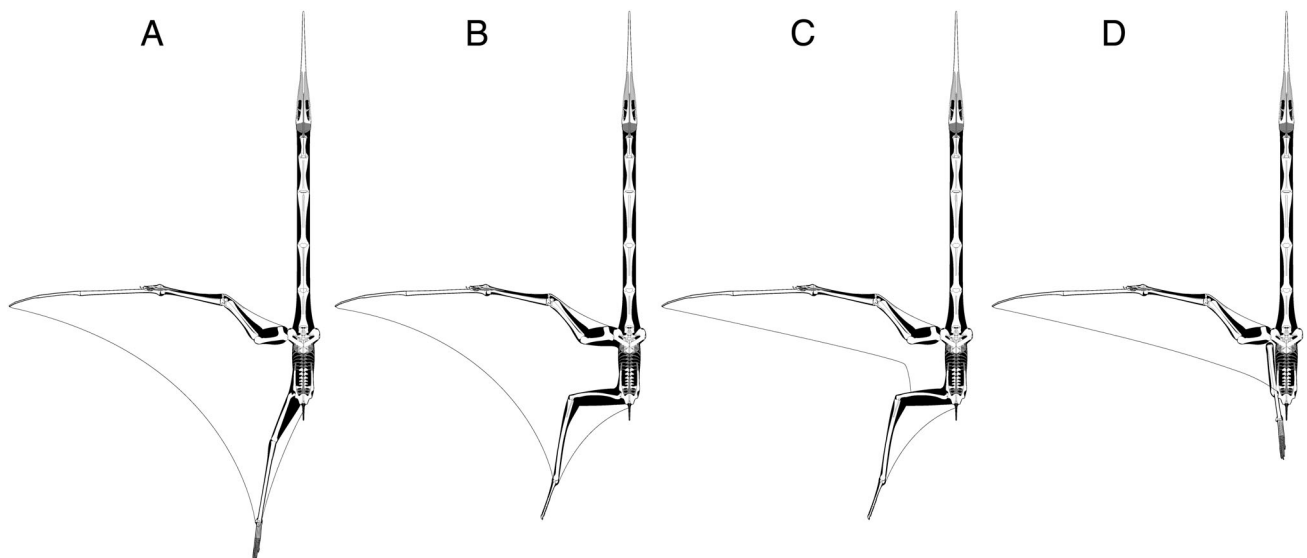


FIGURE 20. Four reconstructions of the pterodactyloid wing. **A**, the 'straight-legged' model. **B**, the 'bat-like' model. **C**, the 'aerodynamic tail' model. **D**, the 'bird-like' model. For explanation, see text.

difficult for the animal to adjust to gusts of wind and indeed high winds in general, maneuverability would be reduced, and its flight speed would have been considerably slower than with a smaller wing area.

**The ‘Bat-like’ Model**—This is an ancient and very common model of authors (Fig. 20B), dating to the first known reconstructions of pterosaurs in the earliest 1800s (Taquet and Padian, 2004), but still dominant in scientific literature (e.g., Wilkinson, 2008; Witton and Naish, 2008; Hone and Henderson, 2014; Tokita, 2015; Palmer, 2017; Britt et al., 2018). It differs from the previous model in that the femur is stretched laterally in a horizontal plane, which requires an unrealistic degree of abduction, rotation, and extension at the hip joint, by comparison with extant ornithodirans (Manafzadeh and Padian, 2018). The knee is bent 90° so that the tibia is directed posteriorly, and as a consequence the soles of the feet face medially. The wing area is very high, and the aspect ratio and wing loading are correspondingly high.

It has been frequently shown that bat hind limbs are utterly different in structure and function than those of all other tetrapods, so they are inappropriate models for pterosaurs (Padian, 1983b, 1991). One key is the hip joint: in bats, the femoral head faces ‘anteriorly,’ that is to say, in the opposite direction of the distal condyles at the knee, whereas in all other tetrapods the head curves medially, so there is a 90° difference in orientation. Correlated with this, the greater and lesser trochanters on the bat femur are equally developed and situated on opposite sides of the femoral head, whereas in other tetrapods these trochanters are lateral to the head. The result is that in the hip joint, the bat femur naturally extends laterally and its distal condyles point posteriorly. The knee is basically a hinge joint, but the ankle is not mesotarsal. Rather, it is capable of substantial rotation, and the metatarsal and phalangeal rows are parallel, not as in ornithodirans. Moreover, the claws are very large and recurved, and sharply attenuated (Padian, 1983b, 1991). There are no diagnostic similarities between the hind limbs of bats and pterosaurs (or birds, or any ornithodirans), but many critical differences.

Rotating the hind limb into a fully ‘bat-like’ pose was untenable for another important reason. Numerous recent anatomical studies of tetrapod joints have shown how soft tissues, often neglected in paleobiological analyses, can fundamentally constrain joint mobility (range of motion) in ways that cast doubt on or even falsify reconstructions based on bones alone (Hewitt et al., 2001, 2002; Hutson and Hutson, 2012; Arnold et al., 2014). It should be remembered that synovial joints comprise not just bones and cartilage, but also an outer joint capsule that holds the bones together and encompasses the synovial cavity. In the hip, several ligaments are an integral part of this capsule, and they are positioned so as to constrain movements of the joints in ways that increase stability. In amniotes, the hip joint capsule takes the form of a ring of connective tissue that holds the proximal femur inside the acetabulum; in birds and crocodiles, several ligamentous thickenings distributed throughout this capsule have been identified and their homologies to ligaments in other diapsids established (Tsai and Holliday, 2015; Manafzadeh and Padian, 2018). In birds, these ligaments limit range of motion at the hip for all rotational degrees of freedom to less than half of what would be predicted based on osteological morphology alone (Manafzadeh and Padian, 2018). Given the close homological and functional correspondence between the bones and joints of pterosaurs and birds, the extreme rotations necessary at the hip to achieve the traditional ‘bat-like’ model, which appear possible from manipulation of the femur and the acetabulum, would be rendered impossible by ligamentous constraints.

A slighter abduction of the femur to about 60° from the parasagittal plane, and an internal rotation of the hip joint to about 90°, would set the hind limb in a less severe extension but would likely still require unrealistic stretching of ligaments

(typically no more than 10% of relaxed length in vivo [Halilaj et al., 2015] and as little as 5% or less [Beynon and Fleming, 1998]). Hewitt et al. (2001) stretched the three human hip ligaments until they tore and found regional strain at structural failure = ~6–25%, with midsubstance strain at failure = 10.4–11.5%. The latter range is more critical because if any part of the ligament fails, the entire structure fails. Consistent with this, the human inferior glenohumeral ligament midsubstance strain at failure is about 10.9% or 9.3%. In general, then, ligaments cannot be stretched more than about 10%. Any restoration that requires more stretching is unrealistic unless the reconstructed motion is commensurate with known degrees of motion in the extant phylogenetic bracket.

Given these difficulties, the traditional ‘broad-winged’ restoration based on an analogy to bats appears unrealistic. Reconstructions of pterosaur limbs in positions not normal to ornithodirans should be justified by extraordinary evidence.

**The ‘Aerodynamic Tail’ Model**—In this model (Fig. 20C), the legs are extended in a nearly horizontal plane to form a control surface, but they have little or no connection with the brachiopatagium. A narrow uropatagium from the ankle to the anterior part of the biological tail is posited. In this model, the flight position of the femur would be nearly horizontal and extended laterally ca. 90° (but see ligamentous considerations above). The flexion and extension of the knee in this position would be horizontal, requiring the lower leg to rotate via the hip joint to approximately the horizontal plane. Internal rotation of the femur, and retraction and extension of the knee and ankle interacting with aerodynamic loading, would make the hind leg and uropatagium an effective control surface—an aerodynamic tail. We hypothesize that in this configuration, the legs and the uropatagium would also provide a small amount of lift. Although aerodynamically unstable, it would have had the effect of reducing wing loading, without incurring a commensurate increase in drag that would be associated with a broader wing.

Manipulation of the femur against a pelvis reconstructed by Wann Langston indicates that it may have been possible to bring the femur into approximately a horizontal position by abduction and slight internal rotation (ca. 5°) of the hip at the end of its extension. This motion appears to be the most plausible way to move the leg into a plane similar to the wing, although this is a bones-only manipulation that assumes no restriction of range of motion by soft tissues, including ligaments and muscles (see above). In order to test this hypothesized posture, more consideration of the constraints imposed by soft tissue is required.

**The ‘Bird-like’ Model**—In flight, it is most plausible, according to this model (Fig. 20D), that the hind limbs were drawn up bird-like, with the knee anterior to the acetabulum, because this position is most consistent with the terrestrial motions of the hind limb discussed above, and most consistent with the biology of other ornithodirans. No evidence has ever been adduced that pterosaurs could not adopt this pose, and considerable evidence has been adduced that they could (Padian, 1983b, 2008c, 2017). In this position, an attachment of the wing membrane to the hind limb would have been useless, as it is in birds, because it would have formed an inverted pocket of membrane that would have created drag. Therefore, in this model, the trailing edge of the wing is presumed to have attached at some point along the pelvis. The tail has been suggested by some authors as an attachment point, but it has never been made clear how or to what extent the tail would have been incorporated in basal (non-pterodactyloid or long-tailed) pterosaurs, or even in pterodactyloids. There has been no functional study of the mobility of the caudal vertebrae in pterodactyloids or how the tail may have deformed the posterior part of the wing membrane (presumably dorsoventrally if at all). The farther back the attachment, the greater the possible wing area, depending on the shape of the trailing edge of the wing. Attached to the pelvis, the aspect

ratio of the wing is high and its shape is narrowly triangular, with a trailing edge that curves slightly posteriorly as it approaches the body midline (Padian, 1985; Padian and Rayner, 1993). The legs, drawn up under the body as in birds, would have incurred little drag, and as in some birds, the legs and feet could likely have been extended as needed for maneuvers and braking.

Although we present all four historical models in Figure 20, in our view the configurations in Figure 20A and B were unrealistic. J.R.C. and J.C. prefer the model in Figure 20C, and K.P. prefers Figure 20D, for the reasons provided above.

## FUNCTIONAL MORPHOLOGY IN TERRESTRIAL LOCOMOTION

### Posture on the Ground

Several lines of evidence support the hypothesis that pterosaurs evolved from bipedal ornithodiran ancestors that had erect stance and parasagittal gait (Padian, 2008c). This stance and gait were carried through the first pterosaurs (Padian, 1983b, 1991, 2008a, 2008b, 2008c), which, with their foreshortened, horizontal (or nearly so) ornithodiran dorsal vertebral column, subhorizontal femur, long hind limbs, and a tail that could act as a dynamic stabilizer much as in *Deinonychus* (Ostrom, 1969), were well suited for bipedal progression.

When pterodactyls evolved in the Middle Jurassic, the most striking change in their postcranial anatomy from basal pterosaurs was the elongation of the metacarpus, which made it possible for the animals to touch the ground easily with their forelimbs, without changing the habitual horizontal or slightly elevated position of the torso. Nothing else in the distribution of mass or general morphology seems to have changed (apart from an extremely slight anterior shift of the center of mass resulting from the elongation of the metacarpus), and so there is no reason to suspect that pterodactyls 'needed' to walk quadrupedally in order to support the anterior part of the body. *Quetzalcoatlus northropi* was a very large animal, and the head and neck may have put additional weight on the front limbs in terrestrial progression, depending on how they were held and the slope of the dorsal vertebral column.

Quadrupedal trackways that could only have been made by pterodactyls, because the manus prints are placed so far outside the pes prints, were first established by Mazin et al. (1995) based on a very large horizon of hundreds of trackways from an intertidal environment from the Jurassic of Crayssac, France. Unfortunately, the poor competence of the substrate, which was saturated by seawater, and the kinematics of the limbs, particularly the manus, have made interpretation of the trackways difficult: no phalangeal formula can be obtained from any manual or pedal print of any Crayssac trackway (or for that matter of any footprint referred to pterosaurs; Padian, 2003). There is even disagreement on which digits of the manus are being impressed (e.g., Unwin, 1988b; Lockley et al., 1995; Bennett, 1997). However, because the sediments that bear the imprints of these digits are not distorted by kinematic activity, even in this incompetent substrate, it can be concluded that these digits had no role in retraction of the forelimb. They were merely emplaced.

The preceding observations are important for contextualizing the evolution of quadrupedality in pterodactyls, and for understanding their gait and how it was powered. If pterosaurs evolved from bipedal ancestors and were originally bipedal (Padian, 2008c), the elongation of the metacarpus (and the correlated loss of the long tail) was likely related to flight, because nothing in the skeleton suggests any shift of mass or change in terrestrial locomotion that required quadrupedality. The impressions of the forelimb suggest that it bore some weight, but these are not deeply impressed and do not show distortion of the sediment

that would reflect retraction of the limb in forward propulsion, so there is no evidence that the forelimb played a significant role in terrestrial propulsion. We explain below the kinematics of the forelimb and the constraints that prevented this role.

Despite poor preservation, trackways provide the best idea of the constraints and possibilities of terrestrial locomotion in pterodactyls. Unfortunately, the Crayssac trackmaker likely had a wingspan on the order of only about 1 m (Mazin et al., 1995), whereas the smaller specimens of *Quetzalcoatlus* (*Q. lawsoni*) are closer to the 4–5 m range and the large holotype specimen (*Q. northropi*) is likely in the range of 10–11 m, so there would have been a difference of scale in mass and proportions that affected locomotion. Based on a layout of the bones of the smaller range of specimens that constitute *Q. lawsoni*, we estimate an average mass of about 20 kg for individuals of this general size (wingspan about 4.5 m), again acknowledging a great capacity to fluctuate naturally. The weight of the neck and the head, which would have acted as a lever arm on the fulcrum of the joint of the neck with the body, provides some idea of the weight transmitted to the ground through the manus. Under the circumstances, *Quetzalcoatlus* may have relied more on its forelimbs for terrestrial support when resting than pterosaurs the size of the Crayssac trackmaker did. We use this reasoning in considering the motions of the forelimbs on the ground.

### Walking: Hind Limb

No specimen of *Quetzalcoatlus* has a reasonably complete, associated femur, tibia, and metatarsus. TMM 41961-1 has an associated femur and tibia, but the proximal end of the former is incomplete. The femur (F) in this specimen is estimated at 33 cm and the tibia (T) is complete at 55 cm, for a T/F ratio of about 1.4. The left femur in TMM 42422-28 is incomplete at about 32 cm, and we estimate its complete length at about 35 cm; the associated tibiae are 57 and 60 cm, for a T/F ratio of 1.6–1.7; even if the femur were as long as 38 cm, the T/F ratio would be 1.5. This is in the high range of pterosaurs.

All metatarsal material of *Quetzalcoatlus* is isolated, and there is only one reasonably complete metatarsus (TMM 41954-64). Most restorations of *Quetzalcoatlus* feature a metatarsus that is about 20% the length of the tibia and 30% the length of the femur, but this is relatively short for pterosaurs; 30% and 40%, respectively, are more typical of pterodactyls. Given the high T/F ratio in *Quetzalcoatlus*, it would be surprising if the metatarsus was especially short, and so an estimate of metatarsal length at about 15 cm for TMM 41961-1 appears reasonable in proportions (the equivalent length in most published restorations is only about 11 cm). Recalling that the lengths of the pedal phalanges in pterosaurs are approximately equal to the length of the metatarsus (Wellnhofer, 1978:abb. 17; Padian, 2003), one can approximately double the estimated metatarsal length to have a sense of the entire length of the foot, which would have been about 30 cm by this reasoning. (*Rhamphorhynchus* has a longer metatarsus, whereas the toes are slightly longer than the metatarsus in *Pteranodon*, a closer taxon to *Quetzalcoatlus*.)

The only azhdarchid for which a complete hind limb is known is *Zhejiangopterus linhaiensis* (Cai and Wei, 1994). Zhejiang Museum of Natural History ZMNH M1328 has approximate element lengths (in mm) of 155 (femur), 215 (tibia), 57 (MT III), and 42 (digit III). Approximate ratios are T/F = 1.4, MT III/T = 0.265, and MT III/F = 0.37. If the hind limb proportions of *Quetzalcoatlus* were isometric to those of the very much smaller *Zhejiangopterus*, MT III would have been approximately the same length and the estimate of the digits decreased by 25%, or about 4 cm to a length of 11 cm (so 26 cm total for the entire pes).



Outside the azhdarchoids but closely related are the chaoyangopterids (Lü et al., 2008), of which the type specimen of *Jidapterus edentus* (Dong et al., 2003) preserves a complete hind limb. Element lengths (in cm) are 100 (femur), 150 (tibia), 36 (MT III), and 29 (digit III). Approximate ratios are T/F = 1.5, MT III/T = 0.24, and MT III/F = 0.29. If the hind limb proportions of *Quetzalcoatlus* were isometric to those of the very much smaller *Jidapterus*, MT III would have been approximately the same length and the estimate of the digits decreased by 20%, or about 3 cm to a length of 12 cm (so 27 cm total for the entire pes).

The bend in the femoral shaft indicates that the femur was held more horizontally than vertically (animals with columnar hind limbs have straight femora). Positioned at 10° below the horizontal, and at about 30° (± 5°) from the sagittal plane in order to clear the body, the distal femur may have been depressed as low as 45° below the horizontal when walking, although the exact limits are difficult to determine. Larger ratites have an excursion angle of roughly 40–55° (Abourachid and Renous, 2000), but their starting angle depends largely on their size (larger animals have more vertical femora).

As we reconstruct it, in resting posture the femur would have been subhorizontal, the tibia subvertical, and the metatarsus held at a low angle relative to the substrate, and this is consistent with the impression of the heel region in the Crayssac tracks. Even if the foot were naturally digitigrade, which is the case for all other ornithodirans, the angle would have been so low that any natural flexion and extension of the ankle during walking would have impressed the heel, if only for an instant. This has been shown in basal theropod dinosaurs, which are universally known as digitigrade (Gatesy, 2003). Crocodiles also walk with a low metatarsal angle, and they impress their pedes not heel-toe but almost simultaneously as a unit (Brinkman, 1980). Given the proportions and the orientations of the hind-limb segments in *Quetzalcoatlus*, it is clear that protraction and retraction of the tibia would have contributed most strongly to the stride length (the complete gait cycle).

It has been established above and in numerous other publications (e.g., Schaeffer, 1941; Padian, 1983b, 1991, 2008a, 2008b, 2008c; Sereno, 1991; Bennett, 2001b) that the pterosaur hind limb functioned effectively like those of birds and other dinosaurs, in the sense of having erect stance, a parasagittal gait, and joints of the hind limb that were effectively hinges except the hip joint, which in basal pterosaurs featured a quadrangular femoral head as in basal dinosaurs (e.g., Padian, 1986) and a bird-like, rounded femoral head in pterodactyls and their close relatives (Wellnhofer, 1978).

*Quetzalcoatlus* shows no differences from the general pterosaurian-ornithodiran plan in these respects. Pterosaurs are similar to birds and other small dinosaurs in the overall proportions of their hind-limb elements (Padian, 1980:table II-1).

In pterosaurs, the ratio of the tibia to the femur is usually 1.1–1.5, whereas in birds it is 1.4–2.0 and in other small dinosaurs it is usually around 0.8–1.3 (the ratio decreases with size increase in non-avian dinosaurs). For the same animals, respectively, the ratio of the third metatarsal to the tibia is around 0.25–0.60, 0.30–0.65, and 0.45–0.70. Ratios of MT III to the femur are respectively about 0.40–0.75, 0.45–0.85, and 0.7–1.15 (leaving out the penguin, anomalously short in the foot at just over 0.50, but commensurate with the range of other dinosaurs and pterosaurs). Departures from the general overlap in ratios are mainly that birds have a relatively shorter femur and longer tibia and metatarsus than in other ornithodirans.

It should be appreciated that the hind limb effectively controlled the animal's entire pace and stride length, for very practical reasons. As noted above, quadrupedality in pterodactyls was secondary, and initially in the smaller basal pterodactyls there was no need to bear much weight on the forelimbs. As Padian (2003) and Mazin et al. (2003) have noted, pterodactyls would not have walked with the contralateral gait of typical quadrupeds, i.e., LF-RH-RF-LH (LF, left foot; LH, left hand; RF, right foot; RH, right hand), but rather the manus would have to be raised before the ipsilateral foot could be moved, and the foot emplaced before the hand, i.e., LF-LH-RF-RH when considering footfall pattern (LH-LF-RH-RF when considering the sequence of lifting them off the ground). In summary, the sequence is to lift the LH, move and place the LF, and lower the LH, and repeat the cycle for the right side (Fig. 21). We are unaware of any animals that move quadrupedally by first lifting the manus, then lifting and bringing forward the ipsilateral pes (completing the pace length), implanting the pes, and then implanting the manus (and repeating the sequence for the contralateral side). We believe that this is unique among tetrapods (see Biknevicius and Reilly, 2006, and references therein for a full treatment of tetrapod gaits), and that it reflects both the lack of a strong role in terrestrial propulsion by the forelimbs and the very unusual proportions of the limbs with respect to the glenoacetabular distance, which essentially forces the forelimbs to be moved out of the way so that the long hind limb can take a step that is greater than a third of its entire hind-limb length (approximately the length of the glenoacetabular distance).

Figure 22 compares three symmetrical gait patterns of quadrupedal mammals (after Hildebrand, 1976, and other sources) with the postulated gait pattern of pterodactyl pterosaurs such as *Quetzalcoatlus*. The step cycle proceeds left to right, not in space, but in time, documenting the sequence of points of emplacement and lifting of limbs, and durations of each of the four footfalls with respect to each other. Pterodactyls were evidently unique in the sequence of emplacement and lifting of their hands and feet, as described above (see also Biknevicius and Reilly, 2006).

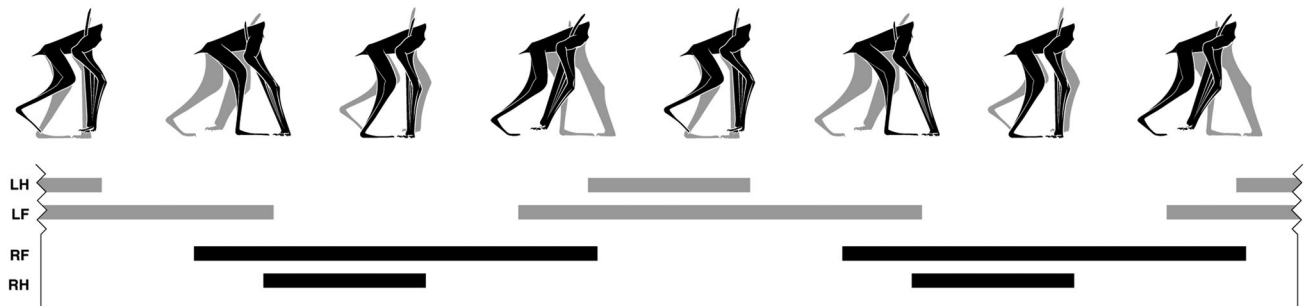


FIGURE 21. Reconstruction of *Quetzalcoatlus* walking quadrupedally in left lateral view. The sequence is to lift the LM, move and place the LP, and lower the LM, and repeat the cycle for the right side. **Abbreviations:** L, left; M, manus; P, pes; R, right.

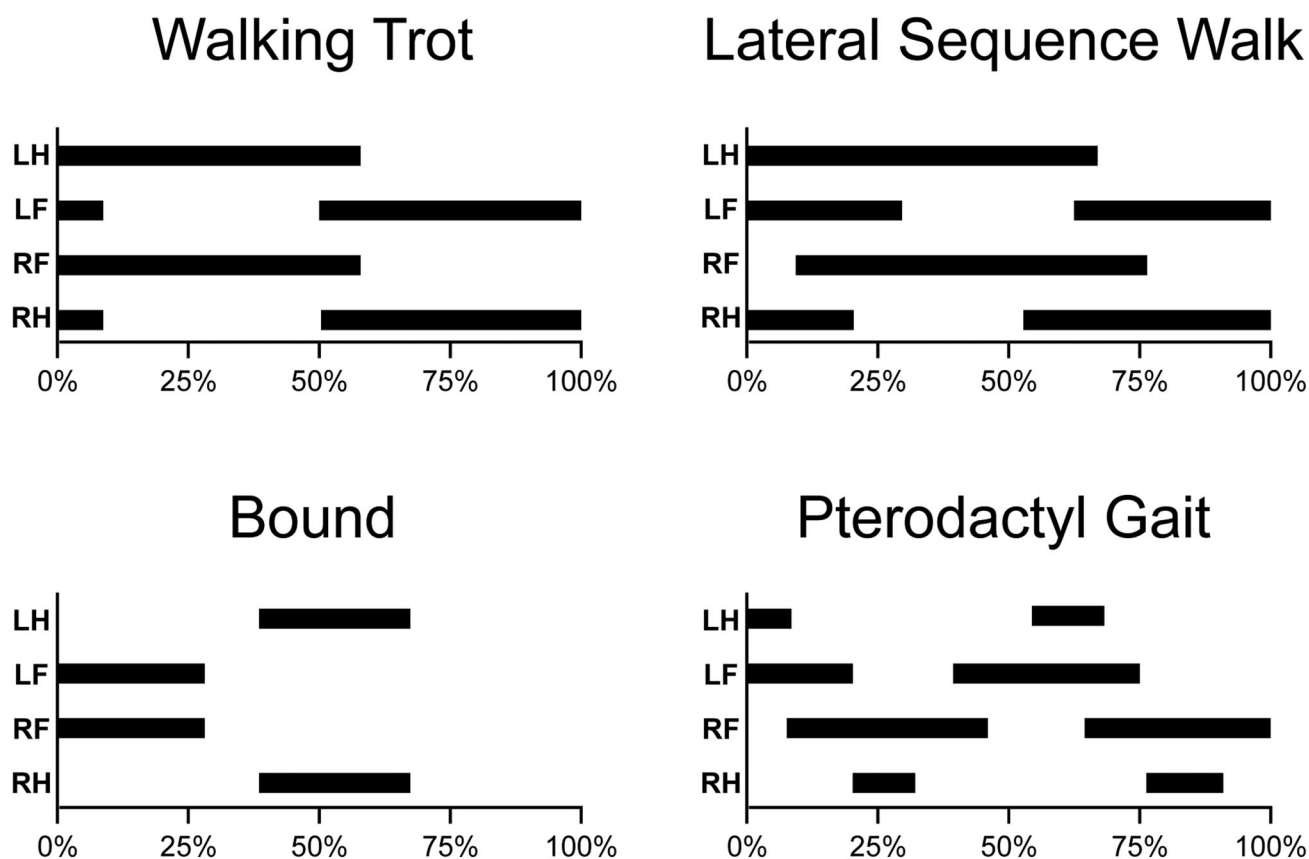


FIGURE 22. Three gait patterns of quadrupedal mammals (after Hildebrand, 1976, and other sources), compared with the postulated gait pattern of pterodactyloid pterosaurs such as *Quetzalcoatlus*. The X-axis measures the percentage of time along the step cycle that a limb is in contact with the ground. For explanation, see text. **Abbreviations:** LF, left foot; LH, left hand; RF, right foot; RH, right hand.

The reasons for this very unusual gait are that (1) the distance between glenoid and hip is so much shorter than the length of either limb that unless the forelimb is lifted out of the way of the hind limb, the animal is confined to steps shorter than the glenoacetabular distance (the femur alone is nearly as long as the glenoacetabular distance); (2) when the humerus is outstretched laterally, the forelimb has very little possibility of protraction and retraction on the ground (see above); (3) the fore-aft excursion of the hind limb is much greater than that of the forelimb; and (4) the hind limb must avoid interfering with the wing during terrestrial progression. For this reason, overstepping (the pes track being located on or anterior to the manus track) is only possible if the manus is first lifted out of the way. Even when the manus track is lateral to the pes track (it may be slightly so or at 2–4 body radii outside it; Mazin et al., 1995), this gait and footfall pattern are preserved in the Crayssac trackmakers. That is to say, the length of the stride (distance between successive prints of the same foot) did not change as the forelimb was adducted and abducted, nor did the morphology of the track change (Mazin et al., 1995). This does not suggest an active role in propulsion, but it does suggest that the whole forelimb needed to be moved to avoid interfering with the hind limb. The motions of the forelimb when extended so far outside the midline were ostensibly the same as when close to it (see next section), differing only in the angle at which the digits were emplaced relative to the midline but, tellingly, not in print morphology. It follows that the role of the forelimbs in stance and gait, if not effectively passive, was at least primarily dependent on the motions of the hind limb. This is also suggested by the landing trackway of the Crayssac

pterodactyloid (Mazin et al., 2009): once the hind limb accomplished the landing, the forelimbs oriented themselves with respect to the hind limb before the animal began to walk.

The MT III/T ratio of *Quetzalcoatlus* is higher than in most non-avian dinosaurs but at the lower range of small theropods and small ornithischians; in contrast, its T/F ratio is higher than any non-avian dinosaur (comparative data from Coombs, 1978). An elongated metatarsus is associated with running and also with ricochet leaping, and dinosaurs with high MT III/T ratios are generally considered ‘cursorial’ (Coombs, 1978). High T/F ratios are also associated with running, and the combination of a very high T/F ratio and a fairly high MT III/T ratio suggests a slight sacrifice of speed to power, the result of concentrating more muscle mass proximally (Alexander, 1989, 2006). We infer from this that the hind limb had good running and leaping capability.

#### Walking: Forelimb

In *Quetzalcoatlus*, when the backbone is angled at about 30° above the horizontal, and the femur is held at 10° below the horizontal and abducted 30° from the midline (which it needs to do in order to clear the body), the knee joint is positioned slightly in front of the shoulder joint (Figs. 19, 21). This is reckoning that in natural position, the glenoid socket was ca. 15 cm lateral to the midline of the body, which is determined by the articulation of the scapula with the notarium and the coracoids with the sternal cristospine. This 15-cm distance represents the body radius across the shoulders (a 30-cm distance between the

glenoid fossae). The distal condyles of the femur, in articulated position, are reconstructed as forming an angle that directs the lower leg slightly medially, so that the feet move closer to the body midline (as in the Crayssac tracks). In order to clear the hind limb, the humerus (at ca. 22 cm length, or about 1.5 body radii) must be substantially extended laterally, and we manipulated the actual material and casts to determine whether and how this would work.

The humerus, when extended laterally, can be rotated forward (pronated) to where the axis of the deltopectoral crest is ca. 35° below the horizontal, placing the axis between its two distal condyles at ca. 45° below the horizontal (and posterior to the vertical axis). At maximal backward rotation (supination), the deltopectoral crest is level with the horizon and the axis of the distal condyles of the humerus form an angle of 10° posterior to the vertical axis (i.e., 80° below the horizontal). So its maximum rotation is about 35°. When the humerus is extended laterally, its maximum depression is ca. 45° below and its elevation 35° above the horizontal (and possibly more). In this level position, the maximum retraction is -45° and possibly up to -80°, if soft tissues allowed, and the maximum protraction is 0°, for a possible fore-aft excursion angle of about 45°.

The elbow is a hinge joint with little possibility of rotation. Its maximum extension is 160°, and it can flex to 90°. As it flexes, the radius slides distally over the ulna (Bramwell and Whitfield, 1974; Padian, 1983b) to displace the outboard segment of the wing by about 25°. Only the slightest rotational movement may have been possible between the syncarpals and the adjacent wing bones, likely limited to absorbing some stresses of flight. However, the intersyncarpal joint may have been able to flex and extend 65–70°, depending on soft tissue restrictions.

In terrestrial progression, the bend near the distal end of the fourth metacarpal has an added effect of helping the distal wing clear the inner wing and torso when folded. When the forearm, the carpus, and the metacarpus are oriented near the sagittal plane (or slightly lateral to it) during walking, the bend in the distal fourth metacarpal is now directed medially. This offsets the MP joint from the inner wing such that the wing finger is directed posterodorsally at a greater angle than the angle between the metacarpus and the substrate, relative to the horizon. This allows the wing finger and the distal wing membrane to clear the inner wing and also the torso medially while still protected by the elbow. Note that in contrast to many authors, our reconstruction of the forelimb implies that in terrestrial locomotion the wing finger was directed between the body wall and the proximal forelimb elements (humerus and radius-ulna), not lateral to the other wing bones as traditionally reconstructed (Fig. 23).

When the humerus is maximally elevated (abducted) and depressed (adducted) (45° maximum range), it can be protracted to 30° behind the vertical axis. At 80° retraction, the humerus can be elevated to 30° above the horizontal and depressed to 45°, giving a potential range of motion of 75°. At 45° retraction, the humerus can be elevated to 30° above the horizontal and depressed to about 55°, giving a potential range of motion of about 85°.

To reconstruct terrestrial motion of the forelimb, we began by placing the distal end of the wing metacarpal at 2 cm above the ground (to account for the spread of the small digits) and with its distal condyles oriented posteriorly (so that the wing finger could be directed behind the elbow and close to the body wall). We then articulated the wrist bones, assuming more or less fixed position, with the wing metacarpal and the radius and the ulna, and assumed a fairly hinge-like motion (because rotation at the wrist was limited). We then fit the humerus against the forearm, using a substantially flexed position of the elbow, and attempted to fit the humerus into the glenoid socket.

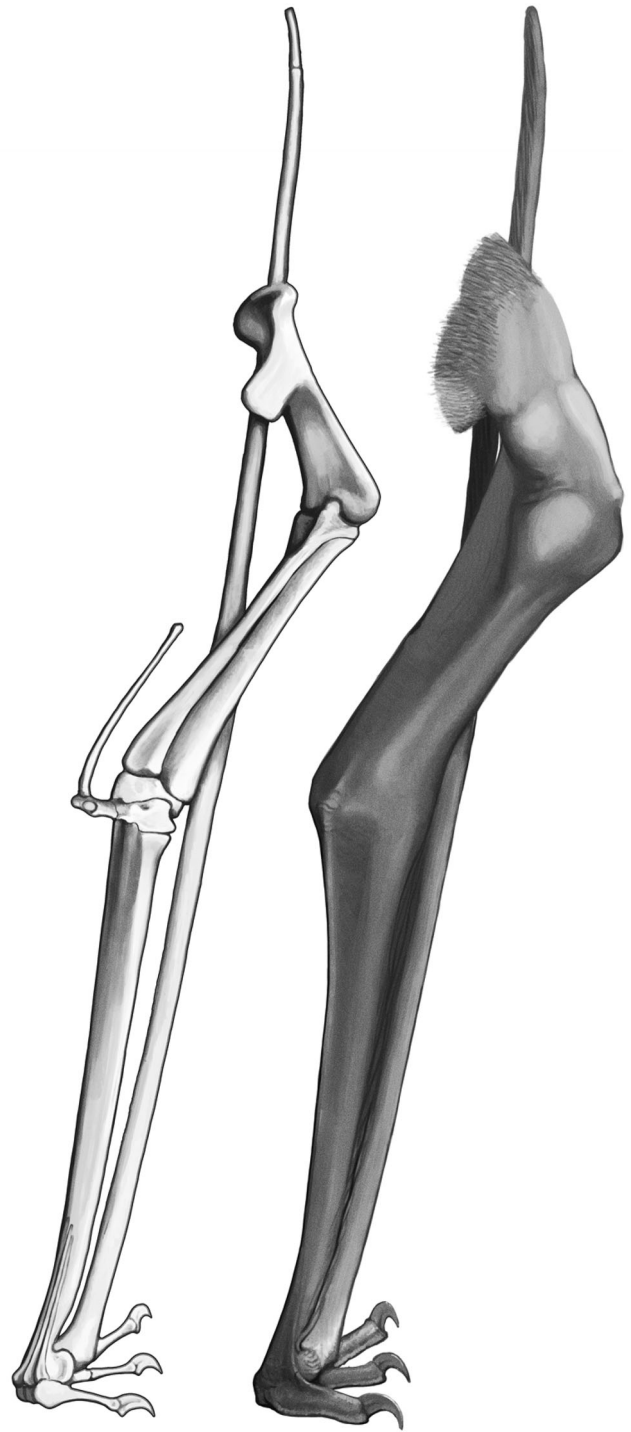


FIGURE 23. Reconstruction of the left forelimb of *Quetzalcoatlus* in lateral view on the ground, showing the spread of the first three digits and the orientation of the wing finger medial to the humerus and the forearm.

We found that, first, it was impossible to place the manus (located by the distal condyles of MC IV) on the ground directly lateral to the glenoid at a distance of 1.5 body radii (22.5 cm). The closest possible position of the manus to the midline is 3 body radii, and this cannot be accomplished unless the glenoid socket is positioned 20 cm higher than the position we initiated, with a

30° elevation of the dorsum and a femur oriented 10° below the horizontal. This problem can be approached in three ways: (1) increasing the anterior elevation of the dorsal column by 20 cm, which places the glenoid socket closer to the knee joint in a horizontal plane; (2) extending the hip (retracting the femur) by 20 cm when beginning the propulsive phase (a retraction of an additional 25°, which is well in line with ratites of various sizes; Abourachid and Renous, 2000); and (3) acknowledging that the hand may not have been able to impress the ground so close to the midline (the reconstruction was based on the Crayssac trackmaker, which was very different in size and configuration). A combination of these approaches is possible, and we do not know what *Quetzalcoatlus* actually did because we have no trackways.

With the glenoid in a more elevated position, the manus may be brought to within 3 body radii of the midline. In this position, the humerus is angled 30° below the horizon and 50° posterior to a lateral position. The elbow is then able to flex and extend (in this position, elevate and depress) the forearm and the metacarpus, but the humerus cannot rotate (pronate and supinate) to any significant degree. The humerus can protract and retract about 20° in this position, which adds only about 6 cm to stride length. Given the possible range of motion of the shoulder and elbow as just described, the forearm and the metacarpus were effectively oriented anteriorly, but they could do little more than elevate and depress at the elbow. This is of critical importance for informing us about how the forelimb worked on the ground.

As shown in the previous section, the hind limb controls the length of the animal's stride. As we have reconstructed the hind limb posture, the pace length (the distance that a foot travels in a single step) could have been about 75 cm and the stride length twice that, or 150 cm. (Other lengths and speeds are possible, but this seemed a reasonable walking gait.)

Given the possible directions and mechanical limitations of motion at the shoulder and other forelimb joints, we find it implausible that the forelimb could have contributed much to terrestrial propulsion through retraction. Roles in braking forward motion, in turning, and in support of the anterior part of the body during quadrupedal standing and walking appear more plausible. The forelimb could not have contributed any significant force to terrestrial propulsion in traditional pose for the following reasons. When the humerus was extended laterally and horizontally, and rotated (pronated) until the glenoid facets prevented further rotation, the manus reached the ground at about 28–30 cm anterior to the glenoid. In this position, the humerus could not further pronate and it could retract only as just noted (6 cm distal excursion), which is insignificant (less than 10%) compared with the estimated hind-limb pace. Such motion combined with flexion at the elbow would adduct and rotate the metacarpus out of the plane of contact with the ground. It appears instead that when the humerus was retracted as far as possible, its motion was a slight elevation and depression, the elbow flexed essentially to elevate and depress the forearm and the metacarpus, and the metacarpus moved very little against the wrist; the effect of this motion was to orient its distal condyles as vertically as possible. In this way, the forelimb was essentially only raised and lowered during walking, and for this reason it was coordinated as described above to follow the pacing of its ipsilateral hind limb. In other words, it was essentially passive and did not contribute substantially to retraction of the forelimb or forward propulsion of the animal. This accords with trackways of pterodactyloids, which, although indistinct about the details of phalanges and digits, do not show a substantial kinematic component to the manual step cycle (Padian and Olsen, 1984; Padian, 2003).

There remains the consideration of the position and role of the first three manual digits in terrestrial locomotion. Specimens of

other pterodactyloids (Wellnhofer, 1978) show that the first three metacarpals terminate just short of the double condyle joint of the distal end of the fourth (wing) metacarpal, and on its medial face. When the metacarpophalangeal joint of the wing finger touches the ground, the first three fingers are positioned medial to it, and the phalanges flex medially. They cannot flex dorsoventrally in this position, nor in flight for that matter. In the Crayssac trackways, one digit appears to be directed anteriorly, one laterally, and one posteriorly. To accomplish this, the first three digits must rotate laterally because their natural position is medial to the wing finger. We reason that the wing finger cannot touch the ground in these footprints, or the first three fingers could not be lateral to it, if preserved specimens and conventional reconstructions are correct. Therefore, the three prongs of the manus print of the Crayssac tracks should be those of the first three digits, but we leave it to others to work out the homologies, given that no phalangeal impressions are distinct enough to help. Some tracks questionably assigned to pterosaurs feature four manual digit impressions (one anterior, two lateral, one posterior), which means either a shift in posture and the inclusion of the wing finger or that these are crocodile tracks (Padian, 2003).

As noted above, because the sediment around the impressions of the small digits in pterodactyloid footprints (Mazin et al., 1995) is not disturbed by their motion, the digits had no role in traction or propulsion during terrestrial locomotion.

#### LAUNCH MECHANICS

There are three main hypotheses about how pterosaurs may have launched themselves from the ground: a running takeoff in bipedal posture, a standing takeoff in bipedal posture, and a standing takeoff in quadrupedal posture. Some of these hypotheses have been more rigorously examined than others, and there are variations on each. Space does not permit us a full review and evaluation of the views provided by various authors, but we offer some general considerations here.

#### Phylogeny and Size

First, the importance of phylogeny: it is well known that pterodactyloids differ from basal pterosaurs in many anatomical respects, and there is also great variation throughout pterosaurs in features and proportions. It is commonly thought that the pterodactyloid bauplan provided greater flight control and maneuverability, but the implications for terrestrial progression are sometimes overlooked. It is not clear how the differences in the deltopectoral crests of pteranodontids and azhdarchids, for example, may have affected flight mechanics and walking, but they appear to have had different ranges of motion.

Second, the importance of size: as linear size absolutely increases, surface area increases by the square, and mass by the cube, of that number in isometrically scaled shapes (Pennycuik, 1972). This means that a larger animal will weigh proportionally more than a smaller one of approximately the same shape, and that the volume and power of its muscles must increase proportionally to keep up with the size increase. It also means that a large pterosaur would face substantially greater functional challenges to performing some activities than a small pterosaur would face. For example, sustained flapping is much more difficult for larger flyers, which is why large birds soar.

Our study deals with an animal with a 5-m wingspan because most of the material clusters around that size range. A 10-m animal might have been up to eight times heavier (the cube of 2, but see below) than a small one of half the linear dimensions and would have required much more power to perform the same functions at the same frequency and amplitude. Because the muscle mass required for such a scaling is prohibitive, some

functions or potentials of smaller animals would have been eliminated or restricted, and other solutions must have been found. These could have included a change in body shape, reduction of mass, and alteration of the wing planform: a giant flying animal proportionally eight times heavier than a smaller one would have had an unsustainable wing loading if it did not change its physical proportions (Pennycuik, 1972).

In all reconstructions of launching, we face speculation about size and the potential actuation of motions. Given that current estimates of the 10-m *Quetzalcoatlus* range from 70 to 250 kg (Habib, 2008; Witton and Habib, 2010), a factor of about 3.5, size-related parameters of function and actuation will vary accordingly.

The largest specimen of *Quetzalcoatlus* is too incomplete for any reliable estimates of mass, which can vary by 50% in flying animals naturally as a result of feeding, pregnancy, starvation, and other factors for individuals with the same wingspan (Padian, unpubl. data on *Pteropus* in the American Museum of Natural History, New York). In our view, a body mass of 150 kg is commensurate with a less expansive wing than traditionally reconstructed (because the legs could not attain a bat-like posture [see above] and could not have been directed fully posteriorly). If the Crayssac trackmaker was roughly the size of a pigeon, its flight muscles may have constituted about 80 g of an animal of about 400 g (Pennycuik and Parker, 1966); flight muscles generally constitute up to 20% of an animal's mass. By this reasoning, the flight muscles of the largest specimen of *Quetzalcoatlus*, roughly 500 times larger in body mass, may have been on the order of 40 kg (14 kg for a light mass estimate of 70 kg, 30 kg for our preferred estimate of 150 kg, and 50 kg for a heavy mass estimate of 250 kg), not counting upstroke muscles and associated skeletal and soft parts or compensation for the increase in wing loading brought on by increased size. However, this assumes proportional isometry, which is not generally true for flying animals: larger flyers change proportions, flap less, use thermals and dynamic lift more when soaring, and reduce mass (Pennycuik, 1972). Marden (1994) showed that in flight muscles, mass-specific power actually increases with body mass, but it is not clear what implications this observation might have for launching, because the 'quadrupedal launch hypothesis' requires a sudden exertion and instantaneous acceleration of forelimb muscles that require enormous power.

Here, we apply our understanding of the functional morphology of *Quetzalcoatlus*, represented by the 5 m size range, to hypotheses about launching. We do not extend our interpretations to other pterosaurs. However, to the extent that their morphologies may have been similar, the same issues will apply. Figure 24 reconstructs a bipedal launch from a standing position, which is favored by K.P., and Figure 25 depicts the animal launching in quadrupedal pose, which is favored by J.R.C. and J.C.

### Running Takeoff in Bipedal Posture

The lengths of the femur and tibia in *Quetzalcoatlus* are close to those of a human just short of 2 m tall. There are many differences: the hind limb is columnar in human, whereas it is flexed in the pterosaur, and the pelvis and the orientation of the spine are completely different. Yet both appear to have had a pace length of about 75 cm during normal walking (we reconstructed this from the articulated hind limb in *Quetzalcoatlus* approximating normal range of motion of flexion and extension at the hip, knee, and metatarsus). Humans can run for short distances at about 7 m/s (~15 mph), and if this were possible for *Quetzalcoatlus*, and if the remaining speed necessary for liftoff could have been generated by the wings, a running liftoff would have been theoretically possible. However, as soon as the animal left the ground, it would no longer gain thrust from the hind limbs, and this would have to be taken up by the wings.

The difficulty is that in a running position, the wing could have been depressed only 20° below the horizontal. This seems unlikely to have been sufficient, because the amplitude of the stroke could have been nowhere near as great as in smaller living birds such as the albatross that use a running, flapping takeoff. Needless to say, head winds would have been a great aid, but we cannot assume that they were always present when the animal needed to launch. If 7 m/s were a sufficient speed for takeoff, and if *Quetzalcoatlus* could reach this speed, there would still be the problem of clearing the ground so that the wings could begin flapping (i.e., the problem of height is not eliminated by running speed). If the wing needed to be depressed 60° below the horizon to flap effectively, the animal would have to bring the torso to an additional height of nearly 2 m by leaping when running. Whether this is possible depends on estimates of the mass and muscle power of the legs, which is a problem outside the scope of this paper. If it was not possible for *Quetzalcoatlus northropi* or other large pterosaurs, it does not necessarily follow that it was impossible for smaller forms.

### Standing Takeoff in Bipedal Posture

Many of the same parameters of the previous model apply here (Fig. 24). Although a leap from fixed position lacks the acceleration from running speed, it allows a greater crouch before takeoff. We estimate that the typical hind limb proportions we use here—femur 36 cm, tibia 58 cm, metatarsus 15 cm, pes 15 cm—would allow the acetabulum to be lowered from a resting position of about 1.25 m to about 45–60 cm above the ground, with the femur in horizontal position—a crouch of about half to two-thirds of the original height. (The angle at the knee is about 45–70°; further flexion dislocates the joint.) This is the maximum crouch available, and it propels the animal vertically. Again, for the wings to clear the ground, the hind limb would have had to propel the acetabulum to a height of at least 3 m. This assumes that the wings would have been able to flap sufficiently to take over from there. Otherwise, a higher leap would have been necessary to compensate for loss of height in the air until the wings could actuate flight. It may be argued that the loss of the large *M. caudofemoralis* in pterodactyloids would raise the question of hip extension power. However, the loss of the long tail in basal maniraptorans, through *Archaeopteryx* to the reduced-tail ornithurine birds such as *Confuciusornis*, had little effect on the morphology of the pelvis. More work is needed on this problem in pterosaurs, but given the functional transition in birds, the burden would seem to be on showing that this would have been a problem for pterodactyloids.

It may also be argued that the potential difficulties of sudden acceleration and bone stress that are of concern for the quadrupedal launch would also apply to a bipedal launch. This is true to some extent, the legs are already built for the motions required in leaping, i.e., rotation of the femur and extension of the knee and ankle. Reconstruction of muscle mass and estimated power is beyond the scope of this paper, but it would appear that the acceleration of the hind limbs to leap into the air would have been less than that required for the forelimbs to actuate a quadrupedal launch (see below).

The caveats at the end of the previous section also apply here.

### Standing Takeoff in Quadrupedal Posture

As far as the hind limbs are concerned, the parameters of the previous model apply here (Fig. 25). In the Habib-Molnar model of the quadrupedal launch (Habib, 2008; Molnar, 2009; hereafter 'quad launch'), nearly all the forward thrust is required to be generated by the forelimbs. As just noted, the maximum hind-limb crouch possible provides a nearly vertical thrust. The 'quad launch' model, based on the very different proportions of

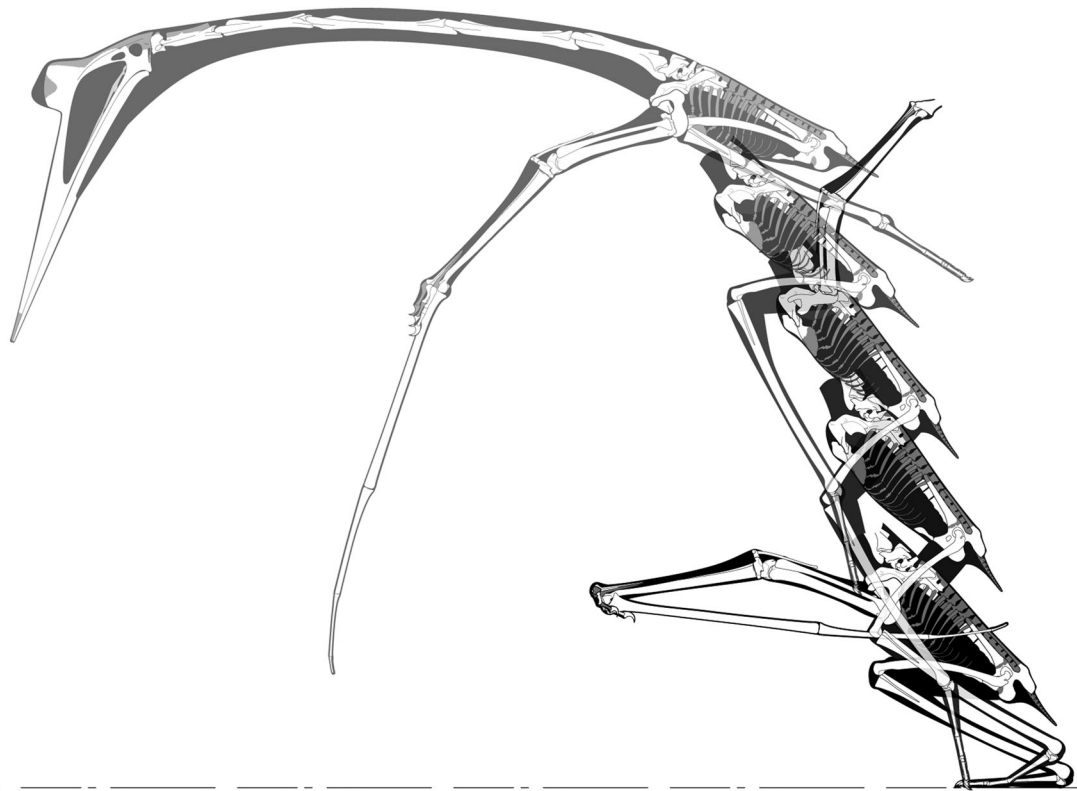


FIGURE 24. Reconstruction of the position of the skeleton in left lateral view as the animal crouches just before a hypothesized bipedal hind-limb launch and as it begins to flap its wings.

an anhanguerid, suggests that the body is held nearly vertical and that the hind limb is columnar, with the knee extended to  $180^\circ$ . (This model can be viewed at [www.youtube.com/watch?v=ALziqtuLxBQ](http://www.youtube.com/watch?v=ALziqtuLxBQ).) The latter position was impossible because the distal condyles of the femur are subterminal (i.e., with their major axis oriented  $90^\circ$  ventral to the femoral shaft) and the femur must be held in a subhorizontal position as noted earlier, rotating between there and subvertical. This applies to all pterosaurs. So the Habib-Molnar model requires hind limb adjustment, although this will likely not change the overall protocol of the model, because the quad launch relies almost entirely on the forelimbs.

The 'quad launch' model for the anhanguerid provides very little contribution from the hind limb. The upward thrust of the legs only tilts the body forward, and because the main muscle mass is concentrated in the pectoral region, the translation of this force pushes the torso forward, over the fulcrum of the forelimb. At this point, its contribution ends. This action is unrealistic for *Quetzalcoatlus* because, as noted above, the knee was substantially flexed and the hind limbs are proportionally much longer. The ratio of the hind limb (femur and tibia only) to the glenoacetabular length is 1.9 in *Pterodactylus*, 2.5 in *Pteranodon*, 2.7 in *Quetzalcoatlus*, but only 1.5 in *Anhanguera*, anomalously small. So for several reasons, if the quad launch works at all for *Anhanguera*, its details cannot be easily transferred to other pterodactyloids. Habib (2008) admits the possible contribution of the hind limb to the quad launch in other pterodactyloids, but none has been specifically studied to date; we accept this possibility, although J.R.C. believes that even in *Quetzalcoatlus* a quad launch would have had very little contribution from the hind limb. This problem requires further attention.

The main question, however, is what the contribution of the forelimb can be. This depends partly on its orientation, partly on the kinematics of the hypothesized gait, and partly on the power that muscles can generate, given the stance from which motion originates. But it may depend most critically on the ability of the forelimb bones to withstand a sudden bending moment perpendicular to their shafts that is sufficient to launch the animal's body mass, which they are not obviously adapted to do, given their thin walls. These parameters are progressively speculative. We showed above that if the humerus is oriented directly laterally from the glenoid socket, the rotation needed to touch the ground with the hand effectively prohibits any further retraction, so the forelimb cannot assist in terrestrial progression in that position. It can, however, be raised and lowered so that the hind limb can step past it as it propels terrestrial movement. This is how we suspect the animal normally walked.

The situation changes, however, if the distal end of the humerus can be retracted and depressed. If the humerus is retracted to  $80^\circ$  behind the horizontal plane of the glenoid and elevated  $30^\circ$  above the horizontal plane, the humerus can be depressed and protracted, bringing the forelimb down and forward until the manus touches the ground (Fig. 25). In this position, the wrist joint is flexed up to  $50\text{--}60^\circ$ ; the ability to do this depends mainly on interpretation of how much mobility was available at the intercarpal joint. This is the initial resting position that we infer. However, it is not likely to have been used in walking, because pterodactyloid footprints (Mazin et al., 1995) show no evidence of retraction of the manus; it is merely an emplacement because there is no distortion of the sediment. So no forces were being exerted on the manus during terrestrial locomotion.

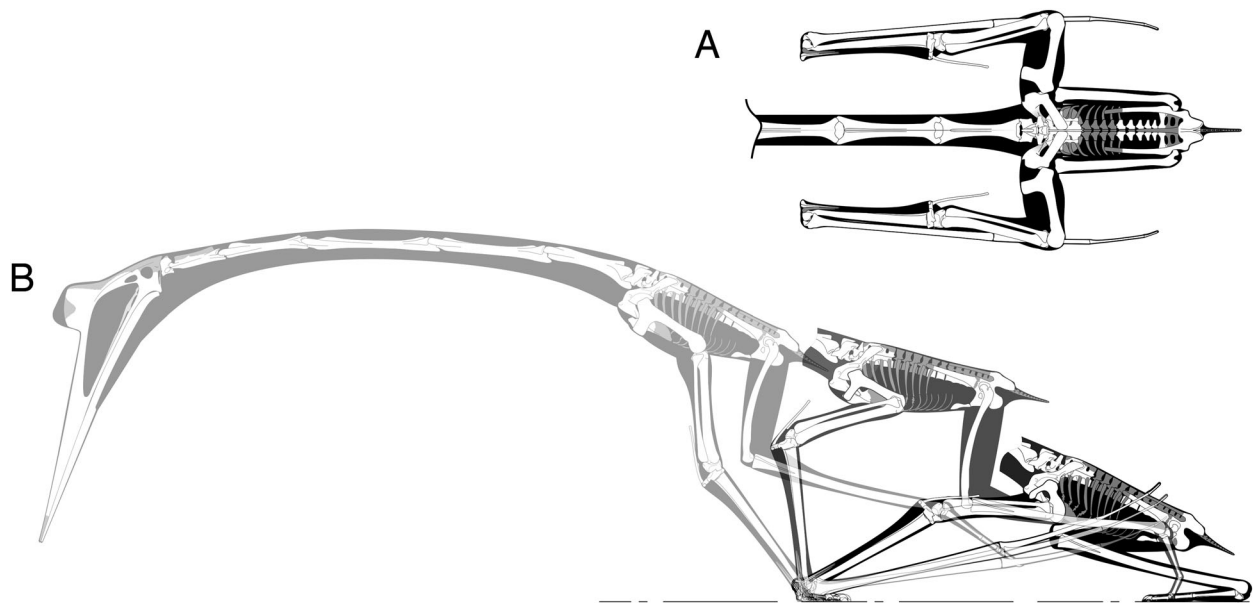


FIGURE 25. Reconstruction of the position of the skeleton in **A**, dorsal and **B**, left lateral views as the animal crouches just before a hypothesized quadrupedal launch and as it thrusts forward with the forelimbs and the hind limbs.

To commence the launch in *Quetzalcoatlus*, as we reconstruct it, the animal would first depress the hip region into a crouch, as described above. The humerus was extended laterally in the transverse plane and  $40^\circ$  below the horizontal. The forearm and the metacarpus are flexed anteriorly to contact the ground, with the anterior side of the metacarpus facing dorsomedially. As it extended the hind limbs into a leap, the humerus would gradually retract  $20^\circ$ , the elbow would flex about  $20\text{--}25^\circ$ , and the wrist would also flex from  $20\text{--}25^\circ$ . The humerus eventually reaches a position where it is depressed  $50^\circ$  below the horizontal and retracted  $45^\circ$  behind the transverse plane. To launch, the elbow extends and the wrist straightens.

Depending on the force that could be generated, the vector of these combined forelimb and hind limb motions should propel the animal upward and forward. In the forelimb, motions of the humerus contribute very little to this stroke; it is a relatively short bone, and most of its power rests in the pectoralis muscles that contribute to flight. The main work has to be done by the elbow as it extends, presumably mainly involving *M. triceps brachii*. This muscle was likely very strong, because it powered the recovery stroke and extension of the elbow during flight. Extension of the wrist joint would have been accomplished by *M. flexor carpi ulnaris* and *M. flexor digitorum* complex (Bennett, 2008:fig. 3). It must be recognized that these muscles and tendons would have had to act with tremendous force and acceleration in order to launch the animal to provide height and thrust sufficient for commencing the flight stroke. If it is expected that this launch would provide sufficient forward thrust to begin a flight trajectory, then it would have to provide an almost instantaneous speed of at least 7 m/s, or whatever speed is postulated for a running takeoff (see above). Estimating the mass and strength of these muscles and quantifying their coordination to produce the quad launch trajectory imagined here is beyond the scope of the present paper. However, we refer readers to the ‘Phylogeny and Size’ section above for an important caveat regarding available muscle power for large and giant flying animals.

#### Why the Vampire Bat Is Not a Good Model for a Pterosaur Quadrupedal Launch

Molnar (2009) notes that her model developed in concert with Michael Habib is based on the launch mechanism of the vampire bat (Schutt et al., 1997). Whether or not a quad launch was possible for pterodactyloids of various sizes and shapes, there are enough differences between bats and pterodactyloids that the comparison is not apt.

Films of the vampire bat (*Desmodus rotundus*) walking and hopping on a treadmill, taken by Daniel Riskin (see [www.youtube.com/watch?v=qWOUZAa5vlQ](http://www.youtube.com/watch?v=qWOUZAa5vlQ)), and Merlin Tuttle’s film of a vampire bat taking off in the wild (see [www.youtube.com/watch?v=kIl\\_bYFMr8o](http://www.youtube.com/watch?v=kIl_bYFMr8o)) show that the hind limbs contribute virtually nothing to the leap and therefore would have had little to give to a full launch. The reason is that in bats, the hind limb is oriented laterally at the hip, so the knee and feet flex and extend laterally; no forward thrust can be provided. The movements of the hind limb only keep the torso level. This is in contrast to the parasagittal orientation and much greater size and strength of the hind limbs in *Quetzalcoatlus* and most other pterosaurs (as noted, the anhangerid used in the Habib-Molnar quad launch has unusually short hind limbs). It was noted above that in *Quetzalcoatlus*, the hind limb should have been able to contribute substantially to both upward and horizontal motion.

The forelimb of the vampire bat mainly executes the leap by rotation and retraction of the laterally oriented humerus against the glenoid. The flexion of the humerus contributes up to 15% of vertical takeoff, mostly overcoming inertia; the rest is accomplished by extension of the elbow (Schutt et al., 1997), which is in a completely different plane than was possible in *Quetzalcoatlus* (see above). The elbow is held more or less in fixed position. The metacarpus in *Desmodus* is not involved in launching, whereas it would be critical to a quad launch in pterodactyloids. In pterosaurs, as noted above, when the humerus is laterally oriented and rotated so that the manus can touch the ground, it cannot be further rotated and retracted. A quad launch is not possible from this position. Even if the humerus is

retracted, as described above for *Quetzalcoatlus*, most of the work of the leap or launch must be done by extension of the elbow and the metacarpus, which the vampire bat does not do. And beyond this, there is the size difference between these small bats and giant pterodactyls, and the resultant effects of scale on performance (see above).

### CONCLUSIONS

A general model of the skeleton on the ground is reconstructed in Figure 26. *Quetzalcoatlus* is the largest known flying animal for which adequate fossil material exists to provide a reliable reconstruction of the skeleton. This material represents nearly all skeletal elements (apart from the free dorsals and the caudal vertebrae, and parts of the skull and pelvis are poorly known), constituting a single giant specimen referred to *Q. northropi* and several hundred bones of a variety of smaller individuals about half its size referred to the new taxon *Q. lawsoni*, plus a skull and cervical series referred to another new taxon, *Wellnhoferus brevirostris* (Andres and Langston, 2021). The giant specimen is represented only by a complete humerus and radius, and a nearly complete wing phalanx, plus other partial material of an ulna and syncarpals. As a result, there is uncertainty in reconstructing its skeletal proportions, and isometry with the smaller specimens cannot be assumed. The mass and the wing area are similarly conjectural, but estimates of the latter must be constrained by the findings that the hind limb could not have been extended, abducted, and rotated to fit bat-like into the plane of the wing, nor could the femur, the tibia, and the pes have been extended posteriorly in the horizontal plane. Rather, the hip and knee could have been flexed as in long-legged flying birds such as storks and herons, and this makes any functional attachment of the wing to the hind limb implausible.

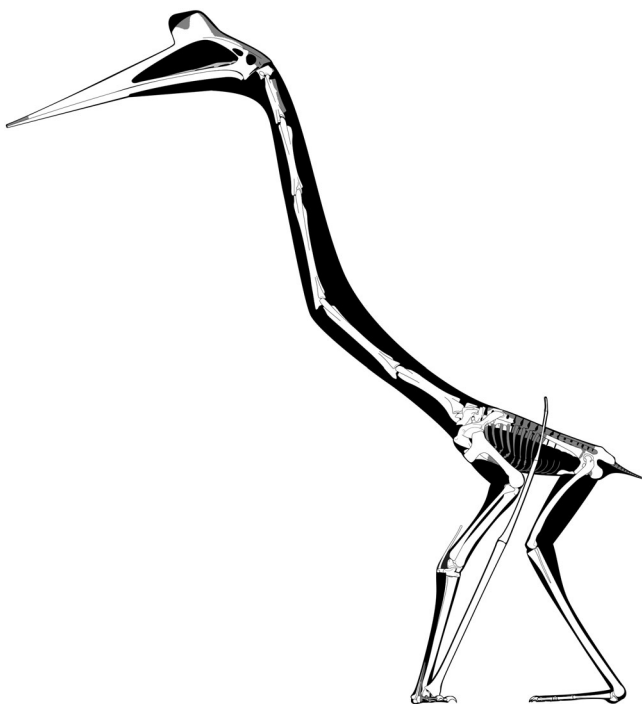


FIGURE 26. Reconstruction of *Quetzalcoatlus lawsoni* in lateral view as posed in quadrupedal terrestrial stance.

Based on reconstructions of the 5-m sample, *Quetzalcoatlus lawsoni* had substantial flapping power actuated from the short and strong wing root of the humerus and pectoral girdle, which was anchored to the notarium and the sternum. At the glenoid, the humerus could have been rotated to some extent but had considerable range of depression and elevation, and its motions controlled much of the orientation of the entire wing. This motion was augmented by flexion of the elbow, which slid the radius distally over the ulna as in other pterosaurs (e.g., Bramwell and Whitfield, 1974), and by flexion and extension mainly at the intrasynsarpal joint and at the metacarpophalangeal joint. These motions also caused elevation and depression of the wing bones at some joints as a result of their orientations.

On the ground, *Quetzalcoatlus* likely adopted a quadrupedal pose, but its walking gait was unlike that of typical quadrupeds. Like other pterodactyls, it would have raised its manus just before the ipsilateral pes was raised, brought forward, and emplaced in a new track, and then the manus would have been emplaced anterior or lateral to it. The action was then repeated for the contralateral limbs. This motion was necessary because when the manus is on the ground, the humerus cannot be rotated to help retract it, and the humerus was not retracted to provide purchase for the manus to contribute to forward locomotion because pterodactyl tracks show no evidence of deep engagement with the substrate (Mazin et al., 1995). The forelimbs functioned something like giant walking sticks; the gait was effectively bipedal because virtually all the power came from the hind limbs.

Three general models of takeoff have been proposed, and all face challenges. A bipedal running launch faces the difficulties of acquiring enough speed to make the effort possible. A standing bipedal launch would have required a leap sufficient to bring the acetabulum at least three hip heights off the ground so that the wingtips could have depressed to at least 60° below the horizon in initiating the flight stroke. However, this leap would have generated more lift than thrust, and if it is assumed that great thrust was necessary for this kind of launch, the model may need to be reconsidered. A quadrupedal launch in *Quetzalcoatlus* would contribute substantial lift from the hind limbs, but the bulk of the forward thrust would have been required to be produced by rapid acceleration of the extension of the elbow and intrasynsarpal joints, and it is not clear whether the muscle power and bone strength were adequate to the task.

*Quetzalcoatlus* has been visualized as a carrion feeder, a fish skimmer, or a large stork. Its jaws are long, thin, attenuated, and perhaps slightly flattened at the beak. These are not the jaws of a carrion feeder. ‘Skimming’ at the water surface has been proposed by various authors, but as noted above, these comparisons are imprecise because birds use several behaviors in feeding at the water’s surface, none of which seems appropriate for *Quetzalcoatlus*. Moreover, as Langston (1981) noted, *Quetzalcoatlus* is found about as far from the seacoast as was possible in the latest Cretaceous (about 400 km), although this does not rule out the possibility of large bodies of fresh water (Lehman, 2021). These waters were likely shallow, and we visualize *Quetzalcoatlus* much like a living stork or heron, wading in shallow water or pacing in meadows, plucking fishes, invertebrates, and small tetrapods with its long, prehensile beak.

The model of *Quetzalcoatlus* as a giant pterosaurian stork is consistent with several aspects of its anatomy. The neck and the head had considerable ability to flex and extend vertically and to some degree laterally. The narrow skull and jaws suggest that prey was relatively small, and the toothless jaws suggest the swallowing of prey whole (see also Witton and Naish, 2008). If the animal plucked its prey off the ground or from shallow water (fishes, amphibians, small reptiles), it could have raised its neck, extended its head vertically, and swallowed. The long, almost



chopstick-like jaws appear adapted for plucking and seizing, but not for mastication. The neck could rotate laterally about 70° and the head another 20°, and the lateral placements of the orbits suggest the ability to see 180° in either direction when rotated. Anterior stereoscopic vision is assumed, but the available skull material cannot test the hypothesis (Kellner and Langston, 1996). The five to seven free dorsals (which are not preserved in *Quetzalcoatlus*, so based on comparisons) are presumed to have had laterally compressed centra with deep procoely that suggests the possibility of lateral rotation in the middle of the back; this likely had no major role in flight but could have allowed postural adjustment on the ground without having to move the entire body. The reconstruction of the Big Bend, Texas, area in the latest Cretaceous suggests a fluvial plain (Kellner and Langston, 1996; Lehman, 2021) in which small vertebrates could have been abundant, and thermals and winds may have provided the means of aerial foraging and travel among food sites for these huge, mainly soaring animals.

#### ACKNOWLEDGMENTS

We are tremendously grateful to the curators, staff, and students of the Texas Vertebrate Paleontology Collections at the University of Texas, Austin. This project would not have been initiated without the support and encouragement of T. B. Rowe, former director and M. Brown, current director. We offer our sincere thanks to them and also to C. Bell, C. Sagebiel, K. Bader, and S. Egberts for help with logistics, history, preparation, and curation. We also thank T. Lehman of Texas Tech University for information on the history of collecting and the provenience of the specimens, and B. Andres, A. Manafzadeh, and K. P. Dial for helpful discussions and references. We benefited greatly from the comments of two anonymous referees and B. Andres. We thank A. Manafzadeh for drafting Figure 22.

Wann Langston first undertook the study of *Quetzalcoatlus* in the late 1970s, after its discoverer and first describer, Douglas Lawson, left the academic field of paleontology. We salute Doug for his persistence, acumen, and interest in excavating and interpreting these amazing specimens. Over the next 35 years, amid other projects, Wann engaged the advice and cooperation of many other scientists and artists as he struggled to understand the anatomy, systematics, functional morphology, flight, and ecology of this remarkable animal. It was a daunting job for one person, and Wann, whose first loves were crocodiles and dinosaurs, proceeded slowly on the giant pterosaur. Apart from his published paper with A. W. A. Kellner on the skull material (Kellner and Langston, 1996) and an early article (Langston, 1981) in *Scientific American*, Wann left only some pages of notes on the anatomy of various bones, many folders of measurements, calculations, drawings, sketches, and hypotheses, and a partial draft (now lost) of a manuscript on bioaerodynamics with J. R. Cunningham. In working on this material, we constantly felt his presence and regretted his absence from the fulfillment of his long labors. We feel certain that he would have joined us in thanking and acknowledging the many other people he consulted and worked with over 30 years, including those listed above and the late P. MacCready, the late J. McMasters, the late H. Ashley, A. Brooks, I. Kroo, S. C. Bennett, G. S. Paul, M. Smith, E. Holley, M. Nicholls, and the late D. Baird, as well as his colleagues at UT B. Rainey, E. Yarmer, K. Davies, and W. Amaral were all involved in the collection, preparation, molding, and casting of these specimens, and no one was more intimately involved than Wann himself.

#### LITERATURE CITED

- Abourachid, A., and S. Renous. 2000. Bipedal locomotion in ratites (Paleognathiformes): examples of cursorial birds. *Ibis* 142:538–549.
- Alexander, R. M. 1989. *Dynamics of Dinosaurs and Other Extinct Giants*. Columbia University Press, New York, 167 pp.
- Alexander, R. M. 2006. *Principles of Animal Locomotion*. Princeton University Press, Princeton, New Jersey, 384 pp.
- Anderson, J. D., Jr. 1997. *A History of Aerodynamics*. McGraw Hill, New York, 478 pp.
- Andres, B. 2021. Phylogenetic systematics of *Quetzalcoatlus* Lawson 1975 (Pterodactyloidea: Azhdarchoidea); pp. 203–217 in K. Padian and M. A. Brown. *The Late Cretaceous pterosaur Quetzalcoatlus Lawson 1975 (Pterodactyloidea: Azhdarchoidea)*. Society of Vertebrate Paleontology Memoir 19. *Journal of Vertebrate Paleontology* 41(2, Supplement).
- Andres, B., and W. Langston. 2021. Morphology and taxonomy of *Quetzalcoatlus* (Pterodactyloidea: Azhdarchoidea); pp. 46–202 in K. Padian and M. A. Brown. *The Late Cretaceous pterosaur Quetzalcoatlus Lawson 1975 (Pterodactyloidea: Azhdarchoidea)*. Society of Vertebrate Paleontology Memoir 19. *Journal of Vertebrate Paleontology* 41(2, Supplement).
- Arnold, P., M. S. Fischer, and J. A. Nyakatura. 2014. Soft tissue influence on ex vivo mobility in the hip of *Iguana*: comparison with in vivo movement and its bearing on joint motion of fossil sprawling tetrapods. *Journal of Anatomy* 225:31–41.
- Bennett, S. C. 1997. Terrestrial locomotion of pterosaurs: a reconstruction based on *Pteraichnus* trackways. *Journal of Vertebrate Paleontology* 17:104–113.
- Bennett, S. C. 2001a. The osteology and functional morphology of the Late Cretaceous pterosaur *Pteranodon*. Part I. General description of osteology. *Palaeontographica, Abteilung A* 260:1–112.
- Bennett, S. C. 2001b. The osteology and functional morphology of the Late Cretaceous pterosaur *Pteranodon*. Part II. Size and functional morphology. *Palaeontographica, Abteilung A* 260:113–153.
- Bennett, S. C. 2003. A survey of pathologies of large pterodactyloid pterosaurs. *Palaeontology* 46:185–198.
- Bennett, S. C. 2007. Articulation and function of the pteroid bone of pterosaurs. *Journal of Vertebrate Paleontology* 27:881–891.
- Bennett, S. C. 2008. Morphological evolution of the wing of pterosaurs: myology and function. *Zitteliana* B28:127–141.
- Bertram, J., and A. Biewener. 1992. Allometry and curvature in the long bones of quadrupedal mammals. *Journal of Zoology* 226:455–467.
- Beynon, B. D., and B. C. Fleming. 1998. Anterior cruciate ligament strain in-vivo: a review of previous work. *Journal of Biomechanics* 31:519–525.
- Biknevicius, A. R., and S. M. Reilly. 2006. Correlation of symmetrical gaits and whole body mechanics: debunking myths in locomotor biomechanics. *Journal of Experimental Zoology* 305A:923–934.
- Bramwell, C. D., and Whitfield, G. R. 1974. *Biomechanics of Pteranodon*. *Philosophical Transactions of the Royal Society of London B* 267:503–581.
- Brinkman, D. 1980. The hind limb step cycle of *Caiman sclerops* and the mechanics of the crocodile tarsus and metatarsus. *Canadian Journal of Zoology* 58:2187–2200.
- Britt, B. B., F. M. Dalla Vecchia, D. J. Chure, G. F. Engelmann, M. F. Whiting, and R. D. Scheetz. 2018. *Caelestiventus hanseni* gen. et sp. nov. extends the desert-dwelling pterosaur record back 65 million years. *Nature Ecology and Evolution* 2:1386–1392.
- Brown, M. A., J. C. Sagebiel, and B. Andres. 2021. The discovery, local distribution, and curation of the giant azhdarchid pterosaurs from Big Bend National Park; pp. 2–20 in K. Padian and M.A. Brown (eds.), *The Late Cretaceous pterosaur Quetzalcoatlus Lawson 1975 (Pterodactyloidea: Azhdarchoidea)*. Society of Vertebrate Paleontology Memoir 19. *Journal of Vertebrate Paleontology* 41(2, Supplement).
- Buffetaut, E., D. Grigorescu, and Z. Csiki. 2002. A new giant pterosaur with a robust skull from the latest Cretaceous of Romania. *Naturwissenschaften* 89:180–184.
- Cai, Z., and F. Wei. 1994. On a new pterosaur (*Zhejiangopterus linhaiensis* gen. et sp. nov.) from Upper Cretaceous in Linhai, Zhejiang, China. *Vertebrata Palasiatica* 32:181–194.
- Chatterjee, S., and R. J. Templin. 2012. Aerodynamics of *Tapejara*, a pterosaur from the Early Cretaceous of Brazil with a large cranial crest. *Acta Geologica Sinica* 86:1377–1388.

- Clark, J. M., J. A. Hopson, R. Hernández R., D. E. Fastovsky, and M. Montellano. 1998. Foot posture in a primitive pterosaur. *Nature* 391:886–889.
- Coombs, W. P., Jr. 1978. Theoretical aspects of cursorial adaptations in dinosaurs. *Quarterly Review of Biology* 53:393–418.
- Costa, F. R., O. Rocha-Barbosa, and A. W. A. Kellner. 2014. A biomechanical approach on the optimal stance of *Anhanguera piscator* (Pterodactyloidea) and its implications for the pterosaur gait on land. *Historical Biology* 26:582–590.
- Currie, P. J., and K. Padian. 1983. A new pterosaur record from the Judith River (Oldman) Formation of Alberta. *Journal of Paleontology* 57:599–600.
- Dong Z., Sun Y., and Wu S. 2003. On a new pterosaur from the Lower Cretaceous of Chaoyang Basin, Western Liaoning, China. *Global Geology* 22:1–7.
- Elgin, R. A., D. W. E. Hone, and E. Frey. 2011. The extent of the pterosaur flight membrane. *Acta Palaeontologica Polonica* 56:99–111.
- Firbas, W., and K. Zweymueller. 1971. Ueber das Hufeitgelenk der Rattiten. *Gegenbaurs morphologische Jahrbuch* 116:91–103.
- Frey, E., and D. M. Martill. 1996. A reappraisal of *Arambourgiana* (Pterosauria, Pterodactyloidea: one of the world's largest flying animals. *Neues Jahrbuch fuer Geologie und Palaeontologie, Abhandlungen* 199:221–247.
- Frey, E., and J. Riess. 1981. A new reconstruction of the pterosaur wing. *Neues Jahrbuch fuer Geologie und Palaeontologie, Abhandlungen* 161:1–27.
- Gatesy, S. M. 2003. Direct and indirect track features: what sediment did a dinosaur touch? *Ichnos* 10:91–98.
- Gatesy, S. M., M. Baeker, and J. R. Hutchinson. 2009. Constraint-based exclusion of limb poses for reconstructing theropod dinosaur locomotion. *Journal of Vertebrate Paleontology* 29:535–544.
- Habib, M. B. 2008. Comparative evidence for quadrupedal launch in pterosaurs. *Zitteliana* B28:159–166.
- Halilaj, E., M. J. Rainbow, D. C. Moore, D. H. Laidlaw, A.-P. C. Weiss, A. L. Ladd, and J. J. Crisco. 2015. In vivo recruitment patterns in the anterior oblique and dorsoradial ligaments of the first carpometacarpal Joint. *Journal of Biomechanics* 48:1893–1898.
- Hertel, F., and K. E. Campbell Jr. 2007. The antitrochanter of birds: form and function in balance. *The Auk* 124:789–805.
- Hewitt, J., F. Guilak, R. Glisson, and T. P. Vail. 2001. Regional material properties of the human hip capsule ligaments. *Journal of Orthopaedic Research* 19:359–364.
- Hewitt, J., F. Guilak, R. Glisson, and T. P. Vail. 2002. The mechanical properties of the human hip joint capsule ligaments. *Journal of Arthroplasty* 17:82–89.
- Hildebrand, M. 1976. Analysis of tetrapod gaits: general considerations, and symmetrical gaits; pp. 203–223 in R. M. Herman, S. Grillner, P. S. G. Stein, and D. G. Stuart (eds.), *Neural Control of Locomotion*. Plenum Press, New York.
- Holliday, C. M., R. C. Ridgely, J. C. Sedlmayr, and L. M. Witmer. 2010. Cartilaginous epiphyses in extant archosaurs and their implications for reconstructing limb function in dinosaurs. *PLoS ONE* 5:e13120.
- Hone, D. W. E., and D. M. Henderson. 2014. The posture of floating pterosaurs: ecological implications for inhabiting marine and freshwater habitats. *Palaeogeography, Palaeoclimatology, Palaeoecology* 394:89–98.
- Hutchinson, J., and S. Gatesy. 2006. Dinosaur locomotion: beyond the bones. *Nature* 440:292–294.
- Hutson, J. D., and K. N. Hutson. 2012. A test of the validity of range of motion studies of fossil archosaur elbow mobility using repeated-measures analysis and the extant phylogenetic bracket. *Journal of Experimental Biology* 215:2030–2038.
- International Commission on Zoological Nomenclature (ICZN). 1999. *International Code of Zoological Nomenclature*, fourth edition. International Trust for Zoological Nomenclature, London, xxix + 306 pp.
- Jensen, J. A., and K. Padian. 1989. Small pterosaurs and dinosaurs from the Uncompahgre Fauna (Brushy Basin Member, Morrison Formation: ?Tithonian), Late Jurassic, Western Colorado. *Journal of Paleontology* 63:364–373.
- Johnston, M. S. 1997. An aeroelastic model for the analysis of membrane wings and its application to yacht sails and *Pteranodon ingens*. Ph.D. dissertation, Department of Engineering, University of Auckland, Auckland, New Zealand, 180 pp.
- Johnston, M.S. 1977. An Aeroelastic Model for the Analysis of Membrane Wings and its Application to Yacht Sails and *Pteranodon ingens*. Ph.D. Thesis, Department of Mechanical Engineering, University of Auckland, New Zealand. 181 pp.
- Kambic, R. E., A. A. Biewener, and S. E. Pierce. 2017. Experimental determination of three-dimensional cervical joint mobility in the avian neck. *Frontiers in Zoology* 14:37. doi: 10.1186/s12983-017-0223-z.
- Kambic, R. E., T. J. Roberts, and S. M. Gatesy. 2014. Long-axis rotation: a missing degree of freedom in avian bipedal locomotion. *Journal of Experimental Biology* 217:2770–2782.
- Kellner, A. W. A. 2004. The ankle structure of two pterodactyloid pterosaurs from the Santana Formation (Lower Cretaceous), Brazil. *Bulletin of the American Museum of Natural History* 285:25–35.
- Kellner, A. W. A., and W. Langston Jr. 1996. Cranial remains of *Quetzalcoatlus* (Pterosauria, Azhdarchidae) from Late Cretaceous sediments of Big Bend National Park, Texas. *Journal of Vertebrate Paleontology* 16:222–231.
- Langston, W., Jr. 1981. Pterosaurs. *Scientific American* 244:122–136.
- Lawson, D. A. 1975. Pterosaur from the latest Cretaceous of West Texas: discovery of the largest flying creature. *Science* 187:947–948.
- Lehman, T. M. 2021. Habitat of the giant pterosaur *Quetzalcoatlus* Lawson 1975 (Pterodactyloidea: Azhdarchoidea): a paleoenvironmental reconstruction of the Javelina Formation (Upper Cretaceous), Big Bend National Park, Texas; pp. 21–45 in K. Padian and M. A. Brown. *The Late Cretaceous pterosaur *Quetzalcoatlus* Lawson 1975 (Pterodactyloidea: Azhdarchoidea)*. Society of Vertebrate Paleontology Memoir 19. *Journal of Vertebrate Paleontology* 41(2, Supplement).
- Lockley, M., T. J. Logue, J. J. Moratalla, A. P. Hunt, R. J. Schultz, and J. W. Robinson. 1995. The fossil trackway *Pteraichnus* is pterosaurian, not crocodylian: implications for the global distribution of pterosaur tracks. *Ichnos* 4:7–20.
- Lü, J., D. M. Unwin, 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.
- Marden, J. H. 1994. From damselflies to pterosaurs: how burst and sustainable flight performance scale with size. *American Journal of Physiology* 266:R1077–R1084.
- MacCready, P. 1985. The great pterodactyl project. *Science and Engineering* 1985(November):16–24.
- Manafzadeh, A. R., and K. Padian. 2018. ROM mapping of ligamentous constraints on avian hip mobility: implications for extinct ornithomimids. *Proceedings of the Royal Society of London B: Biological Sciences* 285:20180727.
- Martin, H. D., A. Savage, B. A. Braly, I. J. Palmer, D. P. Beall, and B. Kelly. 2008. The function of the hip capsular ligaments: a quantitative report. *Arthroscopy* 24:188–195.
- Mazin, J.-M., J.-P. Billon-Bruyat, and K. Padian. 2009. First record of a pterosaur landing trackway. *Proceedings of the Royal Society of London B: Biological Sciences* 276:3881–3886.
- Mazin, J.-M., J.-P. Billon-Bruyat, P. Hantzpergue, and G. Lafaurie. 2003. Ichnological evidence for quadrupedal locomotion in pterodactyloid pterosaurs: trackways from the Late Jurassic of Crayssac (southwestern France). *Geological Society of London Special Publication* 217:283–296.
- Mazin, J.-M., P. Hantzpergue, G. Lafaurie, and P. Vignaud. 1995. Des pistes de ptérosaures dans le Tithonien de Crayssac (Quercy, Lot). *Comptes Rendus de l'Académie des Sciences, Paris* IIA 321:417–424.
- Molnar, J. 2009. How giant reptiles flew: visualizing quadrupedal launch in pterosaurs. M.A. (Medical and Biological Illustration) thesis, Johns Hopkins University, Baltimore, Maryland, 70 pp.
- Munk, M. M. 1979. The aerodynamic forces on airship hulls. *NASA Reference Publication* 1050:111–126.
- Norberg, U. M. L., and R. A. Norberg. 2012. Scaling of wingbeat frequency with body mass in bats and limits to maximum bat size. *Journal of Experimental Biology* 215:711–722.
- Ong, C.-H., and S. W. Tsai. 1999. Design, testing and manufacture of a bend-twist D-spar. *Sandia National Labs Publication* 99-1324:1–111.
- Ostrom, J. H. 1969. Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. *Peabody Museum of Natural History Bulletin* 30:1–165.
- Palmer, C. 2017. Inferring the properties of the pterosaur wing membrane. *Geological Society of London Special Publications* 455:57–68.
- Padian, K. 1980. Studies of the structure, evolution, and flight of pterosaurs (Reptilia: Pterosauria). Ph.D. dissertation, Yale University, New Haven, Connecticut, 309 + xiv pp.

- Padian, K. 1983a. Osteology and functional morphology of *Dimorphodon macronyx* (Buckland) (Pterosauria: Rhamphorhynchoidea), based on new material in the Yale Peabody Museum. Yale Peabody Museum Postilla 189:1–44.
- Padian, K. 1983b. A functional analysis of flying and walking in pterosaurs. *Paleobiology* 9:218–239.
- Padian, K. 1985. The origins and aerodynamics of flight in extinct vertebrates. *Palaeontology* 28:423–433.
- Padian, K. 1986. On the type material of *Coelophysis* (Saurischia: Theropoda), and a new specimen from the Petrified Forest of Arizona (Late Triassic: Chinle Formation); pp. 45–60 in K. Padian (ed.), *The Beginning of the Age of Dinosaurs: Faunal Change across the Triassic-Jurassic Boundary*. Cambridge University Press, New York.
- Padian, K. 1991. Pterosaurs: were they functional birds or functional bats?; pp. 145–160 in J. M. V. Rayner and R. J. Wootton (eds.), *Biomechanics and Evolution*. Cambridge University Press, Cambridge, U.K.
- Padian, K. 2003. Pterosaur stance and gait, and the interpretation of trackways. *Ichnos* 10:115–126.
- Padian, K. 2008a. The Early Jurassic pterosaur *Dorygnathus banthensis* (Theodori 1830). *Special Papers in Palaeontology* 80:1–64.
- Padian, K. 2008b. The Early Jurassic pterosaur *Campylognathoides* Strand, 1928. *Special Papers in Palaeontology* 80:65–107.
- Padian, K. 2008c. Were pterosaur ancestors bipedal or quadrupedal?: morphometric, functional, and phylogenetic considerations. *Zitteliana* 28B:21–28.
- Padian, K. 2017. Structure and evolution of the ankle bones in pterosaurs and other ornithomirans. *Journal of Vertebrate Paleontology*. doi: 10.1080/02724634.2017.1364651.
- Padian, K., and P. E. Olsen. 1984. The track of *Pteraichnus*: not pterosaurian, but crocodylian. *Journal of Paleontology* 58:178–184.
- Padian, K., and J. M. V. Rayner. 1993. The wings of pterosaurs. *American Journal of Science* 293-A:91–166.
- Padian, K., and R. Wild. 1992. Studies of Liassic Pterosauria, I. The holotype and referred specimens of the Liassic pterosaur *Dorygnathus banthensis* (Theodori) in the Petrefaktensammlung Banz, northern Bavaria. *Palaeontographica, Abteilung A* 225:59–77, 5 pls.
- Pennycuik, C. J. 1972. *Animal Flight*. Arnold/Houghton and Stoddard, London, 64 pp.
- Pennycuik, C. J. 1990. Predicting wingbeat frequency and wavelength of birds. *Journal of Experimental Biology* 150:171–185.
- Pennycuik, C. J., and G. A. Parker. 1966. Structural limitations on the power output of the pigeon's flight muscles. *Journal of Experimental Biology* 45:489–498.
- Rayner, J. M. V. 1979. A new approach to animal flight mechanics. *Journal of Experimental Biology* 80:17–54.
- Ricqlès, A. J. de, K. Padian, J. R. Horner, and H. Francillon-Viellet. 2000. Paleohistology of the bones of pterosaurs (Reptilia: Archosauria): anatomy, ontogeny, and biomechanical implications. *Zoological Journal of the Linnean Society* 129:349–385.
- Schaeffer, B. 1941. The morphological and functional evolution of the tarsus in amphibians and reptiles. *Bulletin of the American Museum of Natural History* 78:345–472.
- Schutt, W. A., Jr., J. S. Altenbach, Y. H. Chang, D. M. Cullinane, J. W. Hermanson, F. Muradali, and J. F. Bertram. 1997. The dynamics of flight-initiating jumps in the common vampire bat *Desmodus rotundus*. *Journal of Experimental Biology* 200:3003–3012.
- Sereno, P. C. 1991. Basal Archosaurs: Phylogenetic Relationships and Functional Implications. *Society of Vertebrate Paleontology Memoir* 2. *Journal of Vertebrate Paleontology* 11(4, Supplement):1–53.
- Taquet, P., and K. Padian. 2004. The earliest known restoration of a pterosaur and the philosophical origins of Cuvier's *Ossemens Fossiles*. *Comptes Rendus Palevol* 3:157–175.
- Taylor, M. P., and M. J. Wedel. 2013. The effect of intervertebral cartilage on neutral posture and range of motion in the necks of sauropod dinosaurs. *PLoS ONE* 8:e78214.
- Tokita, M. 2015. How the pterosaur got its wings. *Biological Reviews* 90:1163–1178.
- Tsai, H. P., and C. M. Holliday. 2015. Articular soft tissue anatomy of the archosaur hip joint: structural homology and functional implications. *Journal of Morphology* 276:601–630.
- Unwin, D. M. 1988a. New remains of the pterosaur *Dimorphodon* (Pterosauria: Rhamphorhynchoidea) and the terrestrial ability of early pterosaurs. *Modern Geology* 13:57–68.
- Unwin, D. M. 1988b. A predictive method for the identification of vertebrate ichnites and its application to pterosaur tracks; pp. 259–272 in D. D. Gillette and M. G. Lockley (eds.), *Dinosaur Tracks and Traces*. Cambridge University Press, Cambridge, U.K.
- Unwin, D. M., E. Frey, D. M. Martill, J. B. Clarke, and J. Riess. 1996. On the nature of the pteroid in pterosaurs. *Proceedings of the Royal Society of London B: Biological Sciences* 263:45–52.
- Wellnhofer, P. 1970. Die Pterodactyloidea (Pterosauria) der Oberjura Plattenkalke Süddeutschlands. *Abhandlungen der Bayerische Akademie der Wissenschaften, Neues Folge* 141:1–133.
- Wellnhofer, P. 1975. Die Rhamphorhynchoidea (Pterosauria) der Oberjura-Plattenkalke Süddeutschlands, Teil III: Palökologie und Stammesgeschichte. *Palaeontographica, Abteilung A* 149:1–30.
- Wellnhofer, P. 1978. *Handbuch der Palaeoherpetologie*. Teil 19: Pterosauria. Gustav Fischer Verlag, Stuttgart, Germany, 82 pp.
- Wellnhofer, P. 1991. *The Illustrated Encyclopedia of Pterosaurs*. Salamander Books, London, 192 pp.
- Wild, R. 1978. Die Flugsaurier (Reptilia, Pterosauria) aus der Oberen Trias von Cene bei Bergamo, Italien. *Bolletina della Societa Paleontologia Italiana* 17:176–256.
- 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.
- Wilkinson, M. T., D. M. Unwin, and C. P. Ellington. 2006. High lift function of the pteroid bone and forewing of pterosaurs. *Proceedings of the Royal Society of London B: Biological Sciences* 273:119–126.
- Witmer, L. D., S. Chatterjee, J. Franziosa, and T. Rowe. 2003. Neuroanatomy of flying reptiles and implications for flight, posture, and behavior. *Nature* 425:950–953.
- Witton, M. P., and M. B. Habib. 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 D. Naish. 2008. A reappraisal of azhdarchid pterosaur functional morphology and paleoecology. *PLoS ONE* 3:e2271.
- Woodward, H. N., K. Padian, and A. H. Lee. 2013. Skeletochronology; pp. 195–215 in K. Padian and E.-T. Lamm (eds.), *Bone Histology of Fossil Tetrapods: Advancing Methods, Analysis, and Interpretation*. University of California Press, Berkeley, California.

Submitted January 19, 2018; revisions received January 25, 2020; accepted May 5, 2020.

Memoir Editor: Randall Irmis.