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DAVID W. E. HONE & ERIC BUFFETAUT (Guest Editors)

**Flugsaurier: pterosaur papers in honour of
Peter Wellnhofer**

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DAVID W. E. HONE & ERIC BUFFETAUT (Eds)

Flugsaurier: pterosaur papers in honour of Peter Wellnhofer

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Umschlagbild: Reconstitution of a *Rhamphorhynchus* from the Upper Jurassic of Eichstätt, Bavaria. Concept: P. Wellnhofer;
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Were pterosaur ancestors bipedal or quadrupedal?: Morphometric, functional, and phylogenetic considerations

By
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Abstract

Whereas some phylogenetic analyses have suggested that pterosaurs evolved from basal archosauromorphs, most analyses have concluded that they are basal ornithodirans, the sister group to dinosauromorphs. Independently, for over a century it has been debated whether their typical mode of terrestrial progression was bipedal or quadrupedal. In view of the fact that at least some pterodactyloid pterosaurs are now known to have made quadrupedal tracks, the question persists whether pterosaurs evolved from bipedal or quadrupedal ancestors. Phylogenetic analyses suggest ambiguous polarity when outgroups are used to reconstruct the ancestral state: basal archosauromorphs were presumably quadrupedal, whereas basal ornithodirans were presumably bipedal. Morphometric comparisons, however, suggest that basal pterosauromorphs were bipedal; that compared to their pseudosuchian outgroups their hindlimbs became elongated relative to the trunk length, and the forelimbs later lengthened as they assumed a role in aerial locomotion. The humerus became elongated but the forearm increased its length more rapidly so that it exceeded the humerus in length and was usually one of the longest wing elements in non-pterodactyloids. Functional and ichnological evidence confirms that the stance was erect and the gait parasagittal, as in birds and other dinosaurs. Trackways also show that pterosaurs modified their footfall patterns from the traditional reptilian condition, suggesting that the habit was secondary. Comparing forelimb to hindlimb lengths without considering other morphometric and phylogenetic contexts can provide misleading indications of the evolution of limb length in the origin of pterosaurs.

Key words: Pterosauria, functional morphology, morphometrics, phylogeny, locomotion, evolution

Zusammenfassung

Obwohl manche Phylogenetische Analysen andeuten, dass sich die Flugsaurier aus den basalen Archosauromorpha entwickelt haben kommen die meisten Untersuchungen zu dem Schluss, dass es sich um basale Ornithodira, eine Schwestergruppe der Dinosauroomorpha, handelt. Davon unabhängig wird seit mehr als einem Jahrhundert darüber diskutiert ob sie sich terrestrisch überwiegend biped oder quadruped fortbewegten. Da man heute weiß dass manche pterodactyle Flugsaurier quadrupede Spuren hinterließen, bleibt die Frage bestehen ob sie sich aus bipeden oder quadrupeden Vorfahren entwickelt haben. Phylogenetische Analysen bieten keine eindeutigen Ergebnisse wenn Außengruppen zur Rekonstruktion des Ahnenstatus miteinbezogen werden: basale Archosauromorpha waren vermutlich quadruped, basale Ornithodira dagegen biped. Morphometrische Vergleiche deuten darauf hin dass basale Flugsaurier biped waren. Demzufolge verlängerten sich im Gegensatz zur Außengruppe der Pseudosuchia die Hinterbeine relativ zur Schwanzlänge. Die Vorderbeine verlängern sich vermutlich später für die Fortbewegung in der Luft. Der Humerus wird verlängert, der Unterarm jedoch verlängert sich schneller so dass er den Humerus an Länge übertrifft und zum längsten Element im Flügel der nicht-pterodactylen Flugsaurier wird. Funktionelle und ichnologische Untersuchungen beweisen, dass ebenso wie bei Vögeln und anderen Dinosauriern die Haltung aufrecht und der Gang parasagittal war. Auch ihre Fussspuren lassen erkennen dass sich das Schrittmuster von dem der ursprünglichen Reptilien ableitet, wenn man annimmt dass ihre Art sich fortzubewegen sekundär entstanden ist. Irreführende Hinweise in der Evolution der Beinlänge am Ursprung der Flugsaurier können entstehen wenn man Vorderbeine und Hinterbeine, ohne andere morphometrische und phylogenetische Zusammenhänge zu berücksichtigen, vergleicht.

Schlüsselwörter: Flugsaurier, funktionelle Morphologie, Morphometrie, Phylogenie, Lokomotion, Evolution

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1. Introduction

Did pterosaurs evolve from bipedal or quadrupedal ancestors? There have been divergent analyses of the terrestrial ability of pterosaurs (e.g., PADIAN 1983b, 2003; WELLNHOFER 1988; BENNETT 1997a; UNWIN 1997, 1999 and references therein), but the question of the ancestral condition has seldom been approached (PADIAN 1983b, 1991, 1997). Part of the answer lies in the kinematics of the joints of the hindlimb (PADIAN 1983b; WELLNHOFER 1988; BENNETT 1997a), and part in the morphometric ratios of forelimb and hindlimb elements. Some considerations have been based on whether the hindlimbs were involved in the wing, and the effect that this would presumably have on terrestrial locomotion (e.g., UNWIN 1997, 1999). To some extent, authors have integrated ideas about alternative postures based on the condition in presumed phylogenetic relatives (e.g., PADIAN 1983b; SERENO 1991). And sometimes combinations of phylogenetic considerations and actualistic functional comparisons have been used (e.g., PADIAN 1983b, 1991).

Five independent phylogenetic analyses of pterosaurs, *Scleromochlus*, and other archosaurs have concluded that Pterosauria and *Scleromochlus* are ornithodirans (PADIAN 1984; GAUTHIER 1986; SERENO 1991; BENTON 1999; IRMIS et al. 2007; see also HONE & BENTON 2007). BENNETT (1996) reached the same conclusion when he used a phylogenetic analysis of all characters. When he subtracted the pelvic and hindlimb characters, he found that pterosaurs fell out deeper within Archosauromorpha, and argued that (1) these characters were therefore critical to uniting pterosaurs and dinosaurs; (2) they were not critical to structuring the rest of the archosauromorph tree, and (3) they may have been homoplastic in pterosaurs and dinosauromorphs. However, the derived characters of pterosaurs often make it difficult to interpret character states: if some archosaurs have a particular derived state (call it “1” as opposed to a basal state “0”), and pterosaurs have a different derived state (call it “2”), as they often do, does one code pterosaurs as being derived or as not being derived with respect to state 1? For example, if basal archosaurs have five primary (supportive) metatarsals, pterosaurs have four, and dinosaurs have three, do pterosaurs and dinosaurs share a condition of “fewer than five metatarsals,” or should the conditions of four and three be differently coded (and perhaps viewed as independently derived, with no polarity implied)? This is the universal problem of character coding and polarity (although ordered versus unordered states in a tree-building program deal with this question by different means).

PETERS (2000) also reached the conclusion that pterosaurs were not ornithodirans, and found instead that they were nested within what is traditionally considered the Prolacertiformes. It remains to be seen whether other workers can duplicate this result, but a recent analysis by HONE & BENTON (2007) failed to find support for PETERS’ analyses. For the present, because five different analyses have found that pterosaurs are ornithodirans, and the systematic community seems to have largely accepted this, the present paper will proceed with this provisional conclusion, without discounting other possible solutions.

The discovery of a very small, basal and early pterosaur in the Late Triassic Fleming Fjord Formation of East Greenland (JENKINS et al. 2001) provides additional data to approach the

question of posture in the earliest pterosaurs and their ancestors. The holotype of *Eudimorphodon cromptonellus* has relatively short wings, forearms and tibiae, and long metatarsals, and the proximal limb segments (humerus, ulna, femur, and tibia) are of nearly equal length. Although the specimen is probably a juvenile individual, based on its osteohistological features, its proportions do not fit the growth trajectories of other known contemporary pterosaurs, justifying its taxonomic separation (JENKINS et al. 2001). The question is what its limb proportions may tell us about the condition in pterosaur ancestors, and for this, some broader comparative context is necessary.

2. Nomenclature

It is first necessary to explain the nomenclature used in this paper, particularly regarding Ornithodira, Ornithosuchia, and other conventions. GAUTHIER (1986) defined Ornithodira as a taxon-based clade (“*Lagosuchus*”, Pterosauria, Herrerasauridae*, Ornithischia, Sauropodomorpha, and Theropoda”), indicating metataxa by asterisks. SERENO (1991) attempted to redefine it as a node-based clade (“Pterosauria, *Scleromochlus*, Dinosauroomorpha including birds, and all descendants of their common ancestor”), but it still remained taxon-based because it depends on a list of more than two terminal taxa. Both definitions were founded upon nodes that emerged from phylogenetic analyses. Gauthier’s found that *Lagosuchus* was more likely to be the outgroup to pterosaurs + dinosaurs; Sereno’s found *Lagosuchus*/*Marasuchus* closer to dinosaurs than pterosaurs are. Commonality is found in the suggestion that the node Ornithodira should consist of pterosaurs + dinosaurs and all descendants of their most recent common ancestor, because pterosaurs and dinosaurs are major, monophyletic groups.

Priority of definition is generally respected in the phylogenetic system, although the Committee on Phylogenetic Nomenclature of the International Society for Phylogenetic Nomenclature has not yet devoted much attention to settling specific issues. In general, most unofficial emendations of phylogenetic definitions by various authors in the literature have tried to convert original character-based and taxon-based definitions to node-based and stem-based definitions. Regardless of the definition of Ornithodira (now generally accepted as a node), all its component taxa belong *de facto* to the stem-group Ornithosuchia GAUTHIER 1986. This comprises all archosaurs including and closer to birds than to crocodiles.

Some workers have complained that because *Ornithosuchus* and the Ornithosuchidae now apparently belong to the Pseudosuchia (archosaurs closer to crocodiles than to birds: GAUTHIER 1986), the term Ornithosuchia should not be used. Component taxa may shift their positions without affecting the definition of a monophyletic group in the phylogenetic system as it has been understood to this point. However, with the advent of a draft *PhyloCode* (CANTINO & DE QUEIROZ 2000), even Gauthier and de QUEIROZ (2001) now advocate abolishing names such as Ornithosuchia and Ornithodira, but somewhat ironically, because they violate provisions of a code that was not in existence when the names were erected. For practical purposes, I use the term Ornithodira in this work to comprise pterosaurs + dinosaurs and all descendants of their most recent common ancestor.

Table 1: Some comparative lengths of limb elements in basal pterosaurs and other ornithodirans, with *Euparkeria* as an outgroup. Numbers in parentheses involve estimates of nearly complete elements. Only in *Scleromochlus* and pterosaurs is the forearm longer than the humerus. In pterosaurs there is a quantum increase in the forelimb to hindlimb ratio, reflecting the adaptation to powered flight. Abbreviations: f = femur, h = humerus, r = radius, t = tibia. All measurements in mm.

Taxon	h + r	f + t	h+r/f+t	r/h	f
<i>Euparkeria</i>	71.5	103.6	69	89	55.8
<i>Marasuchus</i>	(76.6)	126	61	(.93)	56
<i>Scleromochlus</i>	40.5	66.5	61	1.08	32
<i>Preondactylus</i>	74	83.5	88	1.31	32.5
<i>Eudimorphodon cromptonellus</i>	38.25	(40.2)	95	1.11	19.7
<i>Eudimorphodon rosenfeldi</i>	95.5	91.2	1.05	1.36	37
<i>Eudimorphodon ranzii</i> MCSNB 8950	59.5	45.1	1.32	1.29	19.6
<i>Eudimorphodon ranzii</i> MPUM 6009	61	(44)	1.39	1.35	19
<i>Eudimorphodon ranzii</i> MCSNB 2887	66	50.5	1.31	1.36	22
<i>Eudimorphodon ranzii</i> MCSNB 2888	112	(91)	1.23	1.38	41
<i>Dimorphodon</i>	181	181.4	1.00	1.00	76
<i>Dorygnathus</i>	157	117	1.34	1.34	50
<i>Campylognathoides liasicus</i>	110	85	1.41	1.29	38
<i>Campylognathoides zitteli</i>	152	153	1.00	1.00	65

3. Methods

The question of whether pterosaur ancestors were bipedal or quadrupedal requires more than phylogenetic considerations (Padian 1987a, 1995). First, there is the question of functional morphology. The characters of the hindlimb, apart from their use in systematics, suggest how the limbs worked. The same characters in birds and other dinosaurs (e.g., offset femoral head, bowed femoral shaft, great disparity between tibia and fibula with no significant rotation between them, fusion of astragalus and calcaneum to tibia, mesotarsal ankle, elongated closely appressed metatarsals, and hinges at all joints except the subhemispherical hip) are unexceptionally interpreted as for use in parasagittal locomotion in extinct tetrapods (e.g., basal dinosaurs and dinosauromorphs: ROMER 1971, 1972b; Padian 1983b, 1997; SERENO 1991). Although BENNETT (1996, 1997a, 2001) found that pterosaurs could be related to basal archosauromorphs, he accepted that the hindlimb characters are associated with an erect stance and parasagittal gait, which so far has not been postulated for other basal archosauromorphs with the exceptions of other basal ornithodirans such as *Marasuchus* and *Lagerpeton* (ROMER 1971, 1972b; SERENO 1991). The proximal tarsus of basal dinosauromorphs (*Lagerpeton*, *Dromomeron*, *Marasuchus*, *Pseudolagosuchus*, *Silesaurus*) forms a functional unit with the crus, but is not fused to the tibia (NOVAS 1989; ARCUCCI 1987; SERENO & ARCUCCI 1993, 1994; DZIK 2003; IRMIS et al. 2007). Nevertheless the functional morphology of the ankle can only be mesotarsal, and these coupled with the other correlates of the hindlimb have made the interpretation of erect stance and parasagittal gait uncontroversial.

The characters just listed apply to stance and gait, but they do not by themselves determine whether pterosaurs were strictly bipedal or quadrupedal, or whether they evolved from bipedal or quadrupedal ancestors. These questions can be only tested by an integration of phylogenetic, morphometric, and functional-morphological approaches.

If pterosaurs are ornithodirans, and given that virtually all other basal ornithodirans are recognized as bipeds (SERENO & ARCUCCI 1994), it would be conservative to suggest that pterosaurs evolved from bipedal ancestors (Padian 1983b; SERENO 1991). On the other hand, because the combined length of the humerus and radius of basal pterosaurs is close to that of the femur and tibia (Tab. 1), a feature typical of many quadrupeds, it has sometimes been proposed that pterosaur ancestors were quadrupedal. This is the condition in the outgroups to ornithodirans, and it is consistent with an alternate phylogenetic placement of pterosaurs, such as BENNETT (1996) and PETERS (2000) propose, even though the two questions are logically and materially separate (Padian 1987a, 1995).

The hypothesis that the proportions of pterosaur limbs favor a quadrupedal ancestry would be countered if, as the status of pterosaurs as ornithodirans suggests, the hindlimbs were elongated first in basal ornithodirans (which were bipedal), and then the forelimbs were elongated for flight in pterosaurs.

Therefore, the method used in this analysis is to compare morphometric ratios of independent pterosaur skeletal features with those of their outgroups, as postulated by several phylogenetic hypotheses. The ratios by themselves can only be informative in an evolutionary context if there are alternative hypotheses to test about what aspects of the ratios are changing.

Table 2: Proportions of limbs and gleno-acetabular distances in basal pterosaurs and other basal archosaurs. D, length of dorsal vertebral column; F, femur; FL, proximal forelimb length (humerus plus ulna only); GA, estimated gleno-acetabular length; H, humerus; HL, proximal hindlimb length (femur plus tibia only); R/U, forearm; T, tibia. All measurements in mm. Sources of data: *Tanytrachelos* (OLSEN 1979); *Cosesaurus* (PETERS 2000); *Ticinosuchus* (KREBS 1965); *Chanaresuchus* (ROMER 1972a); *Proterosuchus* (CRUIKSHANK 1972); *Vjushkovia* (CHARIG & SUES 1978); *Euparkeria* (EWER 1965); *Rutiodon* (MCGREGOR 1906); *Desmatosuchus* (PARKER 2008); *Protosuchus* (COLBERT & MOOK 1951); *Scleromochlus* (BENTON 1999 and PADIAN, unpub. data); *Preondactylus* (DALLA VECCHIA 1998); *Peteinosaurus* (WILD 1978); *Dimorphodon* (PADIAN, 1983a and unpub. data); *Eudimorphodon ranzii* (WILD 1978); *Dorygnathus* (PADIAN, unpub. data); *Campylognathoides* (PADIAN, unpub. data); *Marasuchus* (SERENO & ARCUCCI 1994); *Silesaurus* (DZIK 2003, based on a ZPAL composite); *Herrerasaurus* (SERENO & NOVAS 1994; NOVAS 1994); *Coelophysis* (COLBERT 1989); *Lesothosaurus* (SANTA LUCA 1980); *Scutellosaurus* (COLBERT 1981).

Species	-Spec. No.	H	R/U	F	T	D	GA	H + R/U F+T	FL+ HL GA	clade
<i>Tanytrachelos abynis</i>	YPM 7622	25.	11	28	16	59	53†	0.82	1.51	Prolacertiformes
<i>Cosesaurus aviceps</i>	MGB – VI	12	9	19	15.5	33	36	0.61	1.54	Prolacertiformes
<i>Chanaresuchus bonapartei</i>	MCZ 4035	85	76 e	128	94	280†	280†	0.73	1.37	Proterochampsidae
<i>Proterosuchus vanhoepeni</i>	SAM K.140	94	88	149	130	400 e	400 e	0.63	1.14	Proterosuchia
<i>Vjushkovia triplicostata</i>	composite	136†	120†	300†	196†	720†	730†	0.48	1.00	Erythrosuchia
<i>Euparkeria capensis</i>	SAM 5867	38	34	56	48	115†	130†	0.67	1.35	Archosauriformes
<i>Rutiodon carolinensis</i>	composite	245†	150†	295†	150†	765†	760†	0.90	1.10	Pseudosuchia: Phytosauria
<i>Desmatosuchus spurensis</i>	MNA V9300	35	27	59	30	126	122	0.70	1.24	Pseudosuchia: Aetosauria
<i>Ticinosuchus ferox</i>	ZPAL 42	145	164	250	179	449e	545	0.69	1.36	Pseudosuchia: Rauisuchia
<i>Protosuchus richardsoni</i>	AMNH 3024	66	52	100	83	198	190	0.64	1.58	Pseudosuchia: Crocodylomorpha
<i>Scleromochlus taylori</i>	BMNH R3146	20	18	32	35	47	43	0.61	2.49	Ornithodira: ?Pterosauromorpha
<i>Preondactylus buffarini</i>	MFSN 1770	32	42	33	44	50†	54†	0.96	2.80	Pterosauria
<i>Peteinosaurus zambellii</i>	MCSNB 3359	39	48	37	49	82	82	1.01	2.11	Pterosauria
<i>Dimorphodon macronyx</i>	composite	77†	86†	72†	106†	99†	126†	0.92	2.71	Pterosauria
<i>Eudimorphodon ranzii</i>	MCSNB 2888	47	65	41	50 e	103 e	103e	1.23	1.97	Pterosauria
<i>Dorygnathus bathensis</i>	SMNS 51827	52	89	45	58	78	90	1.35	2.69	Pterosauria
<i>Campylognathoides liasicus</i>	CM 11424	50	60	38	47	94 e	107 e	1.29	1.82	Pterosauria
<i>Marasuchus lilloensis</i>	PVL 3871	39	36	58	70	100†	103†	0.55	1.97	Dinosauromorpha
<i>Silesaurus opolensis</i>	ZPAL AbIII	16	19.5	25.5	22	48.5	45	0.75	1.57	Dinosauromorpha
<i>Herrerasaurus ischigualastensis</i>	PVSJ 373	175	167	345	315	542 e	520†	0.50	1.93	Dinosauria: ?Saurischia
<i>Coelophysis bauri</i>	AMNH 7224	134	82	203	221	360	360†	0.51	1.78	Dinosauria: Theropoda
<i>Heterodontosaurus tucki</i>	SAM-K1332	83	67	112	145	172	214	0.58	1.90	Dinosauria: Ornithischia
<i>Scutellosaurus lawleri</i>	MNA V175	69	57 e	93	96	312	308†	0.67	1.02	Dinosauria: Ornithischia

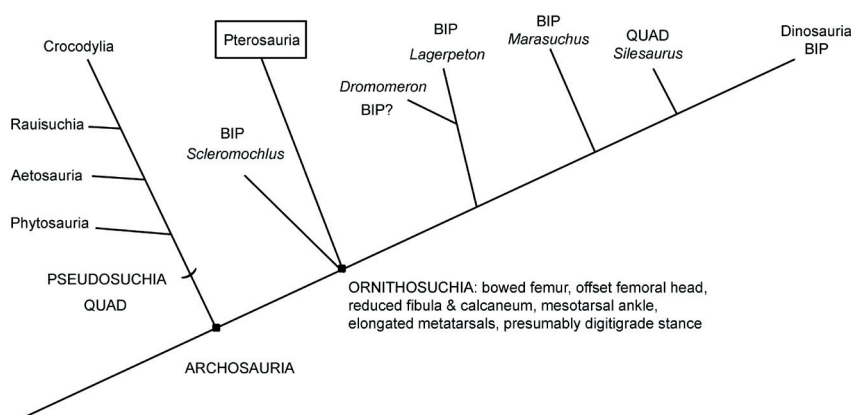


Figure 1: Cladogram of selected archosaurian taxa, based on IRMIS et al. (2007) and other references. Quadrupedality characterizes all non-ornithodiran reptiles, whereas bipedality appears to be basal for ornithodirans, based on a suite of characters associated with erect stance and bipedal gait, and on morphometric ratios of limbs and dorsal vertebral column (see text).

To test this question, it is useful to provide an independent measure of relative limb disparity so that there is some control over what measurement(s) might be changing. The length of the trunk is a standard measurement in archosaurs (e.g., WELLNHOFER 1978), though it is not immune to change itself, and the major limb segments (humerus, forearm, femur, and tibia) are relatively well known and tractable for analysis. In this study, the approximate length of the gleno-acetabular vertebral column (essentially comprising the dorsal and anterior sacral vertebrae) will form the standard of reference against which other skeletal lengths are compared.

Institutional abbreviations: AMNH, American Museum of Natural History, New York; BMNH, Museum of Natural History, London; CM, Carnegie Museum of Natural History, Pittsburgh; MCSNB, Museo Civico di Scienza Naturale, Bergamo; MCZ, Museum of Comparative Zoology, Harvard University; MFSN, Museo Friulano di Scienza Naturale, Udine; MGB, Museo Geologica, Barcelona; MNA, Museum of Northern Arizona, Flagstaff; PVL, Instituto de Geología, Fundación Miguel Lillo, Tucumán, Argentina; MPUM, Dipartimento de Scienze della Terra, University of Milan; PVSJ, Museo de Ciencias Naturales, San Juan, Argentina; SAM, South African Museum (IZIKO), Cape Town; SMNS, Staatliches Museum für Naturkunde, Stuttgart; UZ, Paleontological Museum and Institute, University of Zurich; YPM, Yale Peabody Museum; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

4. Results

Limb proportions and posture. -- Relatively consistent proportional differences between ornithodirans and other archosaurs separate these clades neatly into traditionally accepted bipedal and quadrupedal forms (Fig. 1). All the ornithodirans except *Silesaurus* are bipedal, and all the pseudosuchians are

quadrupedal. The ratio of the four major limb segments (humerus plus forearm plus femur plus tibia) to the gleno-acetabular (GA) length (Tab. 2) is approximately 1.97, 1.93, 1.90, and 1.78 in the ornithodirans *Marasuchus*, *Herrerasaurus*, *Heterodontosaurus*, and *Coelophysis* (respectively), whereas it is only about 1.35 in *Euparkeria* and similarly low in quadrupedal pseudosuchian archosaurs (phytosaur, aetosaurs, crocodiles, and their relatives: Tab. 2). (HAUBOLD [1971a, b] has used the inverse of this ratio as the “coupling value.”) The dorsal vertebral column of *E. cromptonellus* is too incompletely preserved for accurate measurement, but projection from a known dorsal central length of 1.7 mm suggests a GA length of about 3 cm, yielding a ratio of approximately 2.6 (Fig. 2). (Nearly all basal pterosaurs are in the range 2.5–2.8; *Scleromochlus* is about 2.5, far greater than any other basal archosaurs, including dinosaurs and their other close relatives.)

The humerus is longer than the ulna in all basal outgroups to pterosaurs, but in some isolated taxa within other major archosaurian groups (including *Ticinosuchus* [KREBS 1964], the crocodylomorphs *Trialestes* [R. IRMIS, pers. comm.] and *Terrestriusuchus* [CRUSH 1984], and the dinosauromorph *Silesaurus* [DZIK 2003]) the proportions reverse and the ulna becomes longer than the humerus. The humerus is shorter in *Scleromochlus*, which is sometimes considered the sister group to pterosaurs (PADIAN 1984; GAUTHIER 1986; though see BENTON 1999), and in all pterosaurs. The ratio of humerus to ulna is 95% in *Scleromochlus*, but is far lower in more derived pterosaurs. The humerus is shorter than the femur in all outgroups to pterosaurs; it is longer than the femur in all pterosaurs except *E. cromptonellus* and *Preondactylus*, in which the bones are of nearly equal length. The femur is longer than the tibia in *Euparkeria* and all outgroups to ornithodirans, with rare exceptions; it is shorter than the tibia in all basal ornithodirans (nearly 90% in *Scleromochlus* and *E. cromptonellus*, and less than 82% in more derived pterosaurs). The femur/tibia ratio is generally somewhat lower in pterosaurs than in basal

Table 3: Relative proportions of the lengths of major wing bone elements in basal pterosaurs. Abbreviations as in Tables 1 and 2; 1–4 = wing phalanges.

<i>Preondactylus</i> :	$t > r/u > 2 = 3 > f > h > 1 > 4$
<i>Peteinosaurus</i> :	$t \geq r/u > 3 > 2 = 1 > h \geq f > 4$
<i>Dimorphodon</i> :	$3 \geq r/u > t \geq 2 > 1 = 4 > h \geq f$
<i>Anurognathus</i> :	$1 > r/u > t > h > f$
<i>Batrachognathus</i> :	$r/u > h$
<i>Dendrorhynchoides</i> :	$1 > 2 = r/u > h = t$
<i>Eudimorphodon</i> :	$1 \geq 3 = 4 \geq r/u > 2 > t > h > f$
<i>Campylognathoides zitteli</i> :	$2 > 1 > 3 > 4 > t > r/u > h > f$
<i>Campylognathoides liasicus</i> :	$2 > 1 > 3 > 4 > r/u > h > t > f$
<i>Dorygnathus</i> :	$r/u > 2 = 3 > 1 \geq 4 > t > h > f$
<i>Rhamphorhynchus</i> :	$1 \geq 2 > 4 > 3 > r/u > t > h > f$
<i>Sordes</i> :	$r/u > 2 = 3 \geq t > 1 > h > 4 > f$
<i>Scaphognathus</i> :	$r/u \geq 2 \geq 3 \geq 4 \geq 1 > t > f = h$
<i>Pterodactylus</i> :	$t = 1 \geq r/u > 2 > 3 > f > h > 4$

dinosaurs and their relatives. The ulna is shorter than the femur in pterosaurian outgroups; these elements are nearly equal in *E. cromptonellus*, and the ulna is at least 20% longer than the femur in all other pterosaurs. BENNETT (1997b: 285) notes that in *Preondactylus*, one of the most basal pterosaurs, the humerus + ulna is 88% the length of the femur + tibia (in MFSN 1770 this ratio is 96%).

In outgroups to *Scleromochlus* and pterosaurs, the humerus is longer than the ulna and the femur is longer than the humerus. In *Scleromochlus* (contra BENTON 1999) and pterosaurs, the ulna is longer than the humerus, and the humerus is slightly shorter than the femur. In Pterosauria, the ulna is at least 20% longer than the humerus and the femur, and the humerus is approximately as long as the femur. In *Peteinosaurus* and more derived pterosaurs, the ulna/humerus ratio is 1.25 or greater, the humerus is longer than the femur, and the ulna is at least 30% longer than the femur. In *Eudimorphodon* and more derived pterosaurs, the ulna/humerus ratio is 1.35 or greater, and the humerus exceeds the femur in length by 20–25%.

5. Discussion

5.1 Trends in archosaurian limb elongation and vertebral shape

Most workers currently follow the view that pterosaurs are ornithodirans (PADIAN 1984; GAUTHIER 1986; SERENO 1991; BENTON 1999; IRMIS et al. 2007; HONE & BENTON 2007), the sister taxon to dinosaurs (Fig. 1). Using the proportional data from Table 2, some trends in the elongation of limbs in archosaurian evolution can be inferred. In Archosauromorpha basally, the hindlimbs (HL) and the forelimbs (FL) (comprising the propodials and zeugopodials) were each shorter than the gleno-acetabular (GA) length, and so therefore was the ratio of FL + HL to GA length. The femur was longer than the tibia and the humerus longer than the ulna. In basal ornithodirans, the femur became shorter than the tibia and the hindlimb longer than the GA length. The ratio of FL + HL to GA length was more in the range of 1.5–2.0 than 1.0–1.5, as in more basal archosauromorphs. Pterosaurs added to these

trends in three (not entirely independent) ways: the forelimb length became substantially longer than the GA length; the ulna became longer than the humerus, and the ratio of FL + HL to GA length exceeded 2.5.

The basal ornithodiran condition has generally been interpreted as bipedal (PADIAN 1983b, 1991, 1997; SERENO 1991). The elongation of the limbs with respect to the backbone (GA length) could mean that the limb segments became longer; but could the shape of the vertebral column have changed as well? To examine this question I took measurements of dorsal centrum length, height (measured at the ends of the centra), and total height (measured to the top of the vertebral arch) of a range of taxa from basal archosauromorphs (proterosuchians, erythrosuchians, proterochampsians) to basal dinosaurs and pterosaurs, using standard sources in the literature (KUHN 1976; BONAPARTE 1975; WEISHAMPEL et al. 2004; COLBERT 1981; SANTA LUCA 1980; LANGER et al. 1999; WILD 1978). Another interesting trend emerged (Tab. 4). The ratio of centrum height to centrum length was greater than 0.75 in taxa uncontroversially regarded as quadrupedal (all basal archosauromorphs). The ratio was approximately 0.75 or less in all ornithodirans (basal dinosaurs such as *Lagosuchus*, *Syntarsus*, *Saturnalia*, *Heterodontosaurus*, and *Scutellosaurus*), as well as in *Ticinosuchus* and *Euparkeria*, which have sometimes been considered facultative bipeds. The exceptions are *Herrerasaurus* (1.67) and *Staurikosaurus* (1.00), in which the condition has been recognized as derived (LANGER & BENTON 2007). Basal pterosaurs (*Eudimorphodon* and *Peteinosaurus*) fell in with the bipedal ornithodirans, with ratios of 0.52–0.77. When the ratio of the entire vertebral height to centrum length was measured, unquestioned quadrupeds ranged from 2.0–4.0, whereas the ratios ranged from 1.0–2.0 in basal ornithodirans, again with the exceptions of *Herrerasaurus* and *Staurikosaurus*, in which the condition has been recognized as derived (LANGER & BENTON 2007). Again, pterosaurs fell in with the bipedal ornithodirans (ratio 1.2–1.8). Unfortunately the dorsal vertebrae in *Scleromochlus* are not sufficiently preserved to allow the calculations of these ratios.

In ornithodirans, therefore, the hindlimbs appear to have become longer, compared to the basal archosauromorph condition. In addition, at first glance the dorsal vertebrae themselves seem to have attained a higher length to height ratio, which would not account for a decrease in GA length. But comparison of the skeletal elements of a range of archosauromorph taxa (e.g., SERENO 1991: fig. 27) suggests that the length of the dorsal column did not change in ornithodirans from the basal archosauromorph conditions. Rather, instead of the central length increasing in ornithodirans, the heights of the individual vertebrae and of their centra decreased with respect to their central lengths. This does not seem to have resulted in a significant change in relative GA length from the basal archosauromorph condition. Regardless, basal pterosaurs correspond in both vertebral ratios to those of uncontroversial ornithodiran bipeds (Table 4).

5.2 *Scleromochlus taylori*

The poorly preserved but very interesting small reptile *Scleromochlus taylori*, from the Late Triassic of Scotland, has in recent years been implicated in the ancestry of pterosaurs

Table 4: Ratios of centrum height (CH) and total vertebral height (TH) to central length (L) for a variety of archosauromorphs. R = region of dorsal column (a = anterior, m = mid, p = posterior). Sources noted in text.

TAXON	R	CH/L	TH/L
<i>Erythrosuchus africanus</i>	m	1.58	--
<i>Dongusia colorata</i>	a	1.21	--
<i>Shansisuchus shansisuchus</i>	m	1	2.64
<i>Shansisuchus shansisuchus</i>	m	1	--
<i>Shansisuchus shansisuchus</i>	p	1	--
<i>Euparkeria capensis</i>	p	0.76	2
<i>Ticinosuchus ferox</i>	p	0.75	1.94
<i>Stagonolepis robertsoni</i>	a	0.9	3.3
<i>Stagonolepis robertsoni</i>	p	0.8	2.4
<i>Rutiodon carolinensis</i>	a	1	3.4
<i>Rutiodon carolinensis</i>	m	1.15	3.4
<i>Rutiodon carolinensis</i>	p	1.07	3.07
<i>Chanaresuchus bonapartei</i>	a	1.3	3.8
<i>Ctenosauriscus koeneni</i>	m	0.44	12
<i>Marasuchus lilloensis</i>	m	0.52	1.69
<i>Marasuchus lilloensis</i>	m	0.45	1.45
<i>Marasuchus lilloensis</i>	p	0.6	--
<i>Marasuchus lilloensis</i>	a	0.5	1.63
<i>Marasuchus lilloensis</i>	m	0.47	1.53
<i>Herrerasaurus ischigualastensis</i>	m	0.76	2.08
<i>Herrerasaurus ischigualastensis</i>	p	1.67	3.78
<i>Staurikosaurus pricei</i>	a	0.89	--
<i>Staurikosaurus pricei</i>	p	1	3.25
<i>Syntarsus rhodesiensis</i>	a	0.61	1.56
<i>Syntarsus rhodesiensis</i>	a	0.46	1.38
<i>Scutellosaurus lawleri</i>	m	0.55	--
<i>Heterodontosaurus tucki</i>	m	0.5	1.78
<i>Saturnalia tupiniquium</i>	m	0.5	1.2
<i>Eudimorphodon ranzii</i>	p	0.56	1.22
<i>Eudimorphodon ranzii</i>	?	0.6	1.8
<i>Eudimorphodon ranzii</i>	m	0.53	1.72
<i>Peteinosaurus zambellii</i>	p	0.77	1.23

(reviews in Padian 1984, Benton 1999). Padian (1984) proposed a series of synapomorphies linking the two taxa, and these were followed and expanded by Gauthier (1986) and Sereno (1991). Benton (1999) found that *Scleromochlus* was slightly closer to dinosaurs than to pterosaurs, although like other workers he emphasized the difficulties in interpreting these poorly preserved remains. One critical feature is that in *Scleromochlus*, as in pterosaurs, the ulna is longer than the humerus. Benton (1999) found the humerus longer than the ulna, as in most other tetrapods, but he assembled his table of measurements from different specimens of slightly but significantly different lengths. In the specimen in which both

elements are fully preserved without distortion, the ulna is longer than the humerus, a pterosaurian feature (Padian 1984; M.J. Benton, pers. comm.).

Some other characters may complement morphometric features that suggest that *Scleromochlus* is closer to pterosaurs than to dinosaurs. As in pterosaurs, the volume of the skull is at least as great as that of the torso, and there are four elongated, closely appressed metatarsals (Fig. 3C-D). Also unique to pterosaurs and *Scleromochlus*, the ratio of the forelimb and hindlimb segments to the gleno-acetabular length is 2.5 or greater, the ulna is longer than the humerus, and the ratio of the forelimb to the gleno-acetabular length is nearly 1 or greater. It may be argued that these characters do not seem conspicuous individually; but their co-occurrence provides a strong signal of phylogenetic affinity.

The limb proportions of even the most basal pterosaurs are more consistent with those of bipedal archosaurs than of quadrupedal ones. They are most similar to those of *Scleromochlus*, often proposed as a close outgroup to pterosaurs. These comparisons suggest that pterosaur ancestors were bipedal, and they hold whether *Scleromochlus* is a basal pterosaur or a basal dinosaur, or the sister group to both.

Alternatively, if we consider that pterosaurs evolved from quadrupedal basal archosaurs such as Prolacertiformes (Peters 2000), a rather different model of limb evolution must be proposed. In prolacertiforms the humerus is longer than the forearm and the femur is longer than the tibia; the glenoacetabular length is also long, as in most terrestrial quadrupeds. To attain the proportions seen in basal pterosaurs, the relative lengths of humerus and forearm and of femur and tibia would have to have been reversed, and the vertebral column would have had to shorten considerably (or the limb segments increase). These changes are independent of the extensive reorganization of the joints for erect posture and parasagittal gait, for which there is no evidence so far in prolacertiforms.

5.3 Evolution of wing proportions in pterosaurs

The proportions of pterosaur wing bones are remarkably consistent taxonomic indicators: the ratio between most pairs of wing bones, at least at the sub-adult to adult stages, is particular to the genus and often to the species level, and this has enabled the identification and re-identification of many specimens (Padian & Wild 1992). If relative wing element proportions (Tab. 3) are plotted on a cladogram of pterosaurs (Fig. 4), trends in proportional changes can project a more or less basal condition. The information in Figure 4 suggests that the first pterosaurs had a long forearm and a short humerus, and that at this point the humerus was apparently still longer than the fourth wing-phalanx (which is usually the most variable segment in length). The humerus remained the shortest or second shortest element in all taxa. The second and third wing-phalanges were longer than the first, but this was reversed in the Anurognathidae, Campylognathoididae (*Campylognathoides* + *Eudimorphodon*), and *Rhamphorhynchus*; the original condition returned in the Scaphognathinae. The Anurognathidae and especially Campylognathoididae had relatively very short forearms, although this again was reversed in Rhamphorhynchidae (Rhamphorhynchinae and Scaphognathinae). Unwin's (2003) table 2 shows that

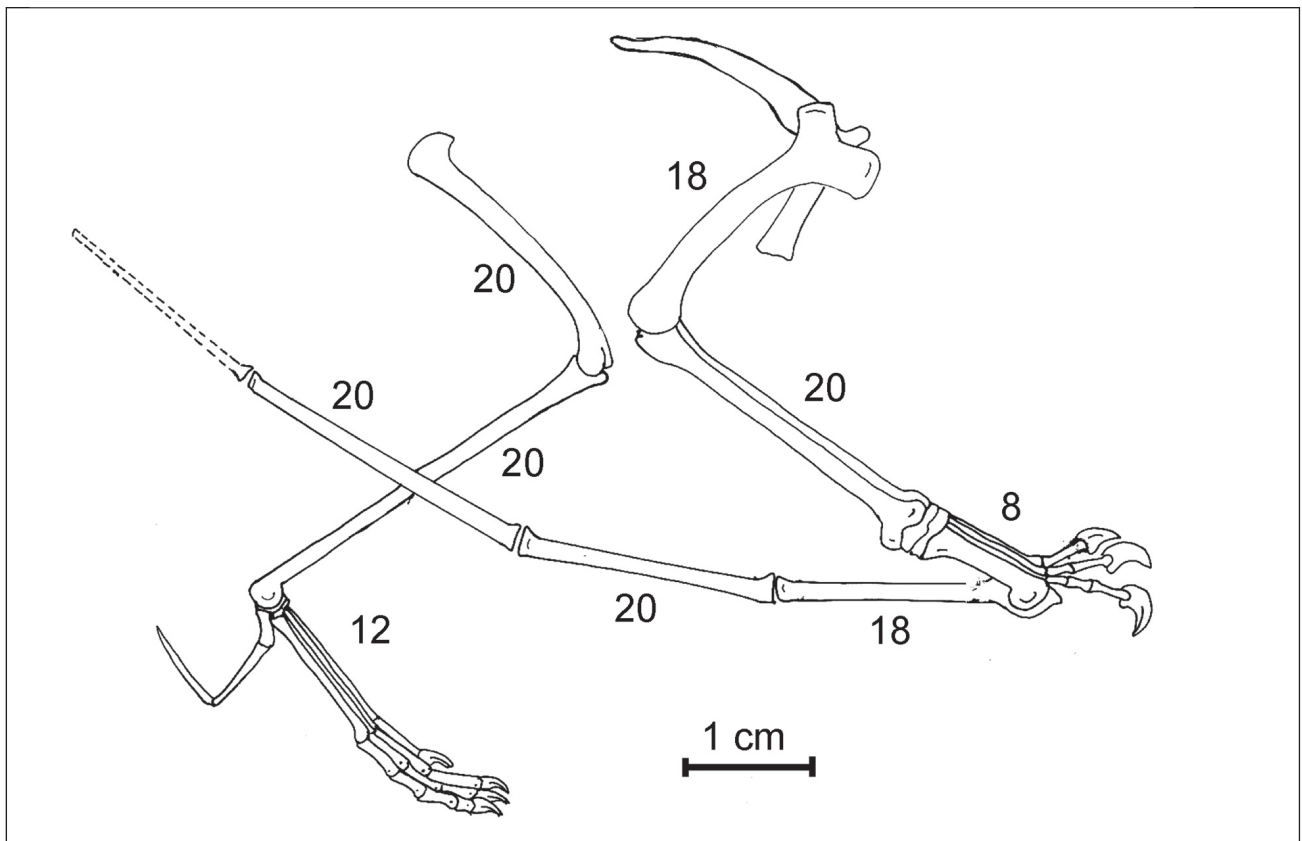


Figure 2: Reconstruction of fore and hind limbs of *Eudimorphodon cromptonellus* JENKINS et al. 2001 (University of Copenhagen Geological Museum MGUH VP 3393), to show relative similarity in length of most limb bones. Wing-phalanx 4 and some smaller phalanges of manus and pes restored. Note relatively short coracoid. Measured lengths (in mm; e = estimated) of some limb bones: humerus, 18.15; ulna, 20.1; wing-phalanges 1–3, 18e, 20.5, 20.5e; femur, 19.7; tibia, 20.5e.

the basal pterosaurs *Preondactylus*, Dimorphodontidae, and Anurognathidae had relatively low forelimb to hindlimb ratios among non-pterodactyloids. This could mean that the forelimbs were not yet very large or that the hindlimbs were particularly large for substantial use in terrestrial locomotion; both explanations, for reasons given above, accord with the hypothesis that pterosaurs had bipedal ancestors.

5.4 Trackways and pterosaur ancestry

Pterosaurs have long been depicted as both bipeds and quadrupeds (e.g., SEELEY 1901). Newly discovered, undisputed tracks of small pterodactyloids from the Late Jurassic of France (MAZIN et al. 1995) unequivocally show a quadrupedal stance. * The pterodactyloid tracks at Crayssac, plus functional studies, show that the hindlimbs were erect and the gait was parasagittal as I predicted (PADIAN 1983b; MAZIN et al. 1995). But these pterodactyloid pterosaurs were apparently not habitual bipeds as I predicted (PADIAN 1983b). If they evolved from bipedal ancestors, as the morphometric and phylogenetic evidence presented here seems to suggest, why would they revert to four legs?

The answer may be found in the very high ratio of pterodactyloid limb proportions to gleno-acetabular length. Both fore and hind limbs (not just the hind limb, as in dinosaurs and other ornithomirans) were each longer than the gleno-acetabular distance (a ratio of 2.56 for humerus + forearm + femur + tibia divided by gleno-acetabular length [Tab. 3]), and the forelimb was even more elongated by virtue of the longer metacarpus that pterodactyloids evolved, greatly increasing the length of the pre-phalangeal segment of the wing (to a ratio of 3.26, greater than any other tetrapod). With such an extraordinarily long pre-phalangeal forelimb, for pterodactyloids touching the ground was evidently easier than not touching it.

The trackway evidence at Crayssac provides another unusual feature of pterosaur locomotion: the manus apparently had to be lifted before the ipsilateral pes overstepped it, so there was not true overstepping (MAZIN et al. 2003; PADIAN 2003). Thus, the footfall pattern was LF-LH-RF-RH, not LF-RH-RF-LH, as in other reptiles. This difference has suggested to some that it is more likely that pterosaurian quadrupedality was secondary (MAZIN et al. 2003; PADIAN 2003) than that it was primitive to the group and its ancestors, and that the footfall pattern changed at some point in pterosaur evolution.

Although the vast majority of pterodactyloid footprints at Crayssac reflect a plantigrade stance, in some tracks only the toes are impressed (MAZIN et al. 2003: fig. 2e,h), suggesting that the toes were impressed first (this would be true even if the tracks in question were merely underprints). The plantigrade

*For reasons noted elsewhere (PADIAN2003), I separate the Crayssac tracks, which I regard as legitimate pterodactyloid tracks, from all other trackways referred to pterosaurs, e.g. the classic *Pteraichnus* tracks of STOKES

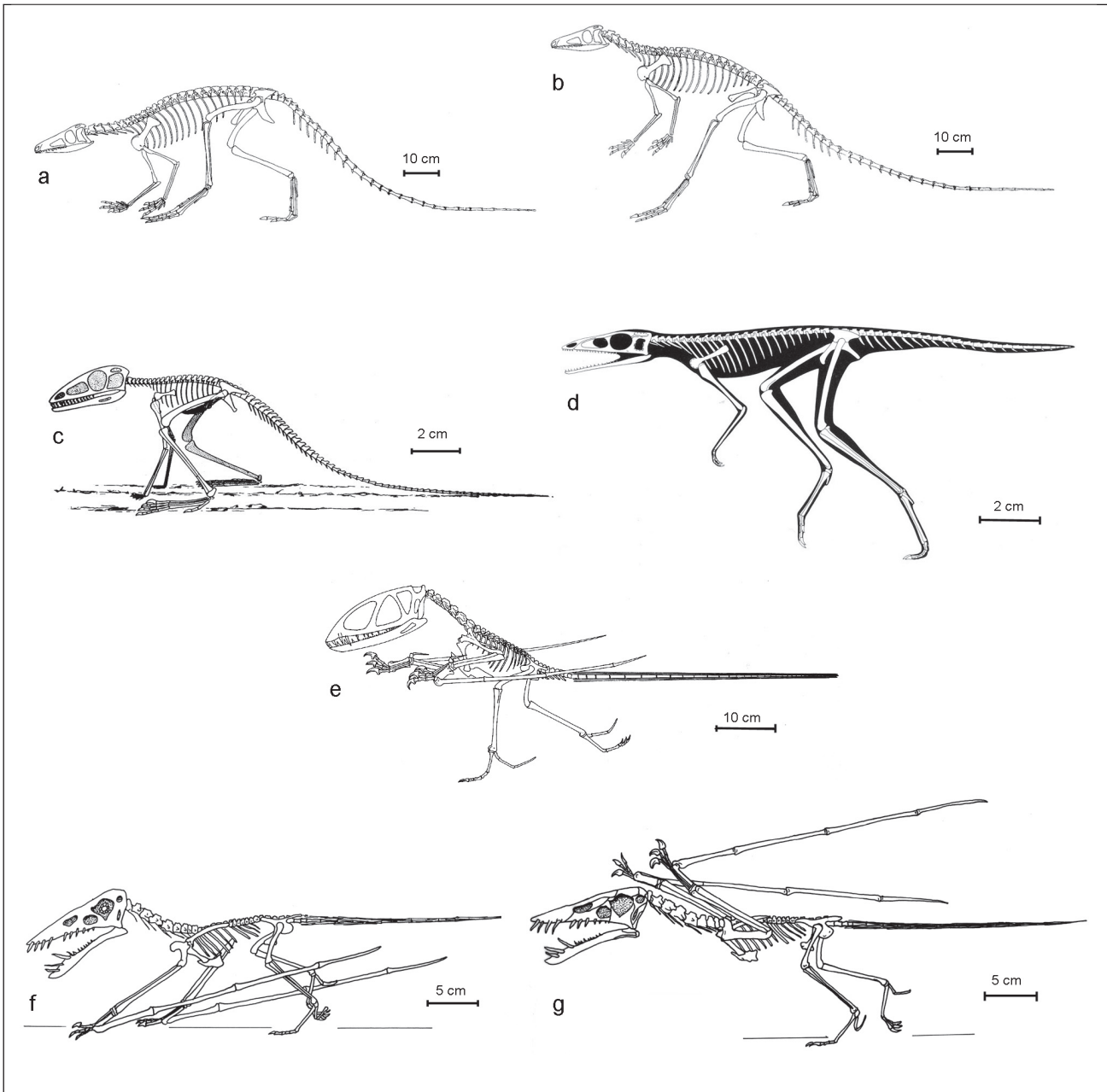


Figure 3: Reconstructions of the basal ornithodirans *Marasuchus* (A–B, after BONAPARTE 1975) and *Scleromochlus* (C, after HUENE 1914; D, after SERENO 1991), and the basal pterosaurs *Dimorphodon* (E, after PADIAN 1983a) and *Dorygnathus* (F–G). Quadrupedality seems an unlikely mode of progression for these taxa because the forelimb elements are so much shorter and sligher than the hindlimbs (A–D), and because the hindlimbs would have to be unnaturally flexed in order to avoid an anterior slope of the vertebral column.

condition can result from a heel-first (as in humans, bears, and badgers) or toe-first condition; apparently pterosaurs used the latter. Crocodiles appear to impress their entire foot at virtually the same instant; they imprint the toes and lift the heel first (BRINKMAN 1980), as digitigrade prints of the basal crocodylomorph ichnogenus *Batrachopus* demonstrate (OLSEN & PADIAN 1986). The pterosaur condition suggests a low metatarsal angle and perhaps a tradition of digitigrady that evolved into a secondary plantigrade impression of the heel. It is noteworthy that among reptiles, with very few exceptions (such as the trackmaker of *Batrachopus* [likely *Protosuchus*: OLSEN & PADIAN 1986] and presumably *Terrestriusuchus* [CRUSH 1984]), only ornithodirans show digitigrady, and there are almost no

exceptions to ornithodiran digitigrady. (Dinosaurs were originally bipedal; several dinosaurian groups became secondarily quadrupedal, but all remained digitigrade, as phylogenetic and functional studies show: PADIAN 1997). If pterosaurs are ornithodirans, as most analyses agree, digitigrady could be presumed to be primitive for pterosaurs, and it would not be clear when the plantigrade posture was first used.

5.5 Body proportions and stance

Although both bipedal and quadrupedal stances have been illustrated for basal ornithodirans, no one has seriously considered that animals such as *Marasuchus* were habitually

or facultatively quadrupedal in gait. A glance at BONAPARTE'S (1975) reconstructions (Fig. 3a,b) underscores the short length and delicate build of the forelimbs, which could not have kept pace with the hindlimbs in normal terrestrial locomotion (See also Tab. 3). Similar problems are seen with HUENE'S (1914) quadrupedal reconstruction of *Scleromochlus*, in contrast to SERENO'S (1991) bipedal version (Fig. 3c,d). In considering reconstructions of pterosaurs in bipedal and quadrupedal pose, it is crucial to separate basal pterosaurs from pterodactyloids, which have an elongated wing metacarpal that adds considerable height to the front end of the animal.

There are relatively few reconstructions of basal pterosaurs in terrestrial progression, either bipedal or quadrupedal. H.G. SEELEY'S illustrations for *Dragons of the Air* (1901), done by his daughter, are too inaccurate to bear consideration, and neither RICHARD OWEN nor German experts on Liassic pterosaurs were in the habit of restoring them in life pose (PADIAN 1987b). John Sibbick's superb paintings for Peter WELLNHOFER'S *Illustrated Encyclopedia of Pterosaurs* (1991: pp. 70, 75, 87) feature three renditions of basal pterosaurs on all fours, but verisimilitude is lacking in the ungainly sprawl of the limbs and the unnaturally acute angle of the knee; cleverly, Sibbick portrays the animals either leaning against a slope (which de-emphasizes how much lower the anterior end would normally be than the posterior end) or, in the case of *Rhamphorhynchus*, has the animal bent over a prey item. It is not clear how closely these reconstructions were based on restorations of articulated skeletons and their functional mechanics.

Elsewhere (PADIAN 1983b, 1991, 1995) I have provided detailed evidence from the structure of the hindlimbs that pterosaurs stood erect and had a parasagittal gait, because their limbs are organized exactly like those of birds and other dinosaurs. My (1983a) restoration of *Dimorphodon* in bipedal pose (Fig. 3e) reflected that erect hindlimb stance plus the disparity between the relative lengths of the hindlimb segments (femur, tibia, metatarsus) and those of the forelimb (humerus, forearm, metacarpus). Restorations of *Dorygnathus* in bipedal and quadrupedal poses (Fig. 3f,g) suggest an ungainly stance on all fours: not only is the shoulder joint substantially lower than the hip joint, but in this position the left forelimb is positioned as far forward as it can go, and it cannot retract directly (PADIAN 1983b). If quadrupedal locomotion were possible in basal pterosaurs, it would have been clumsy, and the forelimb could not have participated much in the normal protraction and retraction of limbs essential to efficient locomotion. I hypothesize from these considerations that basal pterosaurs and their direct ancestors were bipedal, and that facultative quadrupedality (that featured an unusual and secondarily derived footfall pattern) evolved in pterodactyloids, which had a prephalangeal wing much longer than that of non-pterodactyloids, suited for reaching the ground comfortably.

5.6 Arboreal vs cursorial proportions

S.C. BENNETT, in reviewing this paper, suggested that it needed an argument why the limb and body proportions cited here as evidence of bipedal ancestry of pterosaurs could not apply to the arboreal leaping model that he suggested in 1997 (BENNETT 1997b). Although I am not comparing hypotheses about the origin of pterosaur flight in this paper, his is a good

suggestion. As we both acknowledge, many small and mid-sized animals can climb trees without any obvious arboreal specializations; however, to make a case for arboreality still requires specifics. BENNETT (1997b) referred to NAPIER & WALKER'S (1967) morphological correlates of vertical clinging and leaping in primates, and suggested that many of these were shared by pterosaurs, including "small to medium size; pelvis with long iliac blade and short ischium; greatly elongate hindlimbs permitting great flexion and extension; femoral head cylindrical*; femoral condyles posteriorly placed with patellar groove anteriorly placed*; tibia straight, and fibula fused to tibia in *Tarsius* and the Eocene *Necrolemur*; forelimb short with high brachial index (= antebrachium/brachium x 100)*; long hands; and long tail." (I have asterisked characters that BENNETT noted do not apply to pterosaurs; *pace* BENNETT, I think the femoral head is properly regarded as cylindrical in many pterosaurs, including *Rhamphorhynchus*, *Pterodactylus*, and other basal pterodactyloids.) These features, as NAPIER & WALKER noted, apply to primates; they do not necessarily apply to all climbing and leaping animals, such as squirrels or arboreal lizards; moreover, pterosaurs were not primates, so the features cannot be applied to them *ipso facto* because the argument is not based on common ancestry. These features are not necessarily prescriptive of arboreal behavior, nor did BENNETT construct a detailed functional argument for climbing in pterosaurs.

Many of the features and proportions that NAPIER & WALKER listed could also apply to other basal ornithodirans, such as *Marasuchus* and *Lagerpeton*, which are universally presumed to be cursorial bipeds; these same features have even been used to argue for ricochet behavior (e.g., SERENO & ARCUCCI 1994), although there is little evidence for that view. Finally, primates have multidirectional mobility in their wrist and ankle joints; we know little of the wrist joints in basal ornithodirans or whatever the immediate ancestors of pterosaurs were. However, we do know that the ankle joints of pterosaurs and basal ornithodirans, like the knee and metatarso-phalangeal joints, moved almost entirely in a fore-and-aft plane, quite unlike primates and other scansorial animals (except, of course, woodpeckers and similar birds that are quite differently adapted). It may also be noted that basal pterosaurs have very large, recurved manual claws and smaller, less curved pedal claws (e.g., WILD 1978; PADIAN 1983a). These features are characteristic of predaceous, bipedal archosaurs (GAUTHIER 1986), but quadrupeds never seem to have this arrangement (except perhaps some chalicotheres). This could be another indication of the ancestral condition of pterosaurs; in pterodactyloids the manual claws are generally still more recurved than those of the pes, but are not so much larger as they are in basal pterodactyloids (WELLNHOFER 1978).

In light of DIAL'S (2003) seminal Wing-Assisted Incline Running (WAIR) model, it may be wondered whether pterosaurs were capable of the same scansorial running as small precocial birds are. Their hindlimbs are similar in all functional respects related to flight, and if they could have used their forelimbs to generate thrust in the same way (which, inasmuch as pterosaur ancestors eventually evolved flight, must be presumed at some point), the WAIR model could be hypothesized for pterosaurs as well. This would presume bipedal locomotion in their ancestors.

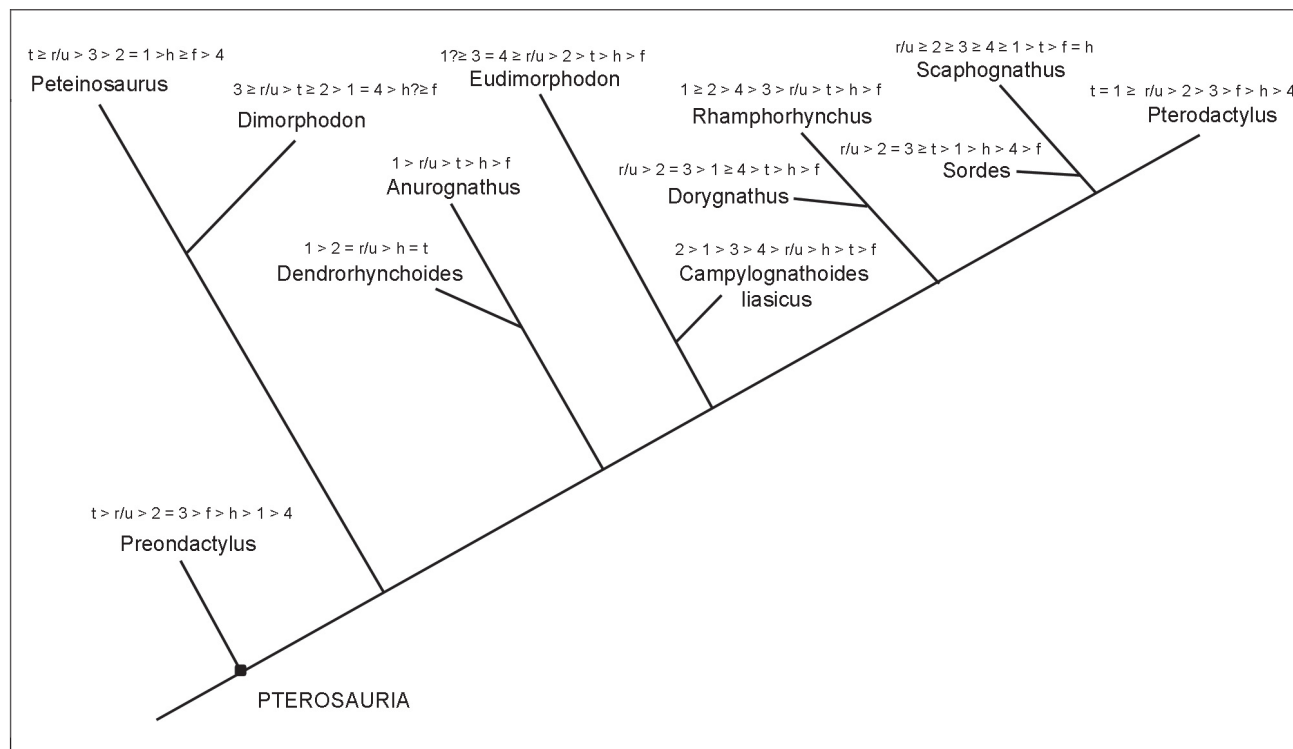


Figure 4: Cladogram of basal pterosaurs, based on UNWIN (2003), showing trends in wing element proportions.

6. Conclusions

As the proportions of *E. cromptonellus* and those of other pterosaurs and archosaurs show, the hindlimbs became elongated relative to the trunk in basal ornithodirans, and the forelimb was then elongated in pterosaurs in connection with flight. Facultative quadrupedality may have ensued secondarily in pterodactyls, in which the proximal forelimb segments were elongated functionally by the hypertrophy of the metacarpals, which placed the hands much closer to the ground than in basal pterosaurs. This inference is supported by the quadrupedal trackways described by MAZIN et al. (1995) in which the manus prints are considerably lateral to those of the pes and similar in stride length, even though the effective length of the forelimb segments out to the base of the fingers is greater than that of the hindlimb in these forms. However, the direct evolution of pterosaurs from quadrupedal forms is not supported by proportional or phylogenetic evidence, whereas their derivation from ancestors with parasagittal gait and bipedal posture is.

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