

On the phylogeny and evolutionary history of pterosaurs

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Abstract: Previous cladistic studies of pterosaur relationships suffer from restricted numbers of taxa and characters, incomplete data sets and absence of information on characters, tree structure and the robustness of trees. Parsimony analysis of a new character data set (60 characters, 20 terminal taxa, 93.75% complete) yielded six trees. In the strict consensus tree *Preondactylus* is the most basal taxon followed, stepwise, by the Dimorphodontidae and the Anurognathidae. Beyond this basal group, more derived pterosaurs (Campylognathoididae (Rhamphorhynchidae + Pterodactyloidea)) share a suite of characters principally associated with elongation of the rostrum. The Pterodactyloidea consists of four major clades. The Ornithocheiroidea is the most basal taxon consisting, stepwise, of *Istiodactylus*, the Ornithocheiridae, *Nyctosaurus* and the Pteranodontidae. The remaining taxa, Ctenochasmatoidea, Dsungaripteroidea and Azhdarchoidea, are weakly united in a clade of non-ornithocheiroid pterodactyloids, but their inter-relationships are difficult to resolve. *Cycnorhamphus* is the basal-most ctenochasmatoid, while the remaining taxa (*Pterodactylus*, Lonchodectidae, Ctenochasmatidae) form an unresolved trichotomy. The Dsungaripteroidea (*Germanodactylus* + Dsungaripteridae) is strongly supported by features of the skull and dentition. The Azhdarchoidea (*Tapejara* [Tupuxuara + Azhdarchidae]) is united by cranial characters such as elevation of the antorbital region, and relative shortening of the wing finger. The pattern of pterosaur evolution suggested by the results of this analysis is broadly similar to traditional ideas, but has greater resolution, more complexity and reveals several previously unrecognized 'events'.

Phylogenetic analysis has had a profound impact on our views of the relationships of extinct vertebrates, both with regard to taxa within principal clades and of these clades to each other (e.g. Benton 1997; Carroll 1997). Moreover, combining the results of such studies with data on the stratigraphic distribution of terminal taxa has often resulted in major changes to our understanding of the history of such clades. Several prominent groups, such as Mammalia and Theropoda, have been subject to intense study, but other taxa, including pterosaurs, an important clade of Mesozoic flying reptiles, have been relatively neglected. The few preliminary cladograms that have been published (Howse 1986; Bennett 1989, 1994; Unwin 1992, 1995a; Kellner 1996a; Peters 1997; Unwin & Lü 1997; Viscardi *et al.* 1999; Unwin *et al.* 2000) suggest a substantially different pattern of evolution from the traditional reconstruction, best epitomized by the *Handbuch* (Wellnhofer 1978), but these new ideas have yet to be explained in detail and, so far, have had little impact on general understanding of pterosaurs.

The current situation is not unusual in that pterosaur systematics has long been a 'poor cousin' to other more contentious aspects of these animals, such as their anatomy, physiology, and flight ability. Early accounts, for example by Meyer (1859) and Seeley (1870) were rather vague and it was not until 1901, more than 100 years after pterosaurs were first recognized, that the major division into "Rhamphorhynchoidea" and Pterodactyloidea was formally proposed by Plieninger. The early twentieth

century saw a burst of activity, with various taxonomies proposed by Williston (1903), Hooley (1913), Arthaber (1919), Nopcsa (1928) and, most importantly, Plieninger (1930). While these studies were quite detailed, there was relatively little discussion of the characters underlying the various taxonomic arrangements, there were no attempts to depict relationships and accounts of the evolutionary history of the group were highly generalized.

The first detailed illustration of pterosaur relationships was published by Young (1964; Fig. 1a) and was followed by a similar reconstruction by Kuhn in 1967 (Fig. 1b). Subsequently, Wellnhofer (1975a) presented a "rhamphorhynchoid" phylogeny, and later combined this with information on pterodactyloids in a tree that has come to represent the traditional view of pterosaur relationships (Wellnhofer 1978; Fig. 2). Wild (1978, fig. 47) also depicted and discussed the general relationships of Late Triassic and Early Jurassic pterosaurs. In all these studies, taxa were aligned in ancestor-descendant lineages on the basis of overall similarity: thus *Anurognathus*, a tall-skulled form with large fenestrae and a steeply oriented quadrate was presumed to have descended from *Dimorphodon*, a similar, tall-skulled form, also with large cranial fenestrae and a subvertical quadrate (Wellnhofer 1975b, 1978).

Howse (1986) published the first phylogenetic study to make use of cladistic techniques (Fig. 3a). This work, based on a subset of pterodactyloids, with *Rhamphorhynchus* as an outgroup, used only characters of cervical vertebrae, but was able to

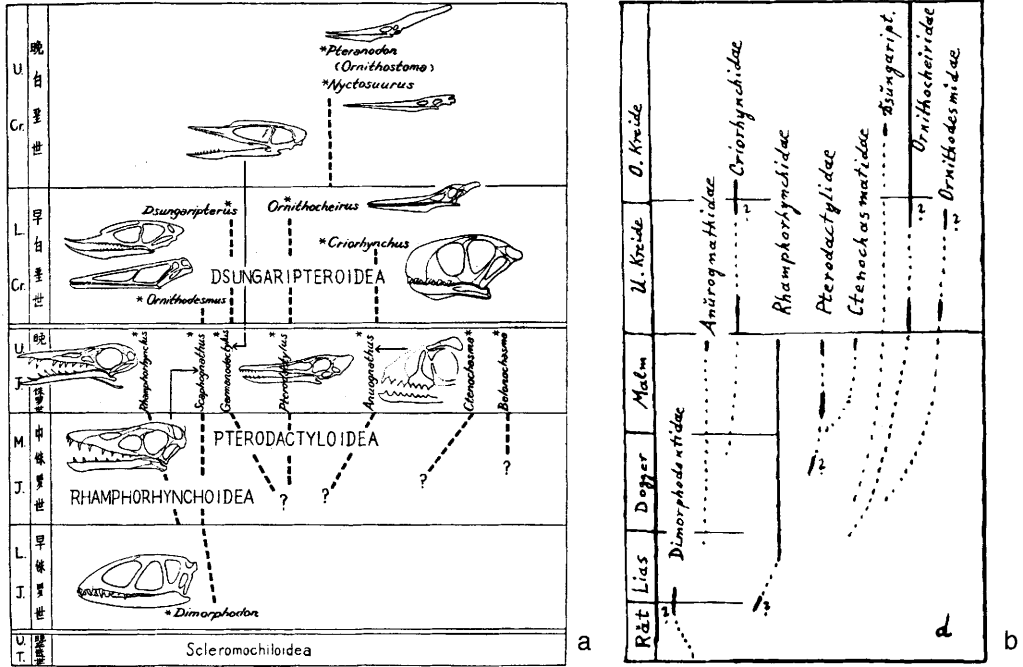


Fig. 1. Traditional evolutionary trees for pterosaurs proposed by (a) Young (1964) and (b) Kuhn (1967).

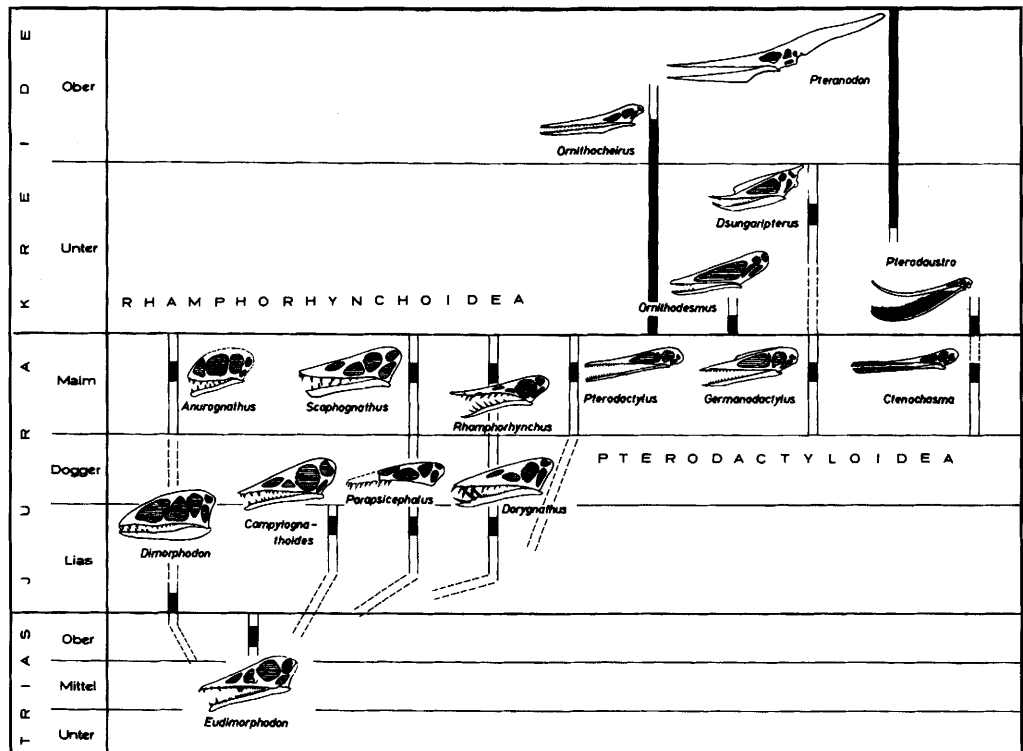


Fig. 2. Pterosaur evolutionary tree reconstructed by Wellnhofer (1978).

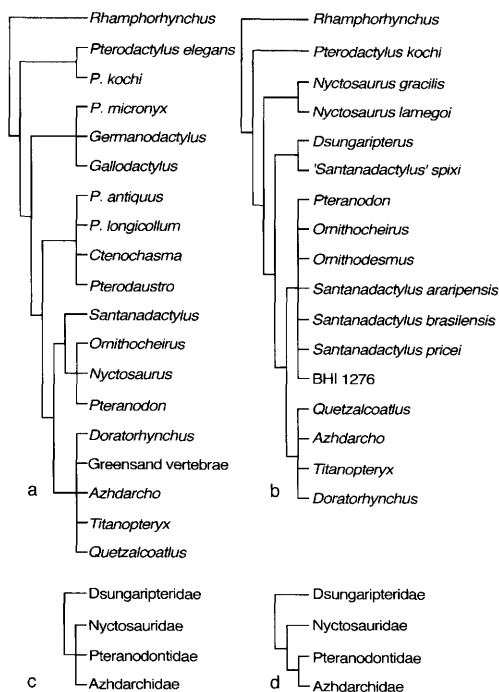


Fig. 3. Cladistic analyses of pterosaur relationships presented by (a) Howse (1986), and (b)–(d) Bennett (1989).

discover groups of long-necked and short-necked forms. Re-analysis of Howse's study by Kellner (1995), using Phylogenetic Analysis Using Parsimony (PAUP) and MacClade 3.03, resulted in little taxonomic resolution and also showed that the trees illustrated did not represent the most parsimonious solution (see also Kellner & Langston 1996).

Bennett (1989) presented the first analysis to utilize PAUP, including 19 taxa (*Rhamphorhynchus* and 18 pterodactyls) and 14 characters, all drawn from postcranial anatomy and using *Rhamphorhynchus* and *Pterodactylus kochi* as outgroups (Fig. 3b–d). Notably, two major clades, *Pteranodontidae* (*Pteranodon*, *Istiodactylus* [= †*Ornithodesmus*] and various ornithocheirids) and Azhdarchidae (*Quetzalcoatlus*, *Azhdarcho*, *Arambourgiania* [= †*Titanopteryx*] and *Gnathosaurus* [= †*Doratorhynchus*]), were recognized. As Bennett observed, however (1989, p. 675), the topology was supported by relatively few characters some of which, such as the appearance of a notarium, may be size related. Moreover, the data set consisted of almost 50% missing data (Kellner 1995), and much of the topology was dependent on interpretation of the polarity of a composite character based on the distal syncarpal. Kellner (1995) and Unwin (1995a) argued that the character state considered by Bennett

as derived probably represented the primitive condition, because it is widely distributed in pterodactyls and even occurs in the outgroups. Importantly, reversing the coding for this character collapses all but one of the groups (Nyctosauridae) in Bennett's original cladogram (Kellner 1995; Wilkinson 1995; Kellner & Langston 1996).

Later, Bennett (1994) published a more substantial study involving 27 taxa (*Rhamphorhynchus* and 26 genera or species of pterodactyls) and 37 characters. The single cladogram (Fig. 4a), reconstructed using MacClade (3.01), is generally similar to the principal cladogram previously published by Bennett (1989, fig. 3.1). A series of predominantly Jurassic pterodactyls form progressively closer sister-taxa to three families of Cretaceous pterosaurs: *Pteranodontidae*, Dsungaripteridae and Azhdarchidae. The content of these families is similar to that in the 1989 cladogram (cf. Figs 3b & 4a) although, notably, *Ornithocheirus* lies outside *Pteranodontidae* and separate from other ornithocheirids, such as *Anhangera*. Also of note is the pairing of Dsungaripteridae with Azhdarchidae, an arrangement not evident in any of Bennett's earlier cladograms (1989, fig. 3). Although more comprehensive than the 1989 study, Bennett's 1994 analysis suffered from the same difficulties: a large amount of missing data and problems with the polarity of some characters, especially those pertaining to the distal syncarpal (Kellner 1995). Analysis of the data set using PAUP supported only a single group, Nyctosauridae (Kellner 1995; Kellner & Langston 1996).

Utilizing data from a taxonomic review of Cretaceous pterodactyls, Unwin (1991) carried out a cladistic analysis of pterosaurs based on 18 taxa and 103 characters. The final cladogram was constructed by hand and a brief account appeared in 1992 (Fig. 4b). This was the first cladistic study to incorporate a broad range of taxa, including "rhamphorhynchoids" and pterodactyls. The study confirmed earlier suggestions that "Rhamphorhynchoides" was paraphyletic, consisting of taxa successively more distant to Pterodactylidae, and recovered a number of pterodactyl clades (Dsungaripteridae, Ornithocheiroidea and Azhdarchidae) that were similar in content to those identified by Bennett (1989, 1994). The principal distinction was in the recognition of a single clade of long-necked forms, the Azhdarchoidea, containing Jurassic pterosaurs such as *Pterodactylus* and *Ctenochasma*, as well as azhdarchids.

In a later analysis of pterosaur interrelationships Unwin (1995a) published a tree based on 60+ characters and 40+ taxa (Fig. 4c). This tree was one of four most parsimonious trees (MPTs) resulting from a PAUP (version 3.1.1) analysis of the data set, although, because of time constraints, details of the

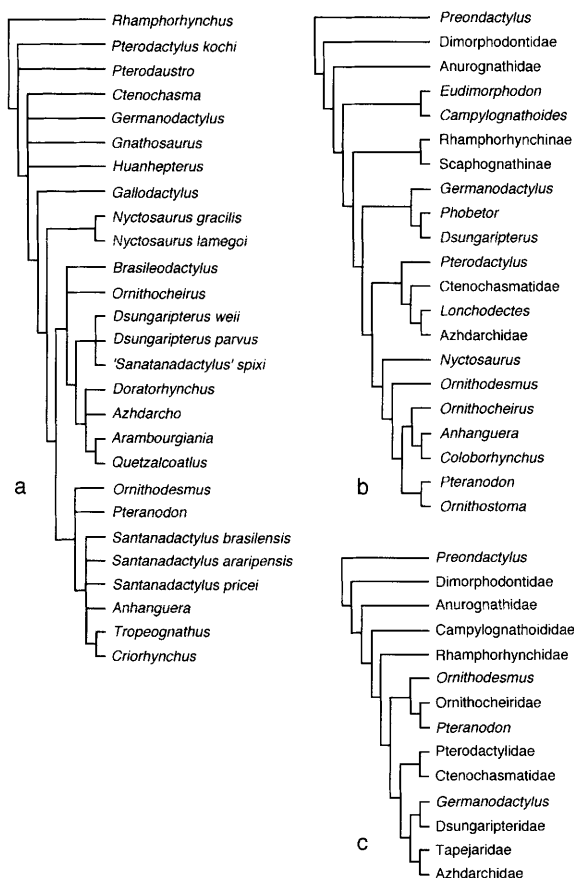


Fig. 4. Cladistic analyses of pterosaur relationships presented by (a) Bennett (1994), (b) and (c) Unwin (1992, 1995a).

statistical analysis were not included in the published material. The favoured tree (Fig. 4c), discussed in some detail by Unwin & Lü (1997), exhibits a similar topology to that previously described by Unwin (1992), except for some changes in the relationships of the major pterodactyloid clades, with the Ornithocheiroidea at the base of Pterodactyloidea, and long-necked pterosaurs split into two distinct groups: azhdarchids with tapejarids and dsungaripteroids as successively more distant sister taxa, and ctenochasmatoids as a sister-taxon to Dsungaripteroidea + Azhdarchoidea.

A second, comprehensive analysis of pterosaur inter-relationships, based on a data set consisting of 32 taxa and 66 characters and analysed using PAUP (version 3.1.1) was briefly outlined by Kellner (1996a; Fig. 5a), but the study upon which this was based (Kellner 1996b) has not yet been published. The structure of the tree is broadly similar to that presented by Unwin (1995a; cf. Figs 4c & 5a), but there are some differences in the arrangement of basal clades of "rhamphorhynchoids". Notably,

Dimorphodon occupies a relatively derived position. Differences are also evident in the arrangement of the main pterodactyloid clades: the Ctenochasmatidae and related forms occupy a basal position while the *Pteranodontoidea* [=Ornithocheiroidea *sensu* Unwin 1995a] is the sister-taxon to Dsungaripteroidea + Azhdarchoidea, although the content of these clades is almost identical to that proposed by Unwin (1995a).

Recently, Peters (1997) presented the results of a study of pterosaur relationships in which *Sharovipteryx* and other prolacertiforms were used as the outgroups. It is not possible to reconstruct a tree from the data presented, but details suggest some similarity to previous trees, at least regarding "rhamphorhynchoids", with, e.g. *Preondactylus*, dimorphodontids, eudimorphodontids and rhamphorhynchids as successively more derived groups. The arrangement and content of clades within Pterodactyloidea appears to be radically different from that in previous studies, e.g. in the unification of dsungaripterids, tapejarids, nyctosaurids and pteranodontids in a single clade, but

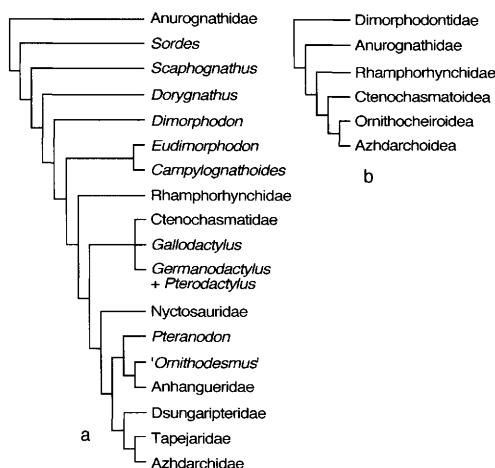


Fig. 5. Cladistic analyses of pterosaur relationships presented by (a) Kellner (1996a) and (b) Viscardi *et al.* (1999).

further assessment of these ideas is not possible at present.

Results of another recent study, based on data culled from published analyses, have been briefly outlined by Viscardi *et al.* (1999). A tree reconstructed from this account (Fig. 5b), exhibits a similar topology to that published by Kellner (1996a). According to Viscardi *et al.* (1999) the composition of the clades differs markedly from previous analyses, but details have not yet been published.

In summary, most cladistic studies published over the last 16 years share some basic topology in common (Unwin & Lü 1997; Unwin *et al.* 2000). “Rhamphorhynchoidea” is paraphyletic and composed of basal forms, e.g. dimorphodontids and anurognathids, and derived taxa such as *Rhamphorhynchus* and its relatives. Pterodactyloidea is monophyletic and most taxa can be assigned to just three or four principal clades (e.g. Dsungaripteridae, Ornithocheiroidea and Azhdarchoidea) dominated by Cretaceous forms. The content, relationships and even names of these clades are highly variable, however, and there are strongly divergent opinions regarding the relationships of Jurassic pterodactyls. While some studies locate these taxa within the major pterodactyloid clades (e.g. *Germanodactylus* as a sister-taxon to Dsungaripteridae, forming the Dsungaripteridae [e.g. Unwin 1995a; Fig. 4c]), in other cases the Jurassic pterodactyls form a cluster of basal taxa lying outside the principal clades (Bennett 1994; Fig. 4a). Moreover, the basic phylogenetic topology outlined above has been directly challenged by Peters (1997) and Viscardi *et al.* (1999).

Published analyses also suffer from other problems. At least eight different cladograms have been presented, but only two of these were accompanied by data matrices and both are substantially incomplete. In addition, there has been relatively little discussion of tree structure, the definition, variation and distribution of characters or the robustness of trees.

This paper presents the results of a new, comprehensive study of the inter-relationships of pterosaurs using cladistic techniques. The aims of this study were to: (1) diagnose terminal taxa using apomorphies and describe their content and stratigraphic range; (2) define, describe and discuss phylogenetically significant characters and their distributions; (3) analyse the relationship of pterosaurs using a data matrix compiled as far as possible from direct study of fossil material; and (4) assess the robustness of the resulting trees and compare them with previous studies.

Institutional abbreviations: AMNH, American Museum of Natural History, New York, USA; BMNH, Natural History Museum, London, UK; BSP, Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany; CAMSM, Sedgwick Museum, Cambridge, UK; CAMMZ, Museum of Zoology, University of Cambridge, Cambridge, UK; DMNH, Denver Museum of Natural History, Denver, USA; FMNH, Field Museum of Natural History, Chicago, USA; GSM, Museum of the Geological Survey, Keyworth, UK; IMCF, Iwaki Coal and Fossil Museum, Iwaki, Japan; IVPP, Institute for Vertebrate Palaeontology and Palaeoanthropology, Beijing, China; JM, Jura Museum, Eichstätt, Germany; MANCH, Manchester Museum, University of Manchester, Manchester, UK; MB, Museum Für Naturkunde, Berlin, Germany; MBH, Museum Bergèr, Harthof bei Eichstätt, Germany; MGUV, Museo del Departamento de Geología, Universidad de Valencia, Valencia, Spain; MNHN, Museum National d’Histoire Naturelle de Paris, France; MPV, Museo Paleontológico Municipal de Valencia, Valencia, Spain; MSA, Museum am Solenhofer Aktienverein, Maxberg bei Solnhofen, Germany; MT, Institut und Museum für Geologie und Paläontologie der Universität Tübingen, Tübingen, Germany; NAMAL, North American Museum of Ancient Life, Lehi, Utah, USA; NHMW, Naturhistorisches Museum, Wien, Austria; NMING, National Museum of Ireland, Dublin, Republic of Ireland; NSM, National Science Museum, Tokyo, Japan; OUM, Oxford University Museum, Oxford, UK; PIN, Palaeontological Institute, Russian Academy of Sciences, Moscow, Russia; PTH, Philosophisch-Theologische Hochschule, Eichstätt, Germany; SM, Natur-Museum und Forschungsinstitut Senckenberg, Frankfurt, Germany; SMNK,

Staatliches Museum für Naturkunde Karlsruhe, Germany; SMNS, Staatliches Museum für Naturkunde Stuttgart, Germany; TMM, Texas Memorial Museum, Austin, Texas, USA; YORM, Yorkshire Museum, York, UK; ZMNH, Zhejiang Museum of Natural History, Hangzhou, China.

Symbol conventions: Citation of a name in single quotation marks indicates that the validity of this taxon has yet to be clearly established, except in the case of '*Phobetor*', which is a valid taxon awaiting a replacement name. Citation in double quotation marks indicates that, here, this taxon is considered to be paraphyletic. Citation within asterisks indicates an alternative name for what is treated here as a valid monophyletic taxon (e.g. Ornithocheiroidea here = *Pteranodontidae* *sensu* Bennett 1989, 1994). Invalid names are prefixed by the symbol †.

Materials and methods

Terminal taxa

The most recent general account of pterosaurs (Wellnhofer 1991a) recognized approximately 100 species and a little over 40 genera. Several new taxa have been described in the last decade (Dalla Vecchia 1993, 1995; Cai & Wei 1994; Frey & Martill 1994; Kellner & Campos 1994; Lee 1994; Padian *et al.* 1995; Howse & Milner 1995; Harris & Carpenter 1996; Campos & Kellner 1997; Ji & Ji 1997, 1998; Buffetaut *et al.* 1998; Clark *et al.* 1998; Mader & Kellner 1999; Unwin & Heinrich 1999; Martill *et al.* 2000; Wang & Lü 2001; Dalla Vecchia *et al.* 2002; Jenkins *et al.* 2001; Wang *et al.* 2002; Carpenter *et al.* 2003; Frey *et al.* 2003), adding to this list. On the debit side, however, taxonomic reviews (Bennett 1994, 1995, 1996a; Howse & Milner 1995; Unwin & Heinrich 1999; Unwin 1991, 2001, 2002; Fastnacht 2001; Carpenter *et al.* 2003) have dismissed significant numbers of invalid taxa.

On the basis of published accounts and examination of fossil material, 93 valid species and a further 8 putatively valid species of pterosaur are recognised here (Table 1 & Appendix 1). Some of these species may eventually disappear into synonymy if they are found to be sexual dimorphs (e.g. Bennett 1992, 2002; Unwin 2001) or part of an ontogenetic sequence (e.g. Wellnhofer 1970; Bennett 1993, 1995, 1996a; Wild 1994; Unwin 1995b) of a previously erected species, but this is unlikely to have a significant impact on the character distributions described below. In this analysis character data was collected for 84 of the 93 species cited in Table 1, of which 65 were studied on the basis of fossil material or casts, while the remainder were assessed from the

Table 1. Classification, based on the phylogenetic relationships shown in Figure 7a, of all valid and potentially valid species of pterosaur

Pterosauria
<i>Preondactylus</i>
<i>P. buffarinii</i>
Macronychoptera
Dimorphodontidae
<i>Dimorphodon</i>
<i>D. macronyx</i>
<i>D. weintraubi</i>
<i>Peteinosaurus</i>
<i>P. zambellii</i>
Caelidracones
Anurognathidae
<i>Anurognathus</i>
<i>A. ammoni</i>
<i>Batrachognathus</i>
<i>B. volans</i>
<i>Dendrorhynchoidea</i>
<i>D. curvidentatus</i>
<i>Jeholopterus</i>
<i>J. ningchengensis</i>
Lonchognatha
Carnylognathoididae
<i>Austriadactylus</i>
<i>A. cristatus</i>
<i>Carnylognathoidea</i>
<i>C. liasicus</i>
<i>C. zitteli</i>
<i>Eudimorphodon</i>
<i>E.romptonellus</i>
<i>E. ranzii</i>
<i>E. rosenfeldi</i>
Breviquartossa
Rhamphorhynchidae
Rhamphorhynchinae
<i>Angustinaripterus</i>
<i>A. longicephalus</i>
<i>Dorygnathus</i>
<i>D. banthensis</i>
<i>D. mistelgauensis</i>
<i>D. purdoni</i>
<i>Nesodactylus</i>
<i>N. hesperius</i>
<i>Rhamphocephalus</i>
<i>R. bucklandi</i>
<i>Rhamphorhynchus</i>
<i>R. 'longiceps'</i>
<i>R. muensteri</i>
Scaphognathinae
<i>Scaphognathus</i>
<i>S. crassirostris</i>
<i>Sordes</i>
<i>S. pilosus</i>
Pterodactyloidea
Ornithocheiroidea
<i>Istiodactylus</i>
<i>I. latidens</i>
Euornithocheira
Ornithocheiridae
<i>Anhanguera</i>

Table 1 (continued)

A. blittersdorffi
A. cuvieri
A. fittoni
A. santanae
 Arthurdactylus
 A. conandoylei
 Brasileodactylus
 B. araripensis
 Coloborhynchus
 C. capito
 C. clavirostris
 C. moroccensis
 C. robustus
 C. sedgwickii
 C. wadleighi
 Haptopterus
 H. gracilis
 Ornithocheirus
 O. mesembrinus
 O. simus
 Pteranodontia
 Pteranodontidae
 Ornithostoma
 O. sedgwicki
 Pteranodon
 P. longiceps
 P. sternbergi
 Nyctosaurus
 N. gracilis
 N. lamegoi
 Lophocratia
 Ctenochasmatoidea
 Cycnorhamphus
 C. canjuersensis
 C. suevicus
 Euctenochasmia
 Pterodactylus
 P. antiquus
 P. kochi
 'P'. *micronyx*
 Lonchodectidae
 Lonchodectes
 L. compressirostris
 L. giganteus
 L. machaerorhynchus
 L. microdon
 L. platysomus
 ? *L. sagittirostris*
 Ctenochasmataidae
 Ctenochasmatinae
 Ctenochasma
 C. gracile
 C. porocristata
 C. roemeri
 ? *Eosipterus*
 E. yangi
 Pterodaustro
 P. guinazui
 Gnathosaurinae
 Cearadactylus
 C. atrox

Table 1 (continued)

Gnathosaurus
 G. macrurus
 G. subulatus
 Huanhepterus
 H. quingyangensis
 Plataleorhynchus
 P. streptophorodon
 'Pterodactylus' *longicollum*
 Dsungaripteroidea
 Germanodactylus
 G. rhamphastinus
 G. cristatus
 Herbstosaurus
 H. pigmaeus
 Kepodactylus
 K. insperatus
 Normannognathus
 N. wellnhoferi
 Tendaguripterus
 T. recki
 Dsungaripteridae
 Domeykodactylus
 D. ceciliae
 Dsungaripterus
 D. weii
 Noripterus
 N. complicidens
 'Phobetor'
 'P. parvus'
 Azhdarchoidea
 Tapejaridae
 Tapejara
 T. imperator
 T. wellnhoferi
 Neoazhdarchia
 Tupuxuara
 T. longicristatus
 T. leonardii
 Azhdarchidae
 Arambourgiania
 A. philadelphiae
 Azhdarcho
 A. lancicollis
 Montanazhdarcho
 M. minor
 Quetzalcoatlus
 Q. northropi
 Q. sp.
 Zhejiangopterus
 Z. linhaiensis

The following taxa are of uncertain validity and in many cases their position within the classification is unclear: 'Araripesaurus castilhoi' Price 1971; 'Mesadactylus ornithosphys' Jensen & Padian 1989; 'Puntanipterus globosus' Bonaparte & Sanchez 1975; 'Santanadactylus araripensis' Wellnhofer 1985; 'Santanadactylus brasiliensis' Buissonjé 1980; 'Santanadactylus pricei' Wellnhofer 1985; and 'Santanadactylus spixi' Wellnhofer 1985.

Table 2. *Morphometric data for terminal taxa used in this study (see Appendix 1)*

	Forelimb/ Hindlimb	Humerus/ Femur	Ulna/ Tibia	Humerus/ Wing metacarpal	Source of data
<i>Preondactylus</i>	2.48	0.98	0.95	0.45	Wild 1984a; Dalla Vecchia 1998
Dimorphodontidae	2.58–2.67	1.04–1.06	0.96–0.98	0.22–0.44	Owen 1870; Wild 1978; Padian 1983; Unwin 1988b
Anurognathidae	>2.64	1.19–1.46	1.15–1.33	0.33–0.34	Döderlein 1923; Riabinin 1948; Wellnhofer 1975b; Ji & Ji 1998; Unwin <i>et al.</i> 2000
Campylognathoididae	4.45–8.72	1.08–1.39	1.00–1.67	0.38–0.62	Plieninger 1895; Wellnhofer 1974; Wild 1978; Dalla Vecchia 1995
Scaphognathinae	3.19–3.40	1.00–1.21	1.36–1.58	0.44–0.50	Wellnhofer 1975b, author
Rhamphorhynchinae	3.40–5.49	1.03–1.48	1.25–1.81	0.39–0.68	Arthaber 1919; Wiman 1923; Salée 1928; Wild 1971; Wellnhofer 1975b, author
<i>Istiodactylus</i>	-	1.1	-	-	Hooley 1913
Ornithocheiridae	3.88 (est.)	1.09	1.36	1	Wellnhofer 1985, 1991b; Frey & Martill 1994; Kellner & Tomida 2000; Wang & Lü 2001, author
<i>Nyctosaurus</i>	4.84	1.06–1.11	1.04–1.18	2.53–2.71	Williston 1903; Brown 1986
Pteranodontidae	4.61	1.05–1.15	1.00–1.06	2.09–2.54	Bennett 2001
<i>Cycnorhamphus</i>	2.99	0.85	0.71–0.75	1.65–1.68	Wellnhofer 1970; Fabre 1976, author
<i>Pterodactylus</i>	2.66–3.25	0.82–1.28	0.80–1.17	0.80–1.79	Wellnhofer 1970; Tischlinger 1994; Frey & Martill 1998; Frey & Tischlinger 2001
Ctenochasmatidae	3.22	0.79–1.33	0.70–1.14	0.91–2.10	Wellnhofer 1970, author
<i>Germanodactylus</i>	2.85–2.90	0.96–0.99	0.86–1.09	1.09–1.18	Wellnhofer 1970, Unwin 1988a, author
Dsungaripteridae	>2.67	0.91	0.62	1.82	Young 1964, 1973; author
<i>Tapejara</i>	2.61	0.78	0.74	1.43	author
<i>Tupuxuara</i>	>2.50	0.78	0.71	1.54	author
Azhdarchidae	2.58	0.62	0.88	2.45	Lawson 1975a; Langston 1981; Cai & Wei 1994, author

published literature. Ideally, phylogenetic analyses should be conducted at the most exclusive level possible (e.g. Bininda-Emonds *et al.* 1998), i.e. the species, in order to reduce *a priori* assumptions of monophyly at higher levels. This is problematic for pterosaurs, however, because many species are incompletely known (Wellnhofer 1978, 1991a), resulting in data sets with high levels of missing entries (e.g. Bennett 1994, p. 70). This, in turn, usually results in large numbers of MPTs. Neither approach to this problem, i.e. exclusion of poorly represented taxa or production of consensus trees, is entirely satisfactory (e.g. Smith 1994).

One partial solution, adopted here, is to group taxa into more inclusive clades. This enables poorly known taxa to contribute phylogenetic information and also improves the completeness of matrices. Consequently, this analysis focused on 19 terminal taxa consisting of 8 genera, 2 subfamilies and 9 families (Appendix 1). Each suprageneric taxon and named ingroup taxon (see below) was formally defined in a phylogenetic sense (Queiroz & Gauthier 1992; Gauthier & Queiroz 2001) and their content specified. Most of these terminal taxa are well established, uncontroversial and can be diagnosed by a series of autapomorphies (Appendix 1), but several (e.g. *Preondactylus*, Scaphognathinae, *Tapejara* and

Tupuxuara) are only weakly supported and two (*Germanodactylus* and *Pterodactylus*) lack any apparent apomorphies and are treated here as metataxa *sensu* Gauthier (1986). Each of the terminal taxa exhibits a unique combination of character states for the 60 characters coded (Table 3), consequently all were included in the parsimony analysis (Wilkinson & Benton 1995).

Characters

A preliminary database of characters was compiled from published cladistic studies (see above) and in some cases from the older literature. These characters were critically assessed by examination of a wide range of fossil material (see Appendix 1 for details of specimens studied) which also led to the discovery of many additional phylogenetically useful characters. Ultimately, the database contained more than 120 characters, including some based on morphometric data (Table 2), but more than half of these were excluded before statistical analysis for the following reasons. Firstly, many published characters were relatively poorly defined and taxa could not be unambiguously scored for character states. In some cases it was possible to modify the character

definition so that scoring was possible, but in other cases this was impossible and the character was rejected. Secondly, the derived state for several binary characters was found to be unique to a single terminal taxon included in this study. These uninformative characters were also excluded. Thirdly, a small subset of characters were only discovered at a late stage of this study and could only be certainly scored for a few taxa. These characters were also excluded, but are mentioned in the text at relevant points.

Finally, 60 osteological characters (Appendix 2), 30 based on cranial and 30 on postcranial anatomy, were selected for this study, primarily because their character states were clear-cut and could be unambiguously coded, and also because they had been assessed on the basis of fossil material for 18 of the 19 terminal taxa (only *Preondactylus* was not examined directly). Additional data was compiled from the literature (see Appendix 1 for citations).

Methods

The taxon-character matrix (Table 3) was analysed using the cladistics package PAUP 3.1.1 (Swofford, 1993), with the 'branch and bound' search option and addition sequence 'furthest'. Runs were executed using both 'Acctran' and 'Deltran' settings. Multiple-state characters were always treated as unordered. Characters that exhibited more than one state for a particular terminal taxon (shown as 0/1 in the matrix) were treated as polymorphic. Character states that could not be coded because of excessive morphological transformation are denoted by 'x' (Table 3). Revised versions of the data set in which 'x' was treated as a discrete character state '3', or as uncertain '?', were analysed separately to assess the significance of this recoding. Continuously variable characters (Table 2) were broken into discrete states on the basis of breaks between distribution peaks.

Rooting of trees was dealt with in two ways. Initially, an outgroup was left unspecified and trees were rooted both by rooting the tree at an internal node with a basal polytomy and by making the ingroup monophyletic. Subsequently, the analyses were rerun using a specified outgroup. Selection of a suitable outgroup is difficult because the relationship of pterosaurs to other diapsids is controversial (Unwin 1999, Brochu 2002). Recent studies (Padian 1984b, 1997; Gauthier & Padian 1985; Gauthier 1986; Benton 1990, 1999; Sereno & Arcucci 1990; Sereno & Novas 1990; Sereno 1991, 1996) have tended to locate pterosaurs within Ornithodira (*sensu* Gauthier 1986), although there is no consensus as to their exact position within this group. Bennett (1996b) has shown, however, that if the hindlimb characters of pterosaurs and dinosauro-

morphs are not treated as homologous, character analysis supports a position near the base of archosauriforms, an idea that was previously suggested by Benton (1982, 1984, 1985) and, more recently, by Atanassov (2001). Peters (1997, 2000) has argued that there is some evidence to support a relationship between pterosaurs and various prolacertiforms, including *Sharovipteryx* and *Cosesaurus*, essentially a modern version of a precladistic hypothesis proposed by Wild (1978, 1984b).

At present it is not clear which, if any, of these hypotheses is correct. Happily, however, with regard to the polarization of characters used for establishing ingroup relationships of pterosaurs, this is largely irrelevant, because pterosaur skeletal anatomy is so derived that in almost all cases the plesiomorphic condition is common to each of the three outgroups used in this study: basal ornithodirans, basal archosauriforms and prolacertiforms.

Support for clades was calculated using bootstrapping techniques. In each case 1000 replicates were made, using the 'branch and bound' search option and the addition sequence 'furthest'. A decay analysis was performed by rerunning the initial data set and increasing the maximum length of permitted trees by a single step each time.

Results

Statistical analyses

Initial runs, which did not include an outgroup, treated 'x' as uncertain ('?') and rooted the tree internally, yielded six MPTs, each 111 steps in length. The first of these trees, together with standard descriptive data, is shown in Fig. 6a. The other five trees were identical except that the Lonchodectidae was variously paired with *Pterodactylus* or the Ctenochasmatidae, or in one case the three formed a trichotomy, and in three of the trees Dsungaripterioidea paired with Ctenochasmatoidae rather than with Azhdarchoidea. The same results were achieved using either the Acctran or Deltran setting. Treating 'x' as a unique character state ('3') resulted in trees 10 steps longer, but otherwise the results were the same.

Including an outgroup (Fig. 6b) resulted in six trees that were identical to those resulting from the 'unrooted' runs, but with a length of 112 steps, slightly different statistical parameters, and resolution of the trichotomy between *Preondactylus*, the Dimorphodontidae and all other pterosaurs. A strict consensus tree of these six trees is shown in Fig. 7a. and a summary of character state changes at each node is given in Table 4. Results of the bootstrap analysis are shown in Fig. 6c.

Table 3. Distribution of character states (0, 1, 2) among the terminal taxa used in this analysis

	5	10	15	20	25	30	35	40	45	50	55	60
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pleonodactylus</i>	0	0	0	0	0	0	0	0	0	0	0	0
Dimorphodontidae	1	1	1	0	0	0	0	0	0	0	0	0
Anurognathidae	1	1	1	0	0	0	0	0	0	0	0	0
Campylognathoididae	1	1	1	0	0	0	0	0	0	0	0	0
Scaphognathinae	1	1	1	1	1	1	1	1	1	1	1	1
Rhamphorhynchinae	1	1	1	1	1	1	1	1	1	1	1	1
<i>Istiodactylus</i>	1	1	1	1	1	1	1	1	1	1	1	1
<i>Nyctosaurus</i>	1	1	1	1	1	1	1	1	1	1	1	1
Ornithocheiridae	1	1	1	1	1	1	1	1	1	1	1	1
Pteranodontidae	1	1	1	1	1	1	1	1	1	1	1	1
Lonchodectidae	1	1	1	1	1	1	1	1	1	1	1	1
<i>Pterodactylus</i>	1	1	1	1	1	1	1	1	1	1	1	1
<i>Cycnorhamphus</i>	1	1	1	1	1	1	1	1	1	1	1	1
Ctenochasmatidae	1	1	1	1	1	1	1	1	1	1	1	1
<i>Germanodactylus</i>	1	1	1	1	1	1	1	1	1	1	1	1
Dsungaripteridae	1	1	1	1	1	1	1	1	1	1	1	1
<i>Tapejara</i>	1	1	1	1	1	1	1	1	1	1	1	1
<i>Tapuxatara</i>	1	1	1	1	1	1	1	1	1	1	1	1
Azhdarichidae	1	1	1	1	1	1	1	1	1	1	1	1

?, uncertainty because of incomplete preservation; 0/1, polymorphism; x, highly transformed morphologies that cannot be assigned to a particular character state.

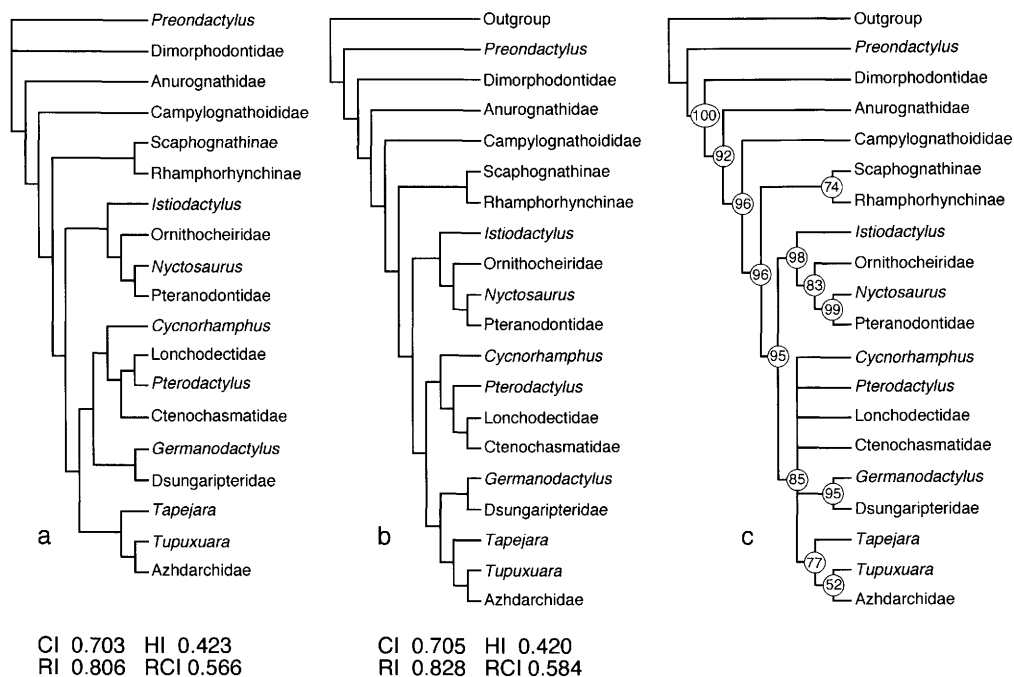


Fig. 6. Cladograms of pterosaur relationships based on a PAUP analysis of the character data matrix shown in Table 3. (a) One of six trees resulting from an unrooted analysis. (b) The same analysis, but including an outgroup. (c) Bootstrap values for the same analysis. Nodes occurring in less than 50% of all trees collapsed to a polytomy. CI, consistency index; HI, homoplasy index; RCI, rescaled consistency index; RI, Retention index.

Tree structure and character analysis

The “Rhamphorhynchoidea” is paraphyletic and consists of a series of clades that are successively closer to Pterodactyloidea (Fig. 7a). Characters used by Kuhn (1967) and Wellnhofer (1978) to define the “Rhamphorhynchoidea” are plesiomorphic for pterosaurs and do not support a monophyletic group.

Clade 1. Pterosauria Kaup 1834 (converted clade name).

Definition. *Preondactylus buffarinii*, *Quetzalcoatlus northropi*, their most recent common ancestor, and all its descendants (Peters 2000).

Content. *Preondactylus*, Dimorphodontidae, Anurognathidae, Campylognathoididae, Rhamphorhynchidae and Pterodactyloidea

Remarks. This clade, the ingroup for this analysis, is generally accepted to be monophyletic and is supported by numerous clear-cut characters, many related to the forelimb (see Romer 1956; Wellnhofer 1978; Padian 1984b; Sereno 1991; Bennett 1994, 1996b; Peters 2000). Surprisingly, Kuhn (1967) argued that pterosaurs were polyphyletic, an idea that was rejected by later workers (Wellnhofer 1978).

Clade 2. Macronychoptera (new clade name).

Etymology: Greek, *macro* = long or large, *onykh* = claw, *pteron* = wing, in reference to the relatively large size of the claws borne by manus digits I–III of pterosaurs in this clade.

Definition. *Dimorphodon macronyx*, *Quetzalcoatlus northropi*, their most recent common ancestor, and all its descendants.

Content. Dimorphodontidae, Anurognathidae, Campylognathoididae, Rhamphorhynchidae and Pterodactyloidea.

Synapomorphies

(1) *The dentary forms more than 75% of the length of the mandible.* (See Unwin 1995a.) In the outgroups and *Preondactylus* (Fig. 8a) the dentary forms approximately half, or less, of the total length of the mandible (Wild 1984a; Dalla Vecchia 1998). In all other pterosaurs (Figs 8b, c & 9–14) the dentary occupies at least 90% of the length of the mandible, except perhaps in *Dsungaripterus* (Bennett 2001), although this development must be homoplastic.

(2) *Coracoid at least 66% the length of the scapula.* In the outgroups, the coracoid is a rounded, plate-like structure. *Preondactylus* has an elongated coracoid that is approximately two-thirds the length

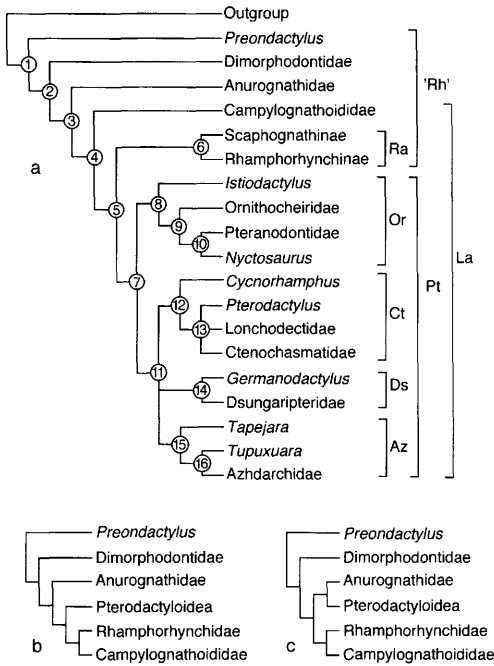


Fig. 7. Strict consensus tree of six trees resulting from PAUP analysis of the character data matrix shown in Table 3 and including an outgroup (a) Apomorphies supporting numbered clades are discussed in the text. Definitions and diagnoses of terminal taxa are given in Appendix 1. Alternative phylogenies depict Pterodactyloidea as (b) a sister-group to Campylognathoidae + Rhamphorhynchidae, or (c) as a sister-group to Anurognathidae. Az, Azhdarchoidea; Ct, Ctenochasmatoidea; Ds, Dsungaripteroidea; La, Lonchognatha; Or, Ornithocheiroidea; Pt, Pterodactyloidea; Ra, Rhamphorhynchidae; "Rh", "Rhamphorhynchoidea".

Table 4. Character (*Ch*) state changes between the nodes shown in Figure 7a

Branch	Ch.	Change
node 0 -> node 1	58	0=>1
node 1 -> node 2	1	0=>1
	2	0=>1
	3	0=>1
	4	0=>1
	5	0=>1
node 2 -> node 3	6	0=>1
	7	0=>1
	8	0=>1
node 3 -> node 4	9	0=>1
	10	0=>1
	11	0=>1
	12	0=>1
	13	0=>1
	14	0=>1

Table 4 (continued)

Branch	Ch.	Change
node 4 -> node 5	15	0=>1
	16	0=>1
	17	0=>1
	18	0=>1
	19	0=>1
	20	0=>1
	21	0=>1
	41	1=>0
node 5 -> node 6	22	0=>1
	23	0=>1
node 5 -> node 7	13	1=>0
	24	0=>1
	25	0=>1
	26	0=>1
	27	0=>1
	28	0=>1
	29	0=>1
	30	0=>1
node 7 -> node 8	31	0=>1
	32	0=>1
	33	0=>1
	34	0=>1
	35	0=>1
	36	0=>1
	37	0=>1
	38	0=>1
node 8 -> node 9	39	0=>1
	40	0=>1
	41	0=>1
node 9 -> node 10	34	1=>0
	42	0=>1
	43	0=>1
	44	0=>1
	45	0=>1
	46	0=>1
node 7 -> node 11	3	0=>1
	5	0=>1
	7	0=>1
	47	0=>1
	48	0=>1
node 11 -> node 12	49	0=>1
	50	0=>1
	51	0=>1
node 12 -> node 13	52	0=>1
	53	0=>1
node 11 -> node 14	54	0=>1
	55	0=>1
	56	0=>1
	57	0=>1
	58	1=>0
	59	0=>1
node 11 -> node 15	3	0=>1
	9	1=>2
	22	0=>1
	37	0=>1
	43	0=>1
	45	0=>1
	60	0=>1
node 15 -> node 16	31	0=>1
	37	0=>1

of the scapula (Wild 1984a; Fig. 16a), although it is still relatively broad and robust compared to the condition in derived pterosaurs (Fig. 16d, e). Other basal pterosaurs such as dimorphodontids (Fig. 16b), also have a relatively short, broad coracoid (Wild 1978, p. 240), but in this case it is slightly more than 70% the length of the scapula, while in anurognathids it reaches 75% the length of the scapula (Unwin *et al.* 2000, fig. 2). In all other pterosaurs the scapula is more slender and rod-like (Fig. 16c-e) and usually approaches, or in some groups even exceeds, the length of the scapula (see character 32).

(3) *Manual phalanges relatively robust compared to pedal phalanges.* In the outgroups, manual and pedal phalanges are usually of similar dimensions and robustness, or the manual phalanges are relatively small. *Preondactylus* also has manual and pedal phalanges, and unguals, of similar dimensions (Fig. 20a), whereas many pterosaurs, including all “rhamphorhynchoids” other than *Preondactylus*, have manual phalanges and unguals that are much more robust than the corresponding pedal elements (Fig. 20b, c). This size disparity is retained in some basal ctenochasmatooids, such as *Pterodactylus* (Fig. 20d), where it is more pronounced in adults than in juveniles, but more derived ctenochasmatooids, such as *Pterodaustro* (Wellnhofer 1991a, p. 131) and dsungaropteroids (e.g. *Germanodactylus*), appear to have manual and pedal phalanges of similar sizes. Clearly, this must represent a character reversal since both these taxa are firmly nested within the Pterodactyloidea.

(4) *Forelimb length more than 2.5 times the length of the hindlimb.* (See Unwin 1995a; Unwin *et al.* 2000.) Outgroup taxa either have forelimbs that are similar in length to the hindlimbs or, in some cases (e.g. prolacertiforms, *Scleromochlus*), the forelimb is much shorter than the hindlimb (femur + tibia + metatarsal III). In *Preondactylus* the forelimb is already highly elongated, as in other pterosaurs, but is slightly less than 2.5 times the length of the hindlimb (Table 2). In all other pterosaurs sufficiently complete for this index to be calculated the forelimb length is at least, and often far greater than, 2.5 times the length of the hindlimb (see Unwin *et al.* 2000, p. 186). Other basal “rhamphorhynchoids”, such as dimorphodontids and anurognathids, also have relatively short forelimbs compared to the hindlimbs, but in more derived clades (Campylognathoididae and Rhamphorhynchidae) they have relatively elongate forelimbs. Remarkably, basal ctenochasmatooids, such as *Pterodactylus*, and azhdarchooids also have relatively short forelimbs (Table 2), although in the latter case this may, in part, be attributable to elongation of the hindlimbs.

(5) *Humerus longer than the femur.* (See Unwin 1995a.) In the outgroups, the humerus is always shorter than the femur. This is also the case in

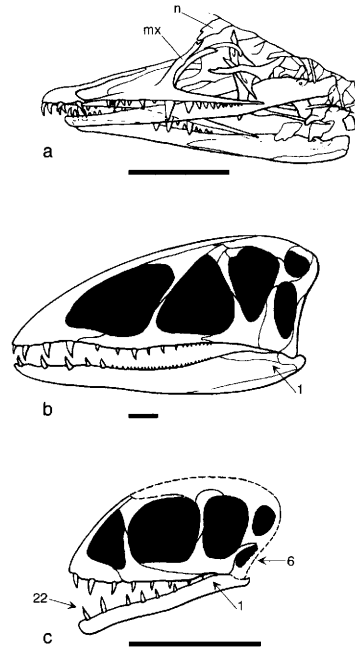


Fig. 8. Skulls of basal pterosaurs drawn to a uniform size and shown in left lateral view. (a) *Preondactylus buffarinii* (after Wild 1984a, reversed), (b) *Dimorphodon macronyx* (after Wellnhofer 1978), (c), *Anurognathus ammoni* (after Wellnhofer 1978). Numbered arrows (here and in Figs 9–20) indicate derived states of characters described in the text. mx, maxilla; n, nasal. Scale bar 20 mm.

Preondactylus (Table 2), but not in any other “rhamphorhynchoid” clades, where the humerus is either the same length or longer than the femur. One exception is the single known specimen of *Eudimorphodon cromptonellus* (Jenkins *et al.* 2001), but in this case the relative shortness of the humerus (92% the length of the femur) may be related to the immaturity of this individual. All known members of the Ornithocheiroidea also have a humerus/femur index greater than 1, whereas, with a few exceptions (some *Pterodactylus*, derived ctenochasmatooids), the humerus is shorter than the femur in other, non-ornithocheiroid pterodactyloids. It seems likely that the primary derived state for pterosaurs (humerus longer than femur) is plesiomorphic for pterodactyloids, because it is present in basal pterodactyloids (ornithocheiroids) and is also universally present in those “rhamphorhynchoid” clades likely to be sister-taxa to Pterodactyloidea (Rhamphorhynchidae, or Campylognathoididae + Rhamphorhynchidae, see below).

Remarks. *Preondactylus* exhibits the plesiomorphic state for the 48 characters that can be scored for this taxon (Table 3) and thus, in agreement with the results of other studies (Unwin 1992, 1995a, Peters

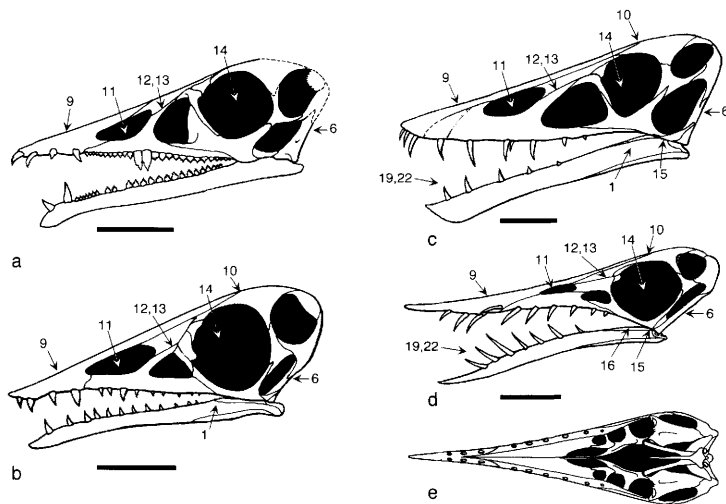


Fig. 9. Skulls of derived “rhamphorhynchoids” drawn to a uniform size and shown in left lateral view (a)–(d) and ventral view (e). (a) *Eudimorphodon ranzii*, (b) *Campylognathoides liasicus*, (c) *Scaphognathus crassirostris*, (d) and (e) *Rhamphorhynchus muensteri*. (All redrawn from Wellnhofer 1978.) Scale bar 20 mm.

1997; Dalla Vecchia 1998), is identified in this analysis as the most basal pterosaur and the sister-taxon to all other ingroup members. In the first description of *Preondactylus*, Wild (1984a) argued, on the basis of morphometric data and characters of the dentition, that this pterosaur was an early member of Rhamphorhynchidae, a proposal that, if correct, would place it in clade 6 of this analysis (Fig. 7a). Comparison with other taxa shows, however, that the dental and morphometric characters cited are found in other pterosaurs (e.g. *Dimorphodon*) and do not support a sister-group relationship for *Preondactylus* and the Rhamphorhynchidae. Dalla Vecchia (1998) corrected some of the meristic data and noted similarities with the dimorphodontid *Peteinosaurus* (Appendix 1), including the shape of the lower jaw and humerus and relative lengths of some of the limb bones. These characters, and a new interpretation of the skull as relatively short and deep (see Appendix 1), further emphasise the basal position of *Preondactylus*, but do not necessarily indicate that it is a dimorphodontid because they may be generally plesiomorphic for pterosaurs. In any case, the subequal size of the phalanges and unguals in the hands and feet of *Preondactylus* contrast sharply with the size disparity evident in these structures in *Peteinosaurus* (cf. Figs 20a and 20b), indicating that these taxa are not congeneric.

Clade 3. Caelidracones (new clade name)

Etymology. Latin, *caelum* = the air or the sky, *draco* = dragon, in reference to Seeley’s (1901) characterization of pterosaurs as ‘dragons of the air’.

Definition. *Anurognathus ammoni*, *Quetzalcoatlus northropi*, their most recent common ancestor, and all its descendants.

Content. Anurognathidae, Campylognathoididae, Rhamphorhynchidae and Pterodactyloidea.

Synapomorphies

(6) *Quadrate inclined anteriorly.* (See Unwin 1995a.) In the outgroups the quadrate is either vertically inclined or the ventral end that articulates with the mandible is located posterior to the dorsal end. In dimorphodontids (Fig. 8b), and apparently also in *Preondactylus* (Wild 1984a; Wellnhofer 1991a; Dalla Vecchia 1998), the quadrate is vertical, the ventral end located directly below the dorsal end when the skull is oriented with its ventral margin horizontal. The single described specimen of *Anurognathus* has been reconstructed with a quadrate in which the ventral end lies somewhat anterior to the dorsal end (Fig. 8c), but this cannot be confirmed at present because this and all other anurognathid skulls (Ryabinin 1948; Ji & Ji 1997; Unwin *et al.* 2000; Wang *et al.* 2002) are strongly compressed and preserved in dorsoventral orientation. It is evident, however, that in all other pterosaurs (Campylognathoididae + Rhamphorhynchidae + Pterodactyloidea) the quadrate slopes forward (Figs 9–13).

(7) *Ulna longer than the tibia.* (See Unwin 1995a; Unwin *et al.* 2000.) The majority of outgroup taxa have an ulna that is shorter than the tibia, as do the basal groups *Preondactylus* and dimorphodontids (Table 2). More derived “rhamphorhynchoids” and all known ornithocheiroids exhibit what is interpreted here, using outgroup comparison, as the

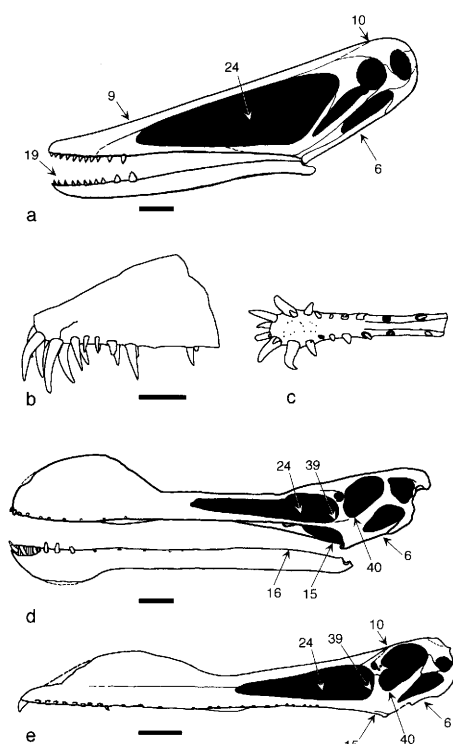


Fig. 10. Skulls of toothed ornithocheiroid pterosaurs drawn to a uniform size and shown in left lateral view (a), (b), (d) and (e), and ventral view (c). (a) *Istiodactylus latidens* (after Wellnhofer 1987), (b) and (c) *Coloborhynchus robustus* (after Fastnacht 2001), (d) *Ornithocheirus mesembrinus* (after Wellnhofer 1978), (e) *Anhanguera blittersdorffi* (after Kellner & Tomida 2000). Scale bar 50 mm.

derived condition with an ulna that is longer than the tibia, but in most non-ornithocheiroid pterodactyloids (with the exception of some specimens of *Pterodactylus* and ctenochasmatids) the tibia is longer than the ulna (see Unwin *et al.* 2000, p. 186). The latter, reflecting elongation of the hindlimb rather than shortening of the forelimb, is most parsimoniously interpreted as a secondarily derived condition. The alternative optimization, that non-ornithocheiroid pterodactyloids retain the primitive condition while the derived condition arose twice (in Anurognathidae + Campylognathoididae + Rhamphorhynchidae and in Ornithocheiroidea), requires location of Pterodactyloidea among the basal clades of Pterosauria and is less parsimonious (see below).

(8) *Fibula less than 80% the length of the tibia.* In outgroup taxa the fibula contacts the calcaneum. In basal pterosaurs the fibula is reduced to a slender, splint-like bone, but certainly contacted the calcaneum in dimorphodontids (BMNH 41347b, BMNH

43051), contrary to published illustrations and in *Campylognathoides* (Fig. 19j). In other clades, including the Anurognathidae (e.g. Unwin *et al.* 2000, fig. 2), *Eudimorphodon* (Wild 1978), Rhamphorhynchidae and Pterodactyloidea, the distal end of the fibula tapered to a fine point that fused with the shaft of the tibia (Fig. 19k). It is more parsimonious to presume that the plesiomorphic condition evident in *Campylognathoides* represents a reversal, because the alternative requires the derived condition to have arisen three times, rather than once.

Remarks. Another synapomorphy that potentially supports this clade is the elongate preacetabular process of the ilium. In *Preondactylus* (Wild 1984a, fig. 3) and in dimorphodontids (Owen 1870; Wild 1978), the preacetabular process of the ilium is shorter or of similar length to the postacetabular process, whereas in anurognathids (e.g. Wang *et al.* 2002, fig. 1) and more derived pterosaurs (Wellnhofer 1978, figs 14 & 15) it is considerably longer.

Wellnhofer (1975a, p. 22; Wellnhofer 1978, Fig. 2) suggested a close relationship between *Anurognathus* and *Dimorphodon*, but characters cited in support of this idea (short, high skull, upright quadrate, large antorbital fenestra) also occur in *Preondactylus* and some of the outgroups, and are probably plesiomorphic for pterosaurs. A close relationship between Anurognathidae and †Criorhynchidae (Kuhn 1967; Fig. 1b) or direct descent of †Criorhynchus from *Anurognathus* (Young 1964; Fig. 1a) must be rejected because †Criorhynchus and Criorhynchidae are invalid taxa and the short, deep skull, first proposed by Arthaber (1919), is incorrect (Wellnhofer 1987; Unwin 2001).

Clade 4. Lonchognatha (new clade name)

Etymology: Greek, *logkhos* = spear, *gnathos* = jaw, in reference to the relatively elongate, spear-shaped jaws of pterosaurs in this clade.

Definition. *Eudimorphodon ranzii*, *Rhamphorhynchus muensteri*, their most recent common ancestor, and all its descendants.

Content. Campylognathoididae, Rhamphorhynchidae and Pterodactyloidea.

Synapomorphies

(9) *Rostrum low with straight or concave dorsal outline.* (See Unwin 1995a; Unwin *et al.* 2000.) Basal pterosaurs and outgroup taxa have short deep rostra, with a high-arched, convex outline in lateral aspect (Figs 8b, c). Campylognathoidids, rhamphorhynchids and pterodactyloids have low elongate rostra, with either a straight or concave dorsal profile (Figs 9–13). *Preondactylus* has also been reconstructed with a low elongate rostrum (Wellnhofer 1991a; Dalla Vecchia 1998), but this is questionable because the elongate subvertical nasal process of the maxilla (Fig. 8a) shows that the snout was probably

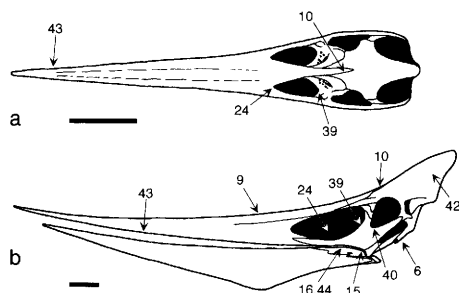


Fig. 11. Skulls of edentulous ornithocheiroid pterosaurs drawn to a uniform size and shown in dorsal view (a) and left lateral view (b). (a) *Nyctosaurus gracilis* (after Williston 1902), (b) *Pteranodon longiceps* (after Bennett 2001). Scale bar 50 mm.

as deep as that of *Dimorphodon* at this point (see Appendix 1).

Some azhdarchoids such as *Tapejara* also have relatively short deep rostra (Fig. 13c), but this probably represents a secondarily derived condition within Pterosauria, especially since the presence of an elongate rostral tip in *Tapejara* appears to indicate the existence of the primary apomorphic state in forms ancestral to Azhdarchoidea.

(10) *Posterior process of premaxillae interfingers between frontals.* (See Unwin 1995a.) In outgroup taxa the posterior process of the premaxillae contacts the nasals but does not extend between them (e.g. Sereno 1991; Benton 1999), whereas in pterosaurs the premaxillae extend further caudally, separating or overlapping the nasals and contacting the frontals. In basal forms, such as dimorphodontids (Fig. 8b) and anurognathids (Fig. 8c), the premaxillae terminate at the contact with the frontals, but in campylognathoidids (Fig. 9a, b), rhamphorhynchids (Fig. 9c, d) and pterodactyls (Figs 10–13) the premaxillae extend even further posteriorly, projecting between the mid-line contact of the frontals. Presumably, this arrangement enabled the skull to resist larger bending loads at the premaxilla-nasal-frontal contacts than in basal pterosaurs, a construction probably related to elongation of the snout.

(11) *External narial opening low and elongate.* Basal pterosaurs have a narial opening that in lateral aspect is as high (dorso-ventrally) or higher than it is long (antero-posteriorly) (Fig. 8a-c). In more derived “rhamphorhynchoids” (Fig. 9), the narial opening is more elongate than it is high, a morphology that is, presumably, correlated with elongation of the rostrum. Most outgroup taxa exhibit a condition wherein the narial opening is more elongate than it is high, thus it could be argued that the short, deep narial opening of basal pterosaurs represents an apomorphic condition and that the coding should be reversed. This has no effect when the outgroup is

excluded, however, and no significant impact on tree structure when an outgroup is incorporated into the analysis.

(12) *Nasal process of maxilla inclined backwards.* In the outgroups and in basal pterosaurs (Fig. 8a-c) the nasal process of the maxilla is oriented vertically. By contrast, in campylognathoidids and rhamphorhynchids, this process slants posterodorsally, its reorientation presumably at least partly associated with elongation of the rostrum. In pterodactyls the nasal process of the maxilla is absent, although its original location can be roughly estimated from the orientation of the maxilla process of the nasal, which is present in some Jurassic taxa (Figs 12b & 13a).

(13) *Broad maxilla-nasal contact.* The nasal of basal pterodactyls has a relatively elongate process that extends downwards to make a narrow contact with the nasal process of the maxilla and thus form the bony buttress separating the narial and antorbital fenestrae (Fig. 8a-c). In campylognathoidids and rhamphorhynchids the maxillary process of the nasal is shortened and the nasal process of the maxilla has a broad contact with the nasal, often extending along a considerable portion of the basal margin of this bone (Fig. 9a-d). In pterodactyls the bony buttress separating the narial and antorbital fenestrae is lost, but the long, narrow maxillary process of the nasal present in some Jurassic taxa (Figs 12b & 13a) suggests that pterodactyl ancestors had a narrow contact between the nasal and maxilla as in basal pterosaurs.

(14) *Orbit larger than antorbital fenestra.* (See Unwin 1995a.) The antorbital fenestra is larger than the orbit in basal pterosaurs (Fig. 8). By contrast, in campylognathoidids and rhamphorhynchids, the orbit is the larger of the two openings (Fig. 9a-d). The orbit is proportionately a little larger in these taxa than in basal pterosaurs, but the main processes contributing to this morphological change are the infilling of the antorbital fenestra as a result of the expansion of the bones surrounding this opening and the reduction in the height of the rostrum anterior to the orbit (Arthaber 1919). The condition in pterodactyls is not directly comparable because of the confluency of the nasal and antorbital fenestrae, but interestingly, where the antorbital fenestra is still discernible in some Jurassic forms (Fig. 12b & 13a), it is relatively large.

Remarks. As noted by Arthaber (1919, p. 412), who commented specifically on *Dimorphodon*, basal pterosaurs (*Preondactylus*, dimorphodontids and anurognathids) have relatively short deep skulls that retain a general construction similar to that seen in the outgroups. Lonchognathans are characterized by fundamental changes in cranial morphology, principally related to elongation of the rostrum: possibly an adaptation for enhancing the ability of these

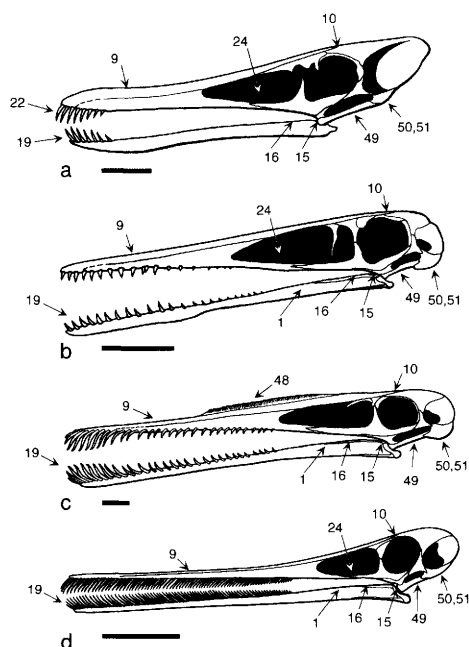


Fig. 12. Skulls of ctenochasmatoid pterosaurs drawn to a uniform size and shown in left lateral view. (a) *Cynorhamphus suevicus*, (b) *Pterodactylus antiquus*, (c) *Gnathosaurus subulatus*, (d) *Ctenochasma gracile*. (All redrawn from Wellnhofer 1978.) Scale bar 20 mm.

pterosaurs to capture prey on or just beneath the water surface during flight. The character polarities adopted here are further supported by ontogenetic patterns described for pterodactyloids such as *Pterodactylus kochi* (Wellnhofer 1970). In this species the rostrum is relatively short and deep in early ontogenetic stages, but becomes long and low in later stages (Wellnhofer 1970, fig. 18).

Clade 5. Breviquartossa (new clade name)

Etymology. Latin, *brevis* = short, *quartus* = fourth, *ossum* = bone, in reference to the relatively short fourth metatarsal of pterosaurs in this clade.

Definition. *Rhamphorhynchus muensteri*, *Quetzalcoatlus northropi*, their most recent common ancestor, and all its descendants.

Content. Rhamphorhynchidae and Pterodactyloidea.

Synapomorphies

(15) *Ventral margin of skull curved downwards caudally.* (See Unwin 1995a.) The ventral profile of the skull essentially follows a straight line in the outgroups, basal pterosaurs (Fig. 8) and campylognathoidids (Fig. 9a, b). By contrast, in rhamphorhynchids and pterodactyloids the caudal region of the skull posterior to the antorbital fenestra is curved downwards such that the ventral articular end of the

quadrate lies well below the level of the ventral margin of the rostrum (Figs 9c, d & 10–13).

(16) *Loss of 'coronoid' eminence on caudal end of mandible.* The dorsal margin of the mandible of outgroup taxa, basal pterosaurs (Figs 8a–c) and campylognathoidids (Figs 9a, b & 14a) bears a low 'coronoid' eminence just anterior to the articular region. In rhamphorhynchids (Figs 9a, b & 14c) and pterodactyloids (Figs 10–13) this eminence is lost and the dorsal margin of each mandible is flat anterior to the articular region.

(17) *Development of bony mandibular symphysis.* (See Unwin 1995a.) The mandibles of outgroup taxa, basal pterosaurs (Figs 8a & 14b) and campylognathoidids (Fig. 14a) contact at their anterior tip and were probably held together by fibrous connective tissue, but do not appear to have been fused. In adult rhamphorhynchids and pterodactyloids, the anterior tips of the mandibles were co-ossified and often formed a symphysis (Fig. 14c–f).

(18) *Mandibular symphysis forms more than 30% the length of the mandible.* (See Unwin 1995a.) As mentioned above, the mandibles of basal pterosaurs and campylognathoidids are unfused, whereas in rhamphorhynchids and pterodactyloids they are fused to form a symphysis. Moreover, in rhamphorhynchines (Fig. 14d) and most pterodactyloids (Figs 14e, f), the symphysis forms more than 30% of the total length of the lower jaw (see also Bennett 2001). Optimization of this character is difficult. It may be apomorphic for clade 5 (Fig. 7a), reversing to the plesiomorphic condition in scaphognathines, *Istiodactylus*, lonchodectids and *Germanodactylus*. Alternatively, the apomorphic condition may have arisen homoplastically in rhamphorhynchines, derived ornithocheiroids, ctenochasmatoids, dsungaripterids and azhdarchoids. The former, more parsimonious, proposal is accepted here.

(19) *Loss of heterodonty in the mandibular dentition.* (See Unwin 1995a.) Typically, in the outgroup taxa, and in basal pterosaurs and campylognathoidids, the rostral end of the mandibular dentition begins with two, large, fang-like teeth (Figs 8a–c & 9a, b). The remaining mandibular teeth are much smaller and usually of similar size. In rhamphorhynchids and pterodactyloids this heterodonty is lost, the first two teeth in each mandible usually being of similar size to the remaining teeth (Figs 9c, d, 10, 12 & 13). Heterodonty reappears in ornithocheiroids (Fig. 10b–d) and in some gnathosaurines (Dong 1982; Leonardi & Borgomanero 1985; Unwin 2000), but the relative enlargement of the teeth at the anterior end of the mandible always extends beyond the first two positions and thus is probably not homologous with the condition in basal pterosaurs.

(20) *Metacarpals I, II and III of equivalent length.* Metacarpals I–III of outgroup taxa, basal pterosaurs

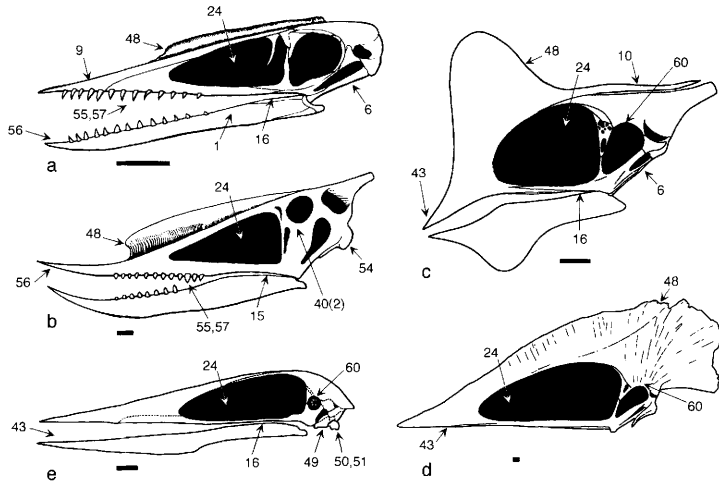


Fig. 13. Skulls of dsungaripteroid and azhdarchoid pterosaurs drawn to a uniform size and shown in left lateral view. (a) *Germanodactylus cristatus* (after Wellnhofer 1978), (b) *Dsungaripterus weii* (after Wellnhofer 1978), (c) *Tapejara wellnhoferi* (after Wellnhofer & Kellner 1991), (d) *Tupuxuara longicristatus* (IMCF 1052), (e) *Zhejiangopterus linhaiensis* (after Unwin & Lü 1997). Scale bar 20 mm.

(Figs 20a, b) and campylognathoidids (Fig. 18a) are of unequal length: most noticeably, metacarpal I is always distinctly shorter than II and III. By contrast, in most rhamphorhynchids and pterodactyloids metacarpals I–III are of equivalent length and their distal terminations are level with each other (Figs 18o, p & 20d). The rhamphorhynchine *Dorygnathus* exhibits the plesiomorphic condition (e.g. Arthaber 1919, fig. 22), by contrast to other rhamphorhynchids, which have metacarpals I–III of the same length. Consequently, it is most parsimonious to assume that the condition in *Dorygnathus* represents a reversal to the plesiomorphic state.

(21) *Short metatarsal IV.* (See Unwin 1995a; Unwin *et al.* 2000.) Metatarsals I–IV of outgroup taxa, basal pterosaurs (Figs 20a, b) and campylognathoidids are of the same, or similar, length, their distal ends terminating level with each other (Unwin *et al.* 2000, p. 192). Metatarsal IV is markedly shorter than I–III in rhamphorhynchids and pterodactyloids (Figs 20c, d).

Remarks. This and some previous studies (Unwin 1992, 1995a; Kellner 1996a; Viscardi *et al.* 1999) have presented evidence in support of a relationship between Rhamphorhynchidae and Pterodactyloidea. Another possibility is that Rhamphorhynchidae is more closely related to Campylognathoididae than to Pterodactyloidea and that this large clade forms a sister-taxon to Pterodactyloidea (Fig. 7b). This hypothesis is supported by character states that are shared by Rhamphorhynchidae + Campylognathoididae and the retention by pterodactyloids of character states otherwise found only in basal pterosaurs.

Thus, Rhamphorhynchidae + Campylognathoididae is supported by derived states for characters 11–14, while basal pterodactyloids (or at least some of them) exhibit the plesiomorphic condition for characters 3, 5 and 7 (Table 3) and a condition that is only slightly derived compared to the plesiomorphic state for character 4 (Table 2). Moreover, stem-group pterodactyloids are likely to have retained the plesiomorphic state for characters 11–14.

Optimizing character states to support the relationships shown in Fig. 7b is less parsimonious than the arrangement shown in Fig. 7a, but this idea merits further study, as does another intriguing possibility, that Pterodactyloidea might share a closer relationship with Anurognathidae than with any other “rhamphorhynchoid” clade. Wellnhofer (1975b, p. 183) noted similarities between the pelvis of *Anurognathus* and pterodactyloids, and two characters utilized in this analysis (character 26, reduction of cervical ribs; character 27, reduction in the length of the caudal series) also support this relationship. If pterodactyloids are assumed to have the plesiomorphic condition for characters 11–14, then a sister-group relationship between Pterodactyloidea and Campylognathoididae + Rhamphorhynchidae has only the same level of support (two characters: 9 and 10) as the pairing of Anurognathidae + Pterodactyloidea.

Clade 6: Rhamphorhynchidae Seeley 1870 (converted clade name)

Definition. *Sordes pilosus*, *Rhamphorhynchus muensteri*, their most recent common ancestor, and all its descendants.

Content. Rhamphorhynchinae and Scaphognathinae.

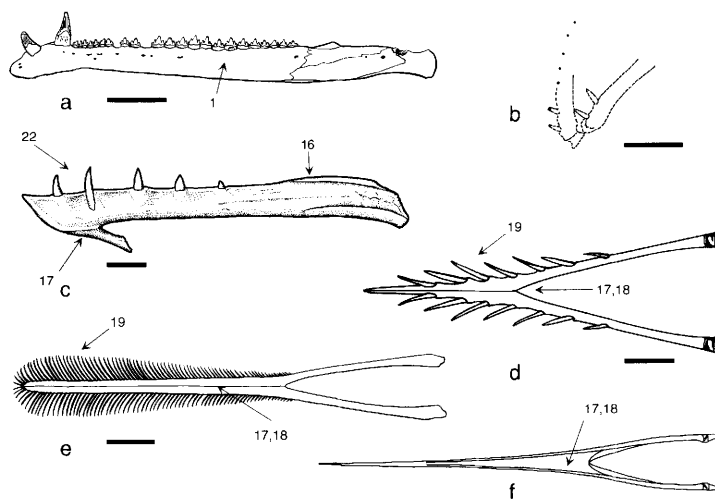


Fig. 14. Pterosaur lower jaws drawn to a uniform size and shown in left lateral view (a)–(c) and dorsal view (d)–(f). (a) *Eudimorphodon ranzii* (after Wild 1978), (b) *Anurognathus ammoni* (after Wellnhofer 1975b), (c) *Scaphognathus crassirostris* (after Wellnhofer 1975b), (d) *Rhamphorhynchus muensteri* (after Wellnhofer 1975c), (e) *Ctenochasma gracile* (after Wellnhofer 1978), (f) *Pteranodon longiceps* (after Bennett 2001). Scale bar 10 mm, except for (f) 100 mm.

Synapomorphies

(22) *Less than 11 pairs of teeth in the rostrum.* All outgroup taxa and most pterosaurs have at least, and often far more than, 11 pairs of teeth in the rostrum (Figs 8a, b, 9a, b, 10, 12 & 13). Rhamphorhynchids have, at most, 9 pairs of rostral teeth (Fig. 9c–e) and in many taxa this number is further reduced. *Anurognathus* (Fig. 8c) also shows a strong reduction in the numbers of rostral teeth with only 8 pairs, but the stratigraphically older form, *Batrachognathus*, has at least 11 pairs of teeth (Ryabinin 1948); thus the condition in *Anurognathus* may be homoplastic with respect to rhamphorhynchids. Several pterodactyloids also exhibit this apomorphy: *Cycnorhamphus* (Fig. 12a) has only 8 pairs of teeth and *Nyctosaurus* (Fig. 11a), pteranodontids (Fig. 11b) and azhdarchoids (Figs 13c–e) are edentulous. This suggests an alternative possibility, that this character is apomorphic for clade 5 (Fig. 7a), although this would require at least three reversals to the primitive condition: in ornithocheiroids, *Pterodactylus* + Lonchodectidae + Ctenochasmatidae, and dsungaripteroids. This is equally parsimonious to the optimization adopted here, and the only grounds for preferring the latter is that reduction in tooth numbers is far more common within clades (e.g. found in campylognathoidids, rhamphorhynchines, ornithocheiroids and dsungaripteroids) than an increase in number (e.g. ctenochasmatids).

(23) *Deltopectoral crest tongue-shaped, with necked base.* Outgroups and all other clades of pterosaur have a deltopectoral crest that is broad-based and either tapers towards its distal, free

margin, or remains of similar depth (Fig. 17a, b, d, g–k). Rhamphorhynchids are distinguished by a deltopectoral crest that is tongue-shaped, with a constricted base and an expanded distal portion (Fig. 17c). This condition is most clearly developed in *Rhamphorhynchus* (e.g. Wellnhofer 1975a; Fig. 17c) but is also evident in *Dorygnathus* (Arthaber 1919) and in *Sordes* (Sharov 1971; Bakhurina 1986, p.33; Ivakhnenko & Korabelnikov 1987, fig. 262). *Nyctosaurus* also has a deltopectoral crest with a constricted base (Williston 1903; Fig. 17i), but the ‘axe-head’-shaped distal expansion and the displacement of the deltopectoral crest further down the shaft clearly distinguishes the nyctosaurid humerus from that of rhamphorhynchids.

Remarks. Comparison with previous systematic studies shows that opinions regarding the content of this clade are variable. Wellnhofer (1978) included *Campylognathoides* together with scaphognathines and rhamphorhynchines in Rhamphorhynchidae, but the former taxon shares characters in common with *Eudimorphodon* (Wild 1978; Appendix 1), which are not found in other pterosaurs, and lacks apomorphies of Rhamphorhynchidae + Pterodactyloidea, or Rhamphorhynchidae.

Sordes, a member of Scaphognathinae (Unwin & Bakhurina 2000; Appendix 1), is considered by Kellner (1996a; Fig. 5a) to be a basal pterosaur, although no character data was cited in support of this, and by Peters (2001) to be a member of the Dimorphodontidae. Among the 12 characters listed by Peters, one (character 9) supports a derived position for *Sordes* with regard to other ‘rhamphorhynchoids’,

one (character 12) is autapomorphic for *Sordes* (Sharov 1971), five (characters 2, 3, 8, 10 and 11) are not consistent with or determinable on the basis of available fossil evidence, four (characters 1, 4, 5 and 7) are not confined to *Sordes* and dimorphodontids and are probably plesiomorphic for pterosaurs, and one (character 6) cannot be unambiguously determined for other pterosaurs. Apart from exhibiting all apomorphies of Scaphognathinae (Appendix 1), *Sordes* also shows the derived state for all characters (1–23) so far described in this analysis, strongly contradicting the possibility of a basal position within Pterosauria.

Clade 7: Pterodactyloidea Plieninger 1901 (converted clade name)

Definition. *Pteranodon longiceps*, *Quetzalcoatlus northropi*, their most recent common ancestor, and all its descendants.

Content. Ornithocheiroidea, Ctenochasmatoidea, Dsungaripteroidea and Azhdarchoidea.

Synapomorphies

(24) *Narial and antorbital fenestrae confluent.* (See Unwin 1995a). In the outgroups and in all “rhamphorhynchoids” (Figs 8 & 9) the narial and antorbital fenestrae are separated by a bony bar consisting of the nasal process of the maxilla and the maxilla process of the nasal. In all pterodactyloids this bony bar is absent (Figs 10–13), although in some Jurassic forms (*Pterodactylus*, *Germanodactylus*) a slender elongate process, presumably homologous with the maxilla process of the nasal of “rhamphorhynchoids” is retained.

(25) *Basipterygoids united to form a median bar of bone.* (See Unwin 1995a.) In the outgroups and in “rhamphorhynchoids” the basipterygoids remain separate (Fig. 9e). In pterodactyloids, however, the basipterygoids fuse to form an elongate median bar of bone (sometimes labelled the basisphenoid, e.g. Wellnhofer 1978) which runs forwards from the basioccipital region to contact the quadrates (Wellnhofer 1978, fig. 6). Occasionally, juvenile pterodactyloids (e.g. ‘*Pterodactylus*’ *micronyx*, Wellnhofer 1970, fig. 8a) exhibit the plesiomorphic condition, with separate basipterygoids.

(26) *Reduction of cervical ribs.* (Howse 1986; Bennett 1994; Unwin 1995a.) Elongate cervical ribs are present in outgroup taxa and in most “rhamphorhynchoids” (Fig. 15b). Cervical ribs are widely thought to be absent in pterodactyloids (Kuhn 1967; Wellnhofer 78; Howse 1986; Bennett 1994), and indeed there is no direct evidence for them in most taxa (Figs 15c–g). Remnants of cervical ribs are found, however, in some ornithocheirids, where they take the form of a small bony arch spanning the gap between the prezygapophysial process and the centrum. Generally, these structures are completely fused to the vertebra and their limits cannot be traced, but they are well seen in the cervical verte-

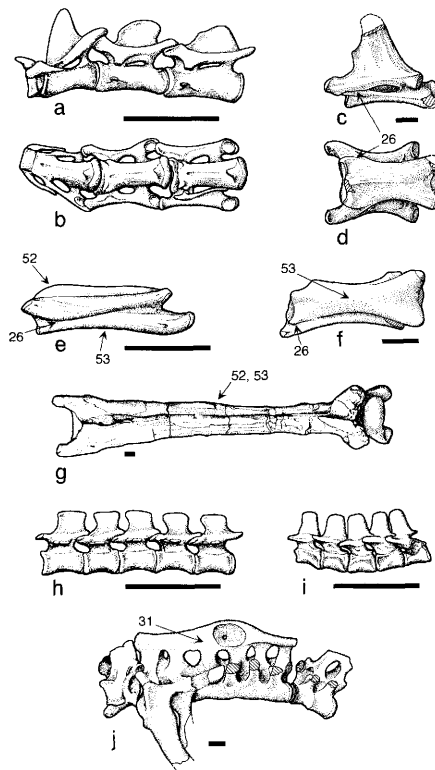


Fig. 15. Cervical and dorsal vertebrae of pterosaurs drawn to a uniform size. Cervical vertebrae shown in left lateral view (a), (c), (e), ventral view (b), (d), (f) and dorsal view (g). Dorsal vertebra shown in left lateral view. (a), (b) and (h) *Rhamphorhynchus muensteri* (after Wellnhofer 1975c), (c) and (d) *Anhanguera santanae* (after Wellnhofer 1991c), (e) and (f) *Pterodactylus antiquus* (after Wellnhofer 1970), (g) *Quetzalcoatlus* sp. (BMNH R2287c), (h) *Quetzalcoatlus* sp. (after Howse 1986), (i) *Pteranodon longiceps* (after Bennett 2001). Scale bar 10 mm.

brae of *Coloborhynchus robustus* (NSM-PV 19892). Their presence can also be inferred in some azhdarchoids, which retain a narrow passage between the prezygapophysial process and the centrum, and whose outer wall is probably formed from a remnant of the cervical rib, now completely fused to the vertebra. Until recently, the condition in anurognathids, where cervical ribs seem to be absent, was difficult to determine because of the poor preservation of the neck region (Ryabinin 1948; Wellnhofer 1975b). New, well-preserved specimens from the Yixian Formation (Ji & Ji 1998; Unwin *et al.* 2000), one with a complete neck (Wang *et al.* 2002), also appear to lack cervical ribs, a synapomorphy that the Anurognathidae share with the Pterodactyloidea (Table 3).

(27) *Caudal vertebral series shorter than dorsal*

series. (see Unwin 1995a; Unwin *et al.* 2000.) The complete caudal series in outgroup taxa and in all “rhamphorhynchoids” except anurognathids easily exceeds in length the complete dorsal series (Bennett 1994). In pterodactyloids the caudal series is sharply reduced to fewer than 15 caudals which usually form a short stubby tail, although in some taxa (e.g. *Dsungaripterus* and *Pteranodon*) the distal caudals are occasionally elongate (Bennett 1987). Despite this variation, the caudal series in pterodactyloids is shorter than the dorsal series in all known taxa. Anurognathids also appear to have a sharply reduced caudal series that is remarkably similar to the tail of pterodactyloids. Ji & Ji (1998) and Ji *et al.* (1999) have argued that a late surviving anurognathid, *Dendrorhynchoides*, from the Lower Cretaceous Yixian Formation has a long tail. More recently, however, Unwin *et al.* (2000) suggested that the tail may be a fake and argued that *Dendrorhynchoides* has a short tail. This interpretation has been supported by Wang *et al.* (2002), who described another anurognathid, *Jeholopterus*, from the Yixian Formation, that also clearly lacks a long tail.

(28) *Pteroid long and slender.* (See Unwin 1995a; Unwin *et al.* 2000.) The pteroid, a rod-like bone that articulates with the medial carpal, is a true bone (Unwin *et al.* 1996) and apparently unique to pterosaurs. In “rhamphorhynchoids” it is a relatively short stubby structure, its total length no greater than 5 times its basal width (Fig. 18a). By contrast, in pterodactyloids the pteroid is highly elongate and always at least 7 times longer than its basal width (Fig. 18b, see also Unwin *et al.* 2000, p. 186) and in many cases proportionately much longer, as for example in *Cycnorhamphus* (Plieninger 1907). The only exception to this pattern occurs in *Rhamphorhynchus*, where the pteroid is relatively elongate in some specimens of *R. muensteri* (Wellnhofer 1975a, fig. 12).

(29) *Wing metacarpal (IV) at least 80% the length of the humerus.* (See Unwin *et al.* 2000.) In all “rhamphorhynchoids”, as in outgroup taxa, the wing metacarpal is relatively short and reaches, at most, only 68% the length of the humerus (Table 2). In all pterodactyloids the wing metacarpal is at least 80% the length of the humerus and often far exceeds the length of the latter (see also Unwin *et al.* 2000).

(30) *Pes digit V with a single phalanx or entirely absent.* (See Bennett 1994; Unwin 1995a; Unwin *et al.* 2000.) The fifth toe is present in most outgroup taxa, although not all (e.g. *Scleromochlus*, Benton 1999), and in all “rhamphorhynchoids” where it consists of two elongate phalanges, but no ungual (Fig. 20b). A single, highly reduced phalanx is retained in some Jurassic pterodactyloids (Fig. 20d), but the fifth toe appears to be entirely absent in other taxa (Wellnhofer 1978, 1991a).

Remarks. In addition to the synapomorphies listed above, this highly distinctive clade of ‘short-tailed’ pterosaurs, recognized as early as the mid-nineteenth century, is supported by numerous other apomorphies including elongation of the skull, forward inclination of the quadrate, and shift of the glenoid from wholly on the scapula to a position between the scapula and coracoid (see also Kuhn 1967; Wellnhofer 1978; Howse 1986; Bennett 1994).

Clade 8. Ornithocheiroidea Seeley 1891 (converted clade name)

Definition. *Istiodactylus latidens*, *Pteranodon longiceps*, their most recent common ancestor, and all its descendants.

Content. *Istiodactylus*, Ornithocheiridae, Pteranodontidae and *Nyctosaurus*.

Synapomorphies

(31) *Development of a notarium.* (See Bennett 1989, 1994; Unwin & Lü 1997.) The dorsal vertebrae of outgroup taxa, all known “rhamphorhynchoids” and some pterodactyloids remain separate and unfused (Fig. 15h, i). In ornithocheiroids early dorsal vertebrae fuse to form a notarium, that in some, but not all cases (e.g. *Nyctosaurus* Bennett 2001) articulates with the distal end of the scapula via an articular facet on a supraneural plate formed from the fused neural processes of the dorsal vertebrae (Fig. 15j).

A similar structure has been reported in *Dsungaripterus* (Young 1964, 1973) and ‘*Phobetor*’ (Bakhurina pers comm. 2001) and also in *Tupuxuara* (IMCF 1052; Kellner & Hasegawa 1993) and azhdarchids (Nesov 1984, Buffetaut 1999). According to Bennett (1989, 1994) all these taxa and ornithocheiroids form a single clade diagnosed by the presence of a notarium. By contrast, the results of this analysis suggest that a notarium developed homoplastically in the Ornithocheiroidea, *Dsungaripteroidea* and *Azhdarchoidea* because it is absent from basal taxa within these clades (*Germanodactylus*, *Tapejara*) and, by inference, from the common ancestor of the Ornithocheiroidea and other pterodactyloids.

Non-homology of the notarium across Pterodactyloidea, as originally suggested by Wellnhofer (1978, p. 53) is supported by several observations. The degree of fusion and number of vertebrae involved is highly variable (Buffetaut 1999, p. 291; Bennett 2001, p. 50). The ornithocheiroid scapula is oriented almost perpendicular to the notarium and occupies a subhorizontal position, whereas in *Tupuxuara*, for example, (IMCF 1052), the scapula is obliquely oriented at 45° to the notarium, and slopes both downwards and forwards to its contact with the coracoid. This is a completely different arrangement from that found in ornithocheiroids, but

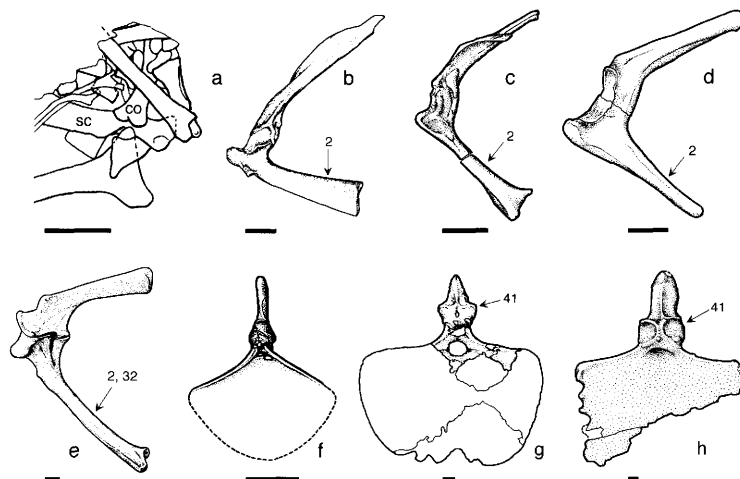


Fig. 16. Pterosaur scapulocoracoids, in left lateral view, and sterna, in dorsal view, drawn to a uniform size. (a) *Preondactylus buffarinii* (after Wild 1984b), (b) *Peteinosaurus zambellii* (after Wild 1978), (c) *Campylognathoides liasicus* (after Wellnhofer 1973), (d) *Cycnorhamphus suevicus* (after Wellnhofer 1978), (e) *Anhanguera santanae* (after Wellnhofer 1991c), (f) *Rhamphorhynchus muensteri* (after Wellnhofer 1975c), (g) *Coloborhynchus robustus* (after Kellner & Tomida 2000), (h) *Pteranodon longiceps* (after Bennett 2001). Scale bar 10 mm. co, coracoid; sc, scapula.

is remarkably similar to the situation in *Pterodactylus kochi* (e.g. Broili 1938), except that the latter taxon has no notarium. Finally, in so far as can be determined from fossil material, all medium to large and giant pterosaurs have a notarium, but they have never been reported in small pterosaurs, suggesting that the principal control on the appearance of this structure is size rather than phylogeny.

(32) *Coracoid longer than scapula.* (See Bennett 1994; Unwin 1995a; Unwin & Lü 1997.) The coracoid is shorter than the scapula in “rhamphorhynchoids” and outgroup taxa (see character 2, Fig. 16a–d). By contrast, in ornithocheiroids the coracoid is longer than the scapula (Fig. 16e), principally as a result of shortening of the scapula as it was reoriented to contact the notarium (see above), rather than through elongation of the coracoid.

(33) *Humerus with warped deltopectoral crest.* (See Padian 1984a, 1986; Bennett 1989, 1994; Unwin 1995a; Unwin & Lü 1997.) In outgroup taxa and all non-ornithocheiroids the deltopectoral crest extends only a short way down the shaft and is a relatively simple, flat, or slightly curved, flange-like structure (Fig. 17a–d, i–k). As first mentioned by Hooley (1913, p. 406) and discussed in some detail by Padian (1984a, 1986) and Bennett (1989, 1994, 2001), ornithocheiroids have a highly distinctive deltopectoral crest that has a long base and bears a terminal expansion that is twisted obliquely to the humeral shaft (Fig. 17g). The only exception is *Nyctosaurus*, but this pterosaur has a highly unusual ‘axe-head’-shaped deltopectoral crest that is unlike that found in any other taxon (Bennett 1994; Fig. 17i) and is thus coded here as a distinct character

state (Table 3). Moreover, in this analysis, *Nyctosaurus* forms a sister-group to Pteranodontidae (Figs 6 & 7) and is thus nested deep within Ornithocheiroidea, suggesting that the unusual morphology of the *Nyctosaurus* humerus was derived from the ornithocheiroid condition.

(34) *Pneumatopore piercing the anconal surface of the proximal part of the humerus.* (See Bennett 1989, 1994, 2001; Unwin 1995a; Unwin & Lü 1997.) In non-ornithocheiroid pterosaurs and outgroup taxa, approximately at the point at which the medial crest meets the shaft, the anconal surface of the proximal end of the humerus does not bear any evidence of a pneumatic opening (Wellnhofer 1978; Fig. 17j), although in some pterodactyloids (e.g. *Lonchodectes*) there is a small foramen, possibly for transmission of vascular or nerve structures, at this point. At the same position some ornithocheiroids have a prominent pneumatic opening (Bennett 1989; Fig. 17h), although this appears to be absent in pteranodontids (Bennett 2001, fig. 69) and *Nyctosaurus* (Williston 1903).

(35) *Distal end of humerus has a triangular outline.* (See Bennett 1989, 1994; Unwin 1995a; Unwin & Lü 1997.) In non-ornithocheiroid pterosaurs the distal end of the humerus has a sub-rectangular or D-shaped outline (Fig. 17e). By contrast, in ornithocheiroids the distal end has a triangular outline (Wellnhofer 1985; Kellner & Tomida 2000, Fig. 17f).

(36) *Ornithocheiroid carpus.* (See Unwin 1995a; Unwin & Lü 1997.) Pterosaurs have a highly unusual wrist construction, consisting of a proximal and distal syncarpal, a medial carpal and a pteroid,

that is unlike that of any other known tetrapod, living or extinct (Wellnhofer 1978, 1985, 1991a, b).

The typical condition, at least for pterodactyloids, is exemplified by wrist material originally described by Wellnhofer (1985) under the name of '*Santanadactylus spixi*', assigned by Bennett (1989, 1994) to the Dsungaripteridae, but probably referable to *Tupuxuara* in that it is remarkably similar to well-preserved remains of this pterosaur (IMCF 1052; Kellner & Hasegawa 1993; Kellner 1996a). In this case, as in other pterodactyloids, including *Pterodactylus*, *Cycnorhamphus*, *Germanodactylus*, '*Phobetor*' (Bakhurina 1982, fig. 1), *Dsungaripterus*, *Azhdarcho* and *Quetzalcoatlus*, the proximal syncarpal has a rectangular outline in proximal aspect (Fig. 18c), with a steeply oriented radial facet, and paired facets for the distal syncarpal that occupy almost the entire distal face of the proximal syncarpal (Fig. 18d). The distal syncarpal is also rectangular in proximal and distal view (Figs 18f, g), with a large, inverted triangular facet for the wing metacarpal on the distal face, bounded posterodorsally by a much smaller, subrectangular facet, which also made contact with the wing metacarpal. In dorsal view (Fig. 18h) the distal syncarpal is relatively short (anteroposteriorly) and blocky, with a short, rounded buttress bearing an articular facet for the medial carpal. *Rhamphorhynchus* (Wellnhofer 1975a, fig. 12) and *Dimorphodon* (Unwin 1988b, fig. 4) also have relatively short, blocky, rectangular syncarpals.

Ornithocheiroids exhibit a derived condition (see also Bennett 2001, p. 90), in which the proximal syncarpal is relatively elongate (anteroposteriorly), and has a proximal face with a pentagonal outline (Fig. 18i), a subhorizontal radial facet and a deep notch in the ventral margin. This syncarpal also has a large posterodistal process (Fig. 18k) that 'hugs' the posterior surface of the distal syncarpal while the distal aspect has a large non-articular area anterior to the facets for the distal syncarpal (Fig. 20j). The latter element is also elongate anteroposteriorly (Fig. 18l–n) and has a distal aspect with a rounded outline (Fig. 18m), and rounded, subequally sized facets for the wing metacarpal. In addition, the buttress bearing the facet for the medial carpal is relatively elongate and narrow and deflected distally (Fig. 18n).

(37) *Reduction of proximal ends of metacarpals I–III.* (See Bennett 1994.) In the outgroup taxa, "rhamphorhynchoids" and many pterodactyloids, metacarpals I–III each articulate with (in pterosaurs) the distal syncarpal (Fig. 18a, b). In those ornithocheiroids in which this region is preserved only a single metacarpal still articulates with the distal syncarpal (Fig. 18o) or, as in the case of *Pteranodon* and *Nyctosaurus*, this contact is also lost (Bennett 2001). In *Pteranodon*, metacarpals I–III are splinted to the distal end of the wing-

metacarpal (Fig. 18p), while in *Nyctosaurus* these elements are apparently lost altogether (Bennett 2000). A similar, but presumably homoplastic pattern is also evident in azhdarchoids. In *Tapejara* only a single claw digit metacarpal contacts the distal syncarpal, while in azhdarchoids even this contact is lost (Bennett 2001, p. 90).

(38) *Femur with stout neck and steeply directed caput.* (See Unwin 1995a; Unwin & Lü 1997.) The femur of derived "rhamphorhynchoids" and non-ornithocheiroid pterodactyloids has a constricted neck and a caput that is directed inwards at approximately 135° to the long axis of the shaft (Fig. 19b–e), interpreted here as the plesiomorphic state for pterodactyloids. Ornithocheiroids are distinguished by a derived condition in which the neck is relatively robust and the caput is directed upward at 160° to the shaft (Fig. 19f, g). The situation in basal pterosaurs is uncertain, but campylognathoidids also have femora with a steeply directed caput and stout collum (Wellnhofer 1978, fig. 16; Fig. 19a). Further fossil material and character analysis is needed to determine if, as it seems, this is a case of homoplasy. *Remarks.* Ornithocheiroids have a remarkably diverse cranial anatomy (Figs 10 & 11), but the unusual morphology of the shoulder girdle and forelimbs and strong reduction in the size of the hindlimbs clearly distinguishes members of this group from all other pterodactyloids. Further putative synapomorphies, in addition to those listed above, include: sagittal cranial crests that have a smooth, rounded free margin (Bennett 1994); a fused atlas-axis (Howse 1986), although this also occurs in *Dsungaripterus* and *Azhdarcho* (Bennett 1989, 1994); radius less than half the diameter of the ulna (Bennett 1994; Kellner & Tomida 2000); the distinctive morphology of the proximal end of wing phalanx 1 (Wellnhofer 1991c, fig. 34; Bennett 2001, fig. 90); and strong medial rotation of the distal end of the femur (Bennett 1989; Unwin & Lü 1997).

Bennett (1994) proposed that the presence of a median ridge on the palate and corresponding median groove on the mandible characterized his *Pteranodontidae* (similar in content to Ornithocheiroidea). These structures are present in ornithocheiroids (Wellnhofer 1985, 1991c), but not in the Pteranodontidae (Bennett 2001; Unwin 2001), in the sense that it is defined here, nor in *Nyctosaurus* (Bennett 2001), and the condition in *Istiodactylus* is unknown. Similar structures are also present in *Dsungaripterus* (Bennett 2001), Lonchodectidae (Unwin 2001), *Tupuxuara* (Bennett 2001), variably in *Azhdarcho* (Nesov 1984), and in *Gnathosaurus macrurus*, although according to Howse & Milner (1995) in the latter they are narrower and sharper than in ornithocheiroids. At present the distribution of this character and its variations are not sufficiently well understood to be phylogenetically useful.

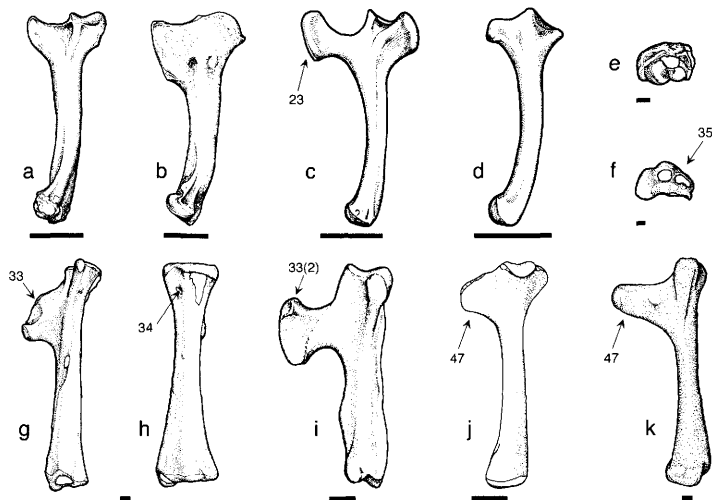


Fig. 17. Pterosaur humeri drawn to a uniform size and shown in anconal view (a), (b) and (j), palmar view (c), (d), (g), (i) and (k), posterior view (h) and distal view (e) and (f). (a) *Peteinosaurus zambellii* (after Wild 1978), (b) *Eudimorphodon ranzii* (after Wild 1978), (c) *Rhamphorhynchus muensteri* (after Wellnhofer 1975c), (d) *Pterodactylus kochi* (after Wellnhofer 1978), (e) ?*Tupuxuara* sp. (after Wellnhofer 1985), (f)–(h) *Coloborhynchus robustus* (after Kellner & Tomida 2000), (i) *Nyctosaurus gracilis* (after Williston 1902), (j) *Lonchodectes* sp. (CAMS M B54.081), (k) *Tupuxuara longicristatus* (IMCF 1052). Scale bar 10 mm.

Several authors (Padian 1984a, 1986; Bennett 1989, 1994; Unwin 1992, 1995a; Kellner 1996a; Unwin & Lü 1997), including some precladistic workers (e.g. Seeley 1891; Williston 1903; Hooley 1913; Arthaber 1922; Plieninger 1930), have recognized this clade, although its name, content and internal relationships vary from author to author. Here, for the first time, it is formally defined and diagnosed in a phylogenetic sense, using the name *Ornithocheiroidea*. This is the earliest available suprafamilial term for the clade and its conception here corresponds reasonably well to previous usage.

Clade 9. Euornithocheira (new clade name)

Etymology. Latin, *eu* = true, *ornithocheira*, from the root *Ornithocheirus*, one of the key members of this clade.

Definition. *Ornithocheirus mesembrinus*, *Pteranodon longiceps*, their most recent common ancestor, and all its descendants.

Content. *Ornithocheiridae*, *Pteranodontidae* and *Nyctosaurus*.

Synapomorphies

(39) *Concave posterior margin of nasoantorbital fenestra.* (See Unwin 1995a; Unwin & Lü 1997). In those outgroup taxa that have an antorbital fenestra, “rhamphorhynchoids” (Figs 8 & 9), all non-ornithocheiroid pterodactyls (Figs 12 & 13) and *Istiodactylus* (Fig. 10a) the antorbital (or in the case of pterodactyls the nasoantorbital) fenestra has a straight posterior margin that meets the ventral margin at (or near) a right angle. In ornithocheirids

(Figs 10d, e), *Nyctosaurus* (Fig. 11a) and pteranodontids (Fig. 11b) this margin has a distinctive, rounded, concave outline, resulting largely from a partial infilling of the angle between the lacrimal and maxilla processes of the jugal. Unwin & Lü (1997) incorrectly cited the derived condition of this character as a synapomorphy of *Ornithocheiroidea*, but it is not present in *Istiodactylus* (Hooley 1913).

(40) *Basal region of orbit infilled.* (See Unwin 1995a; Unwin & Lü 1997). In most outgroup taxa, all “rhamphorhynchoids” and most non-ornithocheiroid pterodactyls the orbit extends virtually to the ventral margin of the skull and the portion of the jugal that borders the base of the orbit is relatively slender (Figs 8, 9, 12 & 13). The orbit is at least partially infilled in *Istiodactylus*, but retains a narrow slit separating the postorbital and lacrimal processes of the jugal (Fig. 10a). By contrast, in ornithocheirids (Wellnhofer 1985, 1987; Fig. 10d, e), *Nyctosaurus* (Fig. 11a) and *Pteranodon* (Eaton 1910; Bennett 2001; Fig. 11b) the angle between the postorbital and lacrimal processes of the jugal is filled with a thin sheet of bone, restricting the orbit to a posterodorsal position within the cheek region.

Infilling of the base of the orbit also occurs in some dsungaripteroids (Fig. 13b), but the process, which involves the development of a bony bar extending from the jugal to the lacrimal (Young 1973; Ivakhnenko & Korabelnikov 1987, fig. 264), seems to be different from that observed in ornithocheirids and is probably not homologous. The results of this analysis, indicating a sister-group

relationship between dsungaripterids and *Germanodactylus*, support this interpretation because there is no evidence of orbital infilling in the latter taxon (Fig. 13a). Consequently, the state in dsungaripterids is coded differently from that in ornithocheiroids (Table 3).

(41) *Coracoid facets on sternum lateral to each other*. (See Bennett 1994). In pterosaurs the sternal cristospine bears coracoid facets that exhibit two morphologies. In rhamphorhynchids and some pterodactyls (Bennett 2001) one facet is located anterior to the other (Fig. 16f), considered here to be the plesiomorphic condition, at least within Pterodactyloidea. By contrast, in ornithocheiroids other than *Istiodactylus*, and in *Tapejara*, the facets are located side by side (Figs 16g, h) and treated here as the derived state. The reverse coding is only marginally less parsimonious, however, and this character needs further exploration.

Remarks. In addition to the apomorphies cited above, this clade is also supported by the derived state for character 18 (see above) in that *Istiodactylus* has a relatively short mandibular symphysis (Hooley 1913), whereas in all euornithocheirans it is more than 30% of the total length of the lower jaw. Other putative synapomorphies of the Euornithocheira include extension of the maxilla process of the jugal to the anterior end of the nasoantorbital fenestra, near exclusion of the squamosal from the post-temporal fenestra, and a spiral mandibular articulation.

An alternative, less parsimonious arrangement, in which *Istiodactylus* is paired with the Ornithocheiridae, is supported by a single character: radius less than half the diameter of the ulna (Bennett 1994). In the topology presented here (Fig. 7a) this character is most parsimoniously optimized as apomorphic for Ornithocheiroidea, and subsequently reversed in Pteranodontidae + *Nyctosaurus*.

Clade 10. Pteranodontia Marsh 1876 (converted clade name)

Definition. *Nyctosaurus gracilis*, *Pteranodon longiceps*, their most recent common ancestor, and all its descendants.

Content. Pteranodontidae and *Nyctosaurus*.

Synapomorphies

(42) *Tall, narrow frontal crest*. (See Bennett 1994). Outgroup taxa and "rhamphorhynchoids" generally lack cranial crests (Figs 8 & 9), although such structures are present in at least one basal pterosaur (Dalla Vecchia 2001; Dalla Vecchia *et al.* 2002). By contrast, many pterodactyls have cranial crests of some type, although their morphology and location is varied (Figs 10–13). Non-ornithocheiroid pterodactyls have large cranial crests that arise from a considerable portion of the dorsal margin of the skull (Figs 12c & 13), usually

involving the premaxillae and possibly also the frontals, and that are continued distally in cartilaginous tissues, though evidence of this is only rarely preserved (Campos & Kellner 1997; Martill & Frey 1998). Within Ornithocheiroidea, ornithocheiroids have relatively small cranial crests that are usually located on the rostrum and the mandibular symphysis (Fig. 10b, d, e), although a small posterodorsally projecting frontoparietal crest occasionally occurs on the posterodorsal apex of the skull (Fig. 10d). The clade *Nyctosaurus* + Pteranodontidae is characterized by the presence of large, usually highly elongate frontal or frontoparietal crests that arise from the dorsal margin of the skull (Bennett 2000, 2001; Fig. 11b). Some individuals have relatively small crests, or in some cases are crestless (Eaton 1910; Miller 1972; Bennett 2001), but this variation is most convincingly interpreted as a sexual dimorphism (Bennett 1992).

(43) *Dentition absent*. (See Bennett 1994; Unwin 1995a; Unwin & Lü 1997). Teeth are present in all outgroup taxa, all known "rhamphorhynchoids" (Figs 8 & 9), and most pterodactyls (Figs 10, 12 & 13). Within Ornithocheiroidea, *Nyctosaurus* and Pteranodontidae are united by the complete absence of teeth in these taxa (Fig. 11). Edentulousness is also an apomorphy of Azhdarchoidea (see below), but as this taxon does not share a close relationship with *Nyctosaurus* or pteranodontids either in this or in other cladistic analyses (e.g. Howse 1986; Bennett 1989, 1994; Unwin 1992, 1995a; Unwin & Lü 1996; Kellner 1996a; Figs 3–5), toothlessness must have evolved at least twice in pterosaurs (Bennett 1994).

(44) *Mandibular rami elevated well above level of lower jaw symphysis*. Viewed in lateral aspect the lower jaw of outgroup taxa, "rhamphorhynchoids" (Figs 8 & 9) non-ornithocheiroids (Figs 12 & 13), *Istiodactylus* (Fig. 10a) and ornithocheiroids (Fig. 10d) is generally straight with the posterior portion usually at the same level as the anterior symphyseal or tooth-bearing section. *Nyctosaurus* and pteranodontids share an unusual condition in which the postsymphysial rami curve upwards, well above the level of the symphysis (Fig. 11). This is related to a second feature of the lower jaw that also distinguishes this clade from other ornithocheiroids: pronounced deepening of the symphysis posteriorly, such that, at the caudal termination of the symphysis, the jaw is much deeper than elsewhere. The lower jaws of other pterosaurs are of even depth or achieve the greatest depth in the region of the jaw articulation (Figs 8–10, 12 & 13), the only exception being *Zhejiangopterus* (Fig. 13e), which exhibits a condition similar to that in *Nyctosaurus* and *Pteranodon*, although this must be homoplastic since this azhdarchoid is not thought to share a close relationship with these pterosaurs (Figs 3–7).

(45) *Pneumatic opening in palmar surface of proximal part of humerus*. Outgroup taxa and “rhamphorhynchoids” appear to lack any pneumatization of the humerus (Fig. 17a–c) or other appendicular elements, but this does occur in some pterodactyls (see character 34). *Nyctosaurus* and pteranodontids (Bennett 1989, 2001, p. 76) are united by the presence of a pneumatic opening that pierces the palmar surface of the humerus just proximal to the base of the deltopectoral crest. This pneumatopore appears to be absent in ornithocheiroids, *Istiodactylus* and most other pterodactyls, but is present in lonchodectids and the Azhdarchoidea (Nesov & Yarkov 1989, pl. 2, fig. 8).

(46) *Hyper-elongation of wing metacarpal*. (See Bennett 1994; Unwin & Lü 1997). The fourth (wing) metacarpal of outgroup taxa and “rhamphorhynchoids” is always shorter than the humerus (Table 2) and in most pterodactyls it is the same or up to twice the length of the humerus. *Nyctosaurus* and pteranodontids, by contrast to other ornithocheiroids, have hyper-elongate wing metacarpals (Bennett 2001) that are more than twice the length of the humerus. This character state is rare in pterosaurs and otherwise only occurs in a single specimen of *Pterodactylus longicollum* (Wellnhofer 1970, exemplar 55) and in azhdarchoids (Table 2; Bennett 1994).

Remarks. Traditionally, *Nyctosaurus* has been allied with *Pteranodon* and the latter's close relative *Ornithostoma* (e.g. Wellnhofer 1978) and this relationship is well supported here. Among characters previously discussed, this relationship is also supported by the complete loss of contact between metacarpals I–III and the distal syncarpal (character 37; see also Bennett 1994, 2001, p. 90), and putatively by the disappearance of the pneumatic opening that pierces the anconal surface of the proximal part of the humerus (reversal of character 34; see also Bennett 1994). Additional derived characters that potentially unite *Nyctosaurus* and Pteranodontidae include a greater degree of infilling of the base of the orbit than in other ornithocheiroids; the presence of marginal ridges on the jaws (Bennett 1994, 2001); beaks long and slender with premaxillae and dentaries tapering to points (Bennett 1994, 2001); mandibular symphysis approximately two-thirds the length of the mandible (Bennett 1994, 2001); and the absence of a palatal ridge and mandibular groove (though see comments above).

Several cladistic studies indicate alternative relationships for *Nyctosaurus*, either as a sister-taxon to all other ornithocheiroids (Unwin 1992, 1995a; Unwin & Lü 1997), or to a larger clade consisting of dsungaripterids, azhdarchoids and ornithocheiroids (Bennett 1989, 1994; Kellner 1996a). Characters of the humerus and notarium, structures in which nyctosaurids differ somewhat from other ornitho-

cheiroids, are relatively important in these analyses, but their impact is diluted by the inclusion of greater numbers of characters in this study. A detailed description of this pterosaur, currently being prepared by Chris Bennett (pers. comm.) may throw some more light on this problem.

Clade 11. Lophocratia (new clade name)

Etymology. Greek, *lophos* = crest, *kratos*, = head. The name refers to the prominent cranial crest borne by many members of this clade.

Definition. *Pterodaustro guinazui*, *Quetzalcoatlus northropi*, their most recent common ancestor, and all its descendants.

Content. Ctenochasmatoidea + Dsungaripteroidea + Azhdarchoidea

Synapomorphies

(47) *Humerus with elongate, rectangular deltopectoral crest*. The deltopectoral crest of outgroup taxa and “rhamphorhynchoids” is generally flange-like, and does not project far from the shaft of the humerus (Fig. 17). Dimorphodontids (Fig. 17a) and rhamphorhynchids (Fig. 17c) do not conform to this basic pattern, but in the former the deltopectoral crest is triangular in outline, while in the latter it is distinctly necked and has a rounded, tongue-like distal termination. Lophocratians have a distinctive deltopectoral crest morphology, consisting of an elongate process (measured from the base to the free margin) that has a rectangular outline with a “squared-off” free margin (Fig. 17d, j, k). The same morphology occurs consistently throughout non-ornithocheiroid pterodactyls but there is some variation in the length of the crest and its proximity to the proximal end of the humerus.

(48) *Extensive sagittal cranial crest*. (See Unwin & Lü 1997). Outgroup taxa, “rhamphorhynchoids” and ornithocheiroids either lack cranial crests (Figs 8, 9 & 10a) or, if present, they are relatively small, with smooth, rounded free margins and restricted to the rostrum, symphyseal part of the mandible or the apex of the skull (Figs 10b, d, e & 11b). Ctenochasmatoidea, dsungaripteroids and azhdarchoids are united by the presence, in most taxa, of an extensive sagittal cranial crest (Figs 12c & 13a–d) that extends from anterior to the nasoantorbital fenestra as far as the apex of the skull, or beyond, and is continued dorsally by stiffened integumentary structures (Campos & Kellner 1997; Martill & Frey 1998).

Despite its widespread distribution within Lophocratia, this character is problematic because it appears to be absent in some taxa, including: *Pterodactylus* (Wellnhofer 1970); some species of *Ctenochasma* (Wellnhofer 1970) and the Lonchodectidae (Unwin 2001); *Pterodaustro* (Chiappe *et al.* 2000); and *Zhejiangopterus* (Cai & Wei 1994; Unwin & Lü 1997). In other cases, such as *Cynorhamphus* (Fabre 1976) and some crested

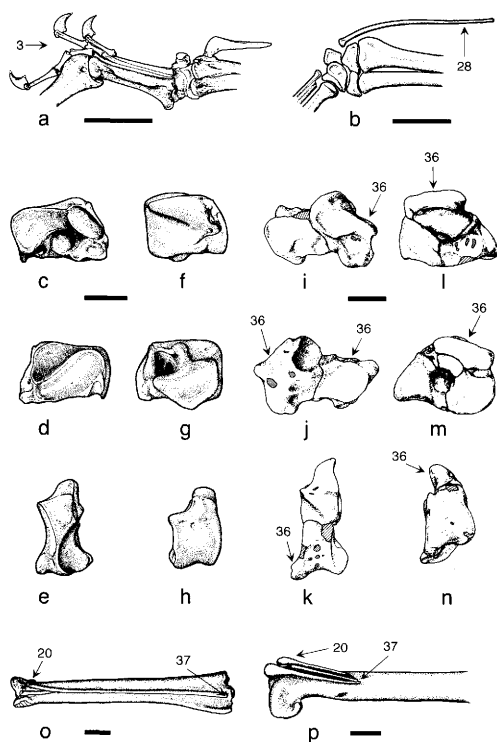


Fig. 18. The carpus and metacarpus of various pterosaurs drawn to a uniform size. (a) Left carpus and metacarpus of *Eudimorphodon ranzii* in posterodorsal view (after Wild 1978), (b) left carpus of *Pterodactylus kochi* in dorsal view (after Wellnhofer 1968), (c)–(e) proximal syncarpal and (f)–(h) distal syncarpal of ?*Tupuxuara* sp. (after Wellnhofer 1985), (i)–(k) proximal syncarpal and (l)–(n) distal syncarpal of *Coloborhynchus robustus* (after Kellner & Tomida 2000). Top row of carpals, proximal view; middle row, distal view; bottom row, dorsal view. (o) right metacarpus of *Anhanguera pricei* in anterior view (after Wellnhofer 1991c) and (p) left metacarpus of *Pteranodon longiceps* in dorsal view (after Bennett 2001). Scale bar 20 mm.

species of the Lonchodectidae (Unwin 2001), the crest has a different morphology or location from that of typical lophocratians (Fig. 12). The absences may be related to sexual dimorphism (Bennett 1992) or to the immaturity of specimens upon which these taxa are based (Bennett 2002), while the unusual crests of some species could be interpreted as further elaboration of the derived condition. Consequently, the plesiomorphic coding assigned to several lophocratians (Table 3) may be inappropriate.

Remarks. Lophocratia is also supported by a series of character reversals including: manual and pedal phalanges of similar dimensions and robustness (reversal of character 3), although azhdarchoids show the derived state for this character; humerus shorter than the femur (reversal of character 5, Table

2), rather than longer as in ornithocheiroids and most “rhamphorhynchoids”; and ulna shorter than the tibia (reversal of character 7, Table 2).

The relationships of the three main clades within Lophocratia (Ctenochasmatoidea, Dsungaripteroidea, Azhdarchoidea) are difficult to resolve. The pairing of Dsungaripteroidea + Ctenochasmatoidea (Fig. 6a) is supported by only a single character state change (reversal of character 3), while in some trees dsungaripterooids and azhdarchoids (Fig. 6b) are united by the derived condition for character 48 (treated as plesiomorphic for most ctenochasmatooids). It could be argued that characters shared by the Dsungaripteridae and the Azhdarchoidea (Kellner 1996a), or the Azhdarchidae (Bennett 1994; characters 11, 13 and 21–24) further support this relationship, but most are widely distributed within lophocratians, while the two remaining apomorphic states (deep supracoracoid flange and a deltopectoral crest that is long and curves ventrally) are absent in basal dsungaripterooids (*Germanodactylus*) and azhdarchoids (*Tapejara*). A basal trichotomy (Fig. 7a) would seem to be the most pragmatic assessment of relationships within Lophocratia at present.

Clade 12. Ctenochasmatoidea Unwin 1995a (converted clade name)

Definition. *Cycnorhamphus suevicus*, *Pterodaustro guinazui*, their most recent common ancestor, and all its descendants.

Content. *Cycnorhamphus*, *Pterodactylus*, Lonchodectidae and Ctenochasmatidae.

Synapomorphies

(49) *Quadrate oriented in subhorizontal position.* (See Unwin 1995a; Unwin & Lü 1997; Kellner cited in Chiappe *et al.* 2000.) The quadrate of outgroup taxa, “rhamphorhynchoids” and most non-ctenochasmatooid pterodactyloids is steeply or vertically oriented with regard to the ventral margin of the skull (see character 6). The quadrate of ctenochasmatooids lies in a subhorizontal position, at an angle of between 160° and 170° to the ventral margin of the skull (Fig. 12). This reorientation of the quadrate reflects a major expansion of the neurocranium in a posteroventral direction, which shifted the opisthotes and their contact with the dorsal end of the quadrate ventrally to a position behind and below the orbit.

Expansion of the neurocranium is a general feature of pterodactyloids, resulting in a relatively larger cranial capacity than in any “rhamphorhynchoid”, but appears to have developed further in ctenochasmatooids than in other clades. The quadrate also occupies a near subhorizontal position in some azhdarchids (e.g. *Zhejiangopterus*, Fig. 13e), but this would appear to be a homoplasy. First, because the construction of the cranial region of the azhdarchid skull is different from that in ctenochasmatooids, with a short robust quadrate and with a frontal

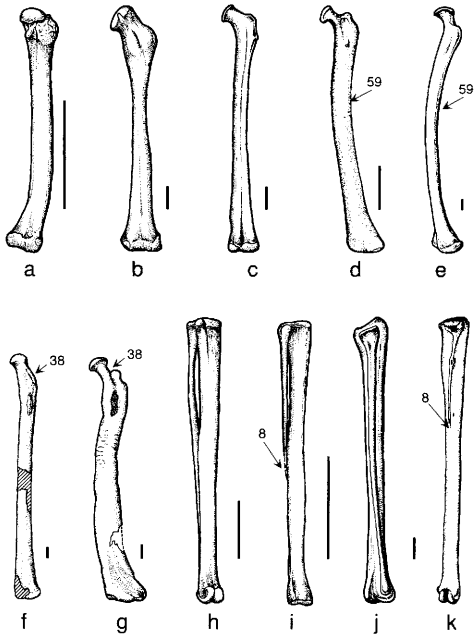


Fig. 19. Pterosaur femora and tibiotarsi drawn to a uniform size and shown in anterior view (a)–(d) and (f)–(i) and lateral view (e), (j) and (k). (a) *Eudimorphodon ranzii* (after Wild 1978), (b) *Dorygnathus banthensis* (after Wellnhofer 1978), (c) *Pterodactylus longicollum* (after Wellnhofer 1970), (d) *Germanodactylus cristatus* (NMING F15005), (e) *Dsungaripterus weii* (after Wellnhofer 1978), (f) *Coloborhynchus robustus* (after Kellner & Tomida 2000), (g) *Pteranodon longiceps* (after Bennett 2001), (h) *Peteinosaurus zambellii* (after Wild 1978), (i) *Eudimorphodon ranzii* (after Wild 1978), (j) *Campylognathoides zitteli* (after Plieninger 1895), (k) *Pteranodon longiceps* (after Bennett 2001). Scale bar 10 mm.

that extends posteroventrally to a point level with the ventral margin of the orbit (Unwin & Lü 1997). Secondly, because sister-taxa to azhdarchids (*Tapejara* and *Tupuxuara*) have more steeply oriented quadrates (Fig. 13c, d), indicating that the condition in azhdarchids is secondarily derived.

(50) *Squamosal located level with or below the base of the lacrimal process of the jugal.* (See Unwin 1995a; Unwin & Lü 1997; Chiappe et al. 2000). In non-ctenochasmatoid pterosaurs the squamosal occupies a position above or opposite the lacrimal process of the jugal (Figs 8–11 & 13). In ctenochasmatoids expansion of the brain case (see character 49) resulted in a marked shift in the position of the squamosal so that, in this clade, it is located at a point below a horizontal line extending posteriorly from the base of the lacrimal process of the jugal. This condition also occurs in some azhdarchids (e.g.

Zhejiangopterus, Fig. 13e), but is interpreted as homoplastic for the same reasons given for character 49).

(51) *Occiput faces ventrally.* (See Unwin 1995a; Unwin & Lü 1997.) In outgroup taxa and “rhamphorhynchoids” the occiput faces posteriorly (Figs 8 & 9) and the cervical vertebrae continue in the line of the long axis of the skull. In pterodactyloids the occiput is reoriented to face posteroventrally, as a result of enlargement of the neurocranium (see above), and the neck forms an obtuse angle with the long axis of the skull (Figs 10 & 13). Ctenochasmatoids are distinguished by an occiput that faces ventrally (Fig. 12a–d) such that the neck is perpendicular (or near-perpendicular) to the long axis of the skull, reflecting the greater degree of enlargement of the neurocranium in this clade (see above). The occiput also faces ventrally in some azhdarchids (e.g. *Zhejiangopterus*, Fig. 13e), but this is interpreted as a homoplasy for the same reasons given as for character 49.

Remarks. This diverse clade comprises various specialized filter-feeding pterosaurs, such as *Ctenochasma* and *Pterodaustro*, together with a number of relatively unspecialized basal forms. The clade is mainly distinguished by characters of the skull that seem to be related to major changes in the shape and size of the brain case. Another potential synapomorphy, present in all ctenochasmatoids except *Pterodactylus kochi* and *P. antiquus*, is a spatulate condition of the jaws, wherein the anterior tip of the rostrum and mandible are dorsoventrally compressed and wider (transversely) than they are deep (dorsoventrally).

Several authors (Kuhn 1967; Wellnhofer 1970; Fabre 1974) have suggested a close relationship between the “Pterodactylidae” (containing *Pterodactylus* and *Cycnorhamphus*) and the Ctenochasmatidae. More recently, Kellner (1996a; see also Chiappe et al. 2000) proposed the name *Archaeopteroactyloidea* for a clade that is practically the same in content and thus synonymous with the Ctenochasmatoida (Unwin 1995a).

Clade 13. Euctenochasmatia (new clade name)

Etymology. Latin, *eu* = true, *ctenochasmatia* from the root *Ctenochasma*, a key member of this clade.

Definition. *Pterodactylus kochi*, *Pterodaustro guinazui*, their most recent common ancestor, and all its descendants.

Content. *Pterodactylus*, Lonchodectidae and Ctenochasmatidae.

Synapomorphies

(52) *Neural arch of mid-series cervicals depressed and with low neural spine.* (See Howse 1986; Bennett 1989, 1994, Unwin 1995a; Unwin & Lü 1997). The neural arch of mid-series cervicals of outgroup taxa (excluding some prolacertiforms),

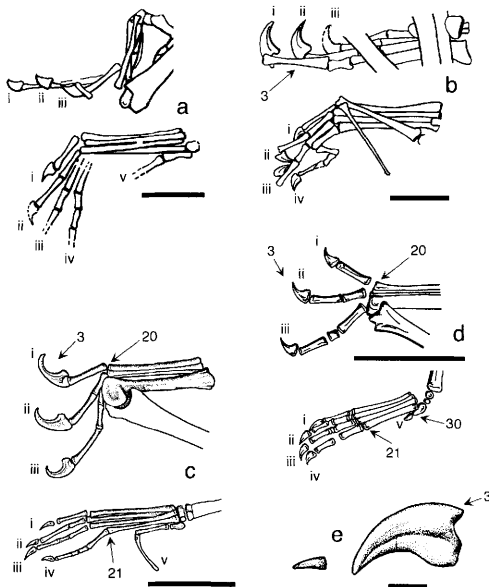


Fig. 20. The left manus and pes of various pterosaurs drawn to a uniform size. (a) *Preondactylus buffarinii* (after Wild 1984a, reversed), (b) *Peteinosaurus zambellii* (after Wild 1978), (c) *Rhamphorhynchus 'longicaudus'* (after Wellnhofer 1975c), (d) *Pterodactylus kochi* (after Wellnhofer 1970, reversed), (e) *Coloborhynchus robustus* (after Kellner & Tomida 2000). Scale bar 10 mm.

“rhamphorhynchoids” and most pterodactyloids including *Cycnorhamphus* (Plieninger 1907, pl. 18) is relatively tall and bears a high neural spine (Fig. 15a, c). In adult individuals of *Pterodactylus* (Fig. 15e), lonchodectids (Owen 1861) and ctenochasmatids (e.g. Broili 1924; Bonaparte 1970; Dong 1982) these vertebrae have a neural arch that is depressed down onto the centrum, and a low, rectangular neural spine (Howse 1986). Significantly, early juvenile individuals of *Pterodactylus kochi* (Wellnhofer 1970, figs 5 & 6) and ‘*P.*’ *micronyx* (Wellnhofer 1970, fig. 9) exhibit the primitive state for this character, with relatively short vertebrae and high neural spines. By contrast, more mature individuals of *P. kochi* (Wellnhofer 1970 pl. 5, fig. 1; Wellnhofer 1987, fig. 1) and ‘*P.*’ *micronyx* (Wellnhofer 1970, pl. 6, fig. 1) exhibit the derived condition (see also Bennett 1996a). The same pattern is evident in *Ctenochasma gracile* and putative juveniles of this species currently assigned to ‘*Pterodactylus elegans*’ (Bennett 1996a).

A morphology similar to the derived condition described above is present in azhdarchids (Fig. 15g); consequently in some previous analyses (Howse 1986; Bennett 1989, 1994; Unwin 1992) azhdarchids and various ctenochasmatoids were grouped together on the basis of this and other char-

acters of the cervical vertebrae. There are some important differences, however, between these two groups. Azhdarchids have a neural arch that is entirely confluent with the vertebral centrum, forming a single tubular structure (Martill *et al.* 1998, figs 5–7), whereas in derived ctenochasmatoids the neural arch, though depressed, remains distinct from the vertebral centrum (Fig. 15e). In addition, a low neural spine is retained throughout the cervical series in the latter group, whereas in the former the neural spine is absent on the fifth cervical at least (Howse 1986). The results of this analysis (Fig. 6 & 7a) also indicate that ctenochasmatoids and azhdarchids do not share a close relationship, and both have sister-groups in which the neural arch and neural spine show the plesiomorphic condition.

(53) *Elongate mid-series cervicals.* (See Howse 1986; Bennett 1989, 1994, Unwin 1995a; Unwin & Lü 1997.) The length of the centrum of mid-series cervicals of outgroup taxa (excluding some long-necked prolacertiforms) “rhamphorhynchoids” and most pterodactyloids, reaches, at most, 3 times the minimum width of the centrum (Fig. 15b, d). In adult individuals of *Pterodactylus*, lonchodectids (Fig. 15f) and ctenochasmatids, centrum length is at least 4 times the width and this index may reach 8 or more in some long-necked derived forms, such as *Pterodaustro* (Wellnhofer 1991a). As for character 52, juveniles of *Pterodactylus kochi*, ‘*P.*’ *micronyx*, and *Ctenochasma gracile* exhibit the plesiomorphic condition with relatively short cervicals.

Similar and, in some cases, even greater degrees of relative elongation of the mid-series cervicals were achieved in azhdarchids (e.g. *Quetzalcoatlus* [Fig. 15g], *Zhejiangopterus* and *Arambourgiania*), but this would appear to be a homoplastic development, for the same reasons given for character 52. *Remarks.* Euctenochasmatia is also partially supported by two character reversals (Table 3). Thus the humerus is shorter than the femur (reversal of character 5) and the ulna is shorter than the tibia (reversal of character 7) in some species of *Pterodactylus* and Ctenochasmatidae (Table 2). Kellner (1996a; see also Chiappe *et al.* 2000) suggested that *Cycnorhamphus* and Ctenochasmatidae were united by the markedly concave outline of the dorsal margin of the skull. The phylogenetic utility of this state, not uniformly present in all ctenochasmatids (e.g. absent in *Gnathosaurus*), but present in some non-ctenochasmatoids (*Pteranodon*), is unclear and needs further study.

This study further confirms the supposed paraphyly of “Pterodactylidae” (Unwin 1995a; Bennett 1996c; Unwin & Lu 1997), in that a pairing of *Cycnorhamphus* and *Pterodactylus*, traditionally the principal members of this family (e.g. Wellnhofer 1978) did not occur in any of the MPTs found here. Encouragingly, however, there is some support for

the location within Ctenochasmatoidea of the Lonchodectidae, a relatively poorly known family of Cretaceous pterodactyloids, whose relationships within Pterodactyloidea have been uncertain (Unwin 2001).

Clade 14. Dsungaripteroidea Young 1964 (converted clade name)

Definition. *Germanodactylus cristatus*, *Dsungaripterus weii*, their most recent common ancestor, and all its descendants.

Content. *Germanodactylus*, the Dsungaripteridae and variously poorly known dsungaripteroids including *Herbstosaurus* (Casamiquela 1975; Unwin 1996), *Kepodactylus* (Harris & Carpenter 1996; Unwin & Heinrich 1999), *Normannognathus* (Buffetaut *et al.* 1998) and *Tendaguripterus* (Unwin & Heinrich 1999).

Synapomorphies

(54) *Distal ends of paroccipital processes expanded.* (See Unwin 1995a; Unwin & Lü 1997.) The occipital region of outgroup taxa, and all non-dsungaripteroid pterosaurs has a rounded outline in lateral view (Figs 8–12 & 13c, e). The distal ends of the paroccipital processes of dsungaripteroids are strongly expanded, resulting in a distinct protuberance in the lateral profile of the occiput (Bakhurina 1986, p. 32; Fig. 13a, b). The reconstruction of *Germanodactylus cristatus* by Wellnhofer (1970, fig. 12), reproduced in Fig. 13a, is based on the holotype specimen preserved on the main slab (BSP 1892 IV 1) and shows an occiput profile with a rounded outline. The rear part of the skull is better preserved on the counterslab (NMING F15005) and shows the strongly expanded paroccipital process and associated protusion in the lateral profile of the occiput. A similar development occurs in *Tupuxuara* (IMCF 1052; Fig. 13d), but this would appear to be a homoplasy since *Tapejara*, which is closer to dsungaripteroids than *Tupuxuara* (Fig. 7a), exhibits the non-derived condition.

(55) *Dsungaripteroid teeth.* (See Unwin 1995a; Unwin & Lü 1997.) Most dentate pterosaurs have simple, sharp-pointed, relatively elongate teeth that taper from the base to the tip, are lightly compressed labiolingually and gently recurved (Figs 8–10 & 12). Dsungaripteroid teeth are relatively short, with a broad, parallel-sided columnar base and a rather obtusely pointed tip (Fig. 13a, b). At least part of the dentition contains teeth of this type in *Germanodactylus* (Wellnhofer 1970, figs 12 & 13) while in dsungaripterids the entire dentition has this morphology, with teeth at the caudal end of the tooth row being particularly squat and obtuse in *Dsungaripterus* (Young 1973) and ‘*Phobator*’ (Bakhurina 1986, p. 32).

(56) *Jaw tips toothless, but followed by a tooth row.* (See Unwin 1995a; Unwin & Lü 1997.) In all

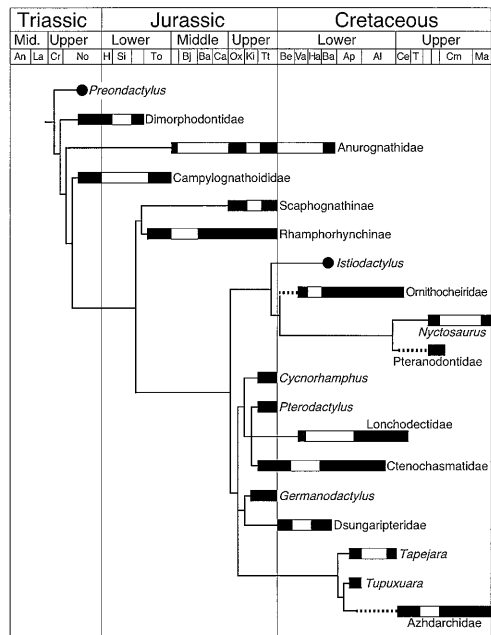


Fig. 21. Pterosaur evolutionary tree constructed from the strict consensus tree shown in Figure 7a and known stratigraphic ranges, indicated by solid shading, of the principal clades (Appendix 1). Possible range extensions based on as yet unverified records are shown by a dashed line. Al, Albanian; An, Anisian; Ap, Aptian; Ba, Barremian; Bj, Bajocian; Bt, Bathonian; Be, Berriasian; Bt, Bathonian; Ca, Callovian; Cr, Carnian; Ce, Cenomanian; Cm, Campanian; H, Hettangian; Ha, Hauterivian; Ki, Kimmeridgian; La, Ladinian; Ma, Maastrichtian; No, Norian; Ox, Oxfordian; Si, Sinemurian; T, Turonian; To, Toarcian; Tt, Tithonian; Va, Valanginian.

other dentate pterosaurs the teeth extend to the tips of the jaws (Figs 8–10 & 12). In dsungaripteroids, however, the jaw tips are toothless (Young 1964; Wellnhofer 1970, fig. 12; Bakhurina 1986, p. 32; Figs 13a, b). The one exception is *Germanodactylus rhamphastinus* (Wellnhofer 1970, fig. 13) which exhibits the plesiomorphic condition, with teeth extending to the tips of the jaws. It is equally parsimonious to treat this as a reversal or as retention of the primitive condition.

(57) *Largest teeth occur in the caudal half of the dentition.* (See Unwin 1995a; Unwin & Lü 1997.) In non-dsungaripteroid pterosaurs teeth with the largest basal diameter occur either towards the midpoint of the tooth row, as in many basal forms such as *Preondactylus* (Fig. 8a) and *Eudimorphodon* (Fig. 9a), some basal pterodactyloids including *Pterodactylus kochi* (Wellnhofer 1968), and some ornithocheirids (Fig. 10d, e), or towards the front of the tooth row, as for example in rhamphorhynchids

(Fig. 9c–e), *Cycnorhamphus* (Fig. 12a) ctenochasmatis (Fig. 12c, d), and some ornithocheirids (Fig. 10b–e). In dsungaripteroids the teeth with the largest basal diameter occur in the caudal half of the tooth row. This pattern is less pronounced in *Germanodactylus* (Fig. 13a), but is clear in dsungaripterids, where the largest teeth occur at the caudal end of the tooth row (Young 1964, 1973; Bakhurina 1986; Ivakhnenko & Korabelnikov 1987; Fig. 13b).

(58) *Limb bones with relatively thick bone walls.* A distinctive feature of pterosaur limb bones that distinguishes them from outgroup taxa is the remarkably thin cortex, which rarely exceeds 2 mm in thickness. The limb bones of dsungaripteroids are similar to those of outgroup taxa in that they have relatively thick walls and only a narrow central lumen. This condition has been observed in *Germanodactylus* (Unwin 1988b), '*Phobator*' (Bakhurina pers. comm. 2001), *Dsungaripterus* (Bennett 1989) and in other material assigned to dsungaripteroids, e.g. *Tendaguripterus* from Tendaguru, Tanzania (Galton 1980; Unwin & Heinrich 1999). Dsungaripteroids are deeply nested within Pterodactyloidea (Figs 6 & 7a); therefore, there can be no doubt, that the evolution of relatively thick bone walls represents a secondarily derived state in dsungaripteroids (Table 3), and not retention of the plesiomorphic condition.

(59) *Strongly bowed femur.* The femur of outgroup taxa tends to be either relatively straight or gently sigmoid. In non-dsungaripteroids it is almost always straight in anterior view (Fig. 19a–c, f, g), but in some non-ornithocheiroid pterodactyloids it may exhibit a gentle forward curvature in lateral view. Dsungaripteroid femora are unusual in that they are markedly curved in two planes: in anterior view there is a distinctive inward bowing of the shaft (Fig. 19d), while in lateral view there is a pronounced forward bowing, most clearly developed in *Dsungaripterus* (Fig. 19e).

Remarks. Young (1964) first proposed that the Late Jurassic pterosaur *Germanodactylus* was related to *Dsungaripterus* from the Early Cretaceous of China. This idea was supported by Wellnhofer (1968, 1970, 1978), and was considerably strengthened by the discovery of a dsungaripterid-like form in the Early Cretaceous of western Mongolia, '*Phobator*', that has an intermediate morphology between *Germanodactylus* and *Dsungaripterus* (Bakhurina 1982, 1986, 1993). Apart from preliminary studies by Unwin (1992, 1995a) other cladistic analyses have so far failed to find evidence to support this hypothesised relationship, although several putative apomorphies have already been pointed out by Young (1964) and Bakhurina (1993).

One additional putative synapomorphy of the Dsungaripterioidea, found in *Germanodactylus* (BSP 1892 IV 1) '*Phobator*' (Ivakhnenko & Korabelnikov 1987, fig. 264) and *Dsungaripterus* (Young 1964,

1973), is a strong anterior bowing of the wing phalanx 1. The plesiomorphic state, a straight or slightly posteriorly bowed wing phalanx 1, is typical for pterosaurs (e.g. Wellnhofer 1978, fig. 13), although some degree of forward bowing is also evident in phalanges probably referable to the rhamphorhynchid *Rhamphocephalus* (Owen 1874).

Clade 15. Azhdarchoidea Unwin 1992 (converted clade name)

Definition. *Tapejara wellnhoferi*, *Quetzalcoatlus northropi*, their most recent common ancestor, and all its descendants.

Content. *Tapejara*, *Tupuxuara* and Azhdarchidae. *Synapomorphies*

(60) *Orbit located well below level of dorsal margin of nasoantorbital fenestra.* (See Kellner 1995; Unwin 1995a; Kellner & Langston 1996; Unwin & Lü 1997.) Viewed in lateral aspect, the dorsal margin of the orbit in the skull of "rhamphorhynchoids" (Figs 8 & 9) and non-azhdarchoid pterodactyloids (Figs 10–12 & 13a, b) approaches close to the dorsal boundary of the skull. By contrast, in azhdarchoids the orbit occupies a relatively low position (Fig. 13c–e) and in azhdarchids, for example, is nearer to the ventral rather than the dorsal margin of the skull. This apparent shift in position can be attributed to a dorsal elevation of the posterior rostral region and the infilling, by ventrolateral extension of the frontal, of the region corresponding to the upper half of the orbit in other pterosaurs.

Remarks. Early cladistic studies (Bennett 1989, 1994; Unwin 1992; Figs 3b & 4b) tended to link azhdarchids with various ctenochasmatis because of the development of long, low cervical vertebrae in both these groups. Kellner and Hasegawa (1993), Kellner (1995, 1996a) and Unwin (1995a) pointed out shared derived features of the skull that are present in both tapejarids and azhdarchids and which suggest that elongate vertebrae had evolved independently in the Ctenochasmatoidea and the Azhdarchoidea. Even though tapejarids were not described until later, Howse (1986) foresaw this phylogenetic arrangement in one of his trees (Fig. 3a), grouping various species of *Pterodactylus* with ctenochasmatis (Ctenochasmatoidea) in one group, and azhdarchids plus some taxa now thought to be ctenochasmatis in a second group. This analysis (Fig. 7a) strongly supports the idea that the acquisition of long necks by ctenochasmatis was entirely independent of the evolution of long necks in azhdarchoids, in part because basal members of both clades have relatively short cervicals.

Azhdarchoidea is well supported by a variety of cranial and postcranial characters. Derived states, although also apomorphic elsewhere within Pterosauria, include: absence of teeth (character 43);

dorsal expansion of the caudal half of the rostrum (see character 9); development of a pneumatic opening in the palmar surface of the proximal part of the humerus (character 45); loss of contact between the distal syncarpal and metacarpals II and III (character 37); and the redevelopment of manual phalanges that are relatively large compared to the pedal phalanges. Additional putative apomorphies include the extension of the frontal anterior to the lacrimal-jugal bar (Fig. 13c–e), and a femur length more than 1.25 times that of the humerus (Table 2).

Clade 16. Neoazhdarchia (new clade name)

Etymology. Latin, *neo* = new, *azhdarchia* from the root *Azhdarcho*, a principal taxon within this clade.

Definition. *Tupuxuara longicristatus*, *Quetzalcoatlus northropi*, their most recent common ancestor, and all its descendants.

Content. *Tupuxuara* and Azhdarchidae.

Remarks. Synapomorphies of the Neoazhdarchia, a clade initially postulated by Unwin and Lü (1997), include: presence of a notarium (character 31), reported in azhdarchids (Buffetaut 1999; pers. obs.) and *Tupuxuara* (Kellner 1996a; Kellner & Hasegawa 1993), but absent in *Tapejara*; and loss of contact between metacarpals I–III and the distal syncarpal (character 37), in contrast to *Tapejara* where at least one metacarpal retains this contact. In addition, the rostrum of *Tapejara* (measured from the anterior margin of the orbit to the anterior end of the premaxillae), forms only 70% of total skull length (anterior tips of premaxillae to occipital condyle), which falls within the range occupied by “rhamphorhynchoids” (58–76%) and is certainly plesiomorphic within Pterodactyloidea. By contrast, neoazhdarchians share a derived condition in which the rostrum forms more than 88% of total skull length.

Kellner (1995, see also Kellner 1989, 1996a; Kellner & Langston 1996) united *Tapejara* and *Tupuxuara* in the Tapejaridae on the basis of two characters: a sagittal premaxillary crest extending from the tip of the snout to the occipital region and a comparatively large nasoantorbital fenestra. The cranial crest of *Tapejara* is rather differently constructed from that of *Tupuxuara* (Fig. 13c, d) and does not extend to the tip of the snout. Moreover this general type of crest is widely distributed within lophocratians (character 48). A comparatively large nasoantorbital fenestra is also present in azhdarchids (Fig. 13e); consequently this character is apomorphic for the Azhdarchoidea (see character 9). Tapejaridae is thus paraphyletic as Unwin & Lü (1997) supposed.

Discussion

Tree robusticity and alternative topologies

Phylogenetic analyses published so far contain little or no discussion of the robustness or likely reliability of the trees presented. The only exception is the brief commentary by Kellner (1995) on previously published trees, though this largely focused on Bennett's work (1989, 1994), and was confined to rerunning data sets and discussion of character states and their distribution. The absolute and relative robusticity of trees recovered in this analysis was assessed using a variety of techniques, some statistical, some purely comparative. Results of these analyses provided insights into the strength of support for principal nodes, the robusticity of the preferred tree (Fig. 7a) compared to the results of other studies and the possible impact of future fossil discoveries.

Quality of the original character data set. The cladistic data set analysed here (Table 2) is 94% complete. This is a far higher value than for other pterosaur data sets reported so far (Bennett 1989, 51%; Bennett 1994, 41%) and generally higher than that for other studies of fossil vertebrates (Wilkinson 1995). Most taxa and most characters have high levels of completeness: only characters 25 and 41 show relatively low values (70% and 60% complete respectively), and only two taxa, *Preondactylus* and the Lonchodectidae, are relatively poorly represented (80% and 58% complete respectively). Neither of the two characters are especially important: character 25 forms part of a large cluster that diagnose Pterodactyloidea; character 41 helps resolve relationships within the well-supported clade Ornithocheiroidea. Likewise, while character distributions represented by the Lonchodectidae have some influence on relationships within the Ctenochasmatoidea they appear to have little impact on general tree topology. Incomplete knowledge of *Preondactylus*, the most basal known pterosaur (Fig. 7a), is more problematic, but in that it is generally similar to dimorphodontids (Dalla Vecchia 1998), which are much better known, this is not a critical issue.

The character data set samples all parts of the skeleton, although the emphasis is on cranial anatomy (50% of all characters), which traditionally (Young 1964; Kuhn 1967; Wellnhofer 1978) has played a critical role in establishing the relationships of pterosaurs. By sharp contrast, previous data sets focus largely (Bennett 1994, 84%) or entirely (Howse 1986; Bennett 1989) on postcranial anatomy.

The character data set also contains data from almost all known species of pterosaur, more than two-thirds of which were inspected directly. The

pterosaur fossil record is often claimed to be poor, in the sense that it is highly incomplete (e.g. Carroll 1987). It could be asserted, therefore, that known taxa significantly under-represent true pterosaur diversity, to the extent that several large clades may remain unknown, thereby compromising phylogenetic analyses. Two lines of evidence suggest that this may not be a significant problem. First, in morphometric studies focused on the wings (Hazlehurst & Rayner 1992) and on the hindlimbs (Elvidge & Unwin 2001), pterosaurs were found to plot in a relatively tight cluster, with no outliers and relatively small gaps between points. This suggests that, at general taxonomic levels (e.g. family or higher), known diversity may be a reasonable proxy for true diversity. Thus, new discoveries are more likely to fit within existing clades, rather than revealing major new lineages and will not usually destabilize the general set of relationships described here.

The history of discovery provides a second independent test regarding our understanding of taxonomic diversity. If major new clades remain to be discovered we might expect to find their representatives in deposits such as the Yixian Formation that sample depositional environments and time intervals from which pterosaurs are poorly known (Unwin *et al.* 2000). Taxonomic studies of Yixian pterosaurs show, however, that the four genera found so far can all be assigned to existing clades: *Dendrorhynchoides* and *Jeholopterus* are anurognathids (Unwin *et al.* 2000; Wang *et al.* 2002), *Haopterus* appears to be an ornithocheirid (Unwin 2001) and *Eosipterus* probably belongs in the Ctenochasmataidae (Unwin *et al.* 2000; Unwin 2002). This observation also applies to other recently discovered assemblages, such as the Crato and Santana Formations (e.g. Fastnacht 2001), and revisions of older assemblages (e.g. Unwin 2001) have also failed to recover evidence of distinctly new clades.

Bootstrap and decay analyses. Results of the bootstrap analysis (Fig. 6c) indicate that nearly all the “rhamphorhynchoid” clades are well supported, with values of >90%. The only exception is the clade Rhamphorhynchidae, although this occurs in almost 75% of all replicates. The situation within Pterodactyloidea is much more variable. A few clades have values of 90% or more, but most are either only moderately well supported or, as for example, in the case of Ctenochasmatoidea, fall below the 50% mark.

A decay analysis, in which the constrained length of the preferred tree was increased in incremental fashion, beginning with the minimum number of steps (112), showed a rapid decline in resolution. In trees only one step longer, Rhamphorhynchidae collapsed, as did the relationships within Azhdarchoidea. The relationships of major pterodacty-

loid clades collapsed to a polytomy in trees only two steps longer, although the clades themselves, and some subclades within them, remained distinct. In trees three steps longer only Ornithocheiroidea was preserved within Pterodactyloidea, although most “rhamphorhynchoid” clades remained distinct. All resolution was lost in trees only five steps longer than the MPT.

Partitioning. The degree to which trees generated from subsets of characters and taxa resemble the preferred tree resulting from the main data set can also provide some insights into the latter’s robusticity. In this study, taxa were partitioned into “rhamphorhynchoid” and pterodactyloid subsets, and characters were divided into cranial and postcranial subsets. Fortunately, the resulting subsets were of roughly similar size. Remarkably, the strict consensus tree of 558 MPTs yielded by the cranial subset was almost identical topologically to the main tree (Fig. 7a), except that the relationships of the four major clades of pterodactyloids were unresolved. Similarly, the strict consensus tree of six MPTs yielded by the postcranial subset showed much the same topology as the main tree. The only notable difference was in the pairing of *Cynorhamphus* with *Dsungaripteroidea* + *Azhdarchoidea*. Analysis of the “rhamphorhynchoids” resulted in a single tree that was identical to the main tree irrespective of whether or not an outgroup and/or a pterodactyloid taxon was included. The pterodactyloid subset yielded varying numbers of MPTs (though never more than 12), depending on which outgroup (the outgroups described above, a basal “rhamphorhynchoid” or a derived “rhamphorhynchoid”) was selected. Strict consensus trees generated from these analyses had an identical, or near identical topology to the main tree.

Stratigraphic congruence. The degree of concordance between the stratigraphic distribution of taxa and their sequence of occurrence in a cladogram offers a means of comparing different trees (Benton 1995). This study found a good correlation between the order of branching (Figs 6 & 7) and the order of appearance of clades in the stratigraphic record (Fig. 21). Only three clades (Anurognathidae, *Istiodactylus* and Lonchodectidae) appear in a different stratigraphic order from that predicted by the results of this analysis. Cladograms by Howse (1986; Fig. 3a), Viscardi *et al.* (1999; Fig. 5b) and Unwin (1992; Fig. 4b) show a similar level of concordance, except for the position of *Nyctosaurus* in the latter work. Other studies are comparably less concordant, especially with regard to *Nyctosaurus*, *Pteranodon*, *Dsungaripterus* and *Pterodaustro* (Bennett 1989, 1994; Figs 3b & 4b) or to *Sordes*, *Dimorphodon* and *Nyctosaurus* (Kellner 1996a; Fig. 5a).

The proportion of predicted stratigraphic range

(also known as ‘ghost range’) compared to known stratigraphic range, a measure of relative completeness (RCI) that can be assessed in various ways (Smith 1994; Benton 1995), provides another method for comparing different trees. The cladogram presented here (Figs 7a & 21), and others described by Howse (1986; Fig. 3a), Unwin (1992, 1995a; Figs 4b, c) and Viscardi *et al.* (1999; Fig. 5b) have relatively small, similarly sized RCIs and few individual lineages with ghost ranges that approach or exceed the known stratigraphic range. Trees presented by Bennett (1989, 1994; Figs 3b & 4c) and Kellner (1996a; Fig. 5a) have larger summed RCIs and a number of individual lineages (e.g. *Nyctosaurus*, *Pteranodon*, Azhdarchidae) with ghost ranges longer than the known stratigraphic range. This is particularly marked in the case of Kellner’s study, wherein a series of “rhamphorhynchoids” (Anurognathidae, *Sordes*, *Scaphognathus* and *Dorygnathus* also have remarkably long ghost ranges.

Summary. Most of the analyses reported above indicate a relatively high degree of robustness for the strict consensus tree (Fig. 7a) and show that it is better supported, or more concordant with alternative lines of evidence, than other cladograms of pterosaur relationships presented so far. This is consistent with the small number of MPTs generated in the main analysis, in contrast to the large numbers of trees generated in previous studies (see Kellner 1996a) and the general concordance of the topology of the strict consensus tree with the results of other phylogenetic studies (see below). The rapid decline in resolution in the decay analysis suggests that the results should be treated with some caution, but does not indicate that they are generally unreliable.

Importantly, a number of well-supported relationships that crop up repeatedly in precladistic and cladistic studies (see below) can be identified. These include the monophyly of Pterosauria, Pterodactyloidea and Ornithocheiroidea, and a basal position for the Dimorphodontidae and similar taxa such as *Preondactylus*. In addition, other clades, including Dsungaripteroidea and *Nyctosaurus* + Pteranodontidae, are also well supported here and, though infrequent in other cladistic studies, were widely accepted in traditional phylogenies (e.g. Young 1964; Kuhn 1967; Wellnhofer 1978). Because these six clades act as a strong constraint on tree shape, if the majority of them are supported by new analyses, much of the basic topology of the consensus tree presented here is likely to persist into the future.

Inevitably, some clades are only weakly supported (e.g. Lophocratia, Ctenochasmatoidea, Neoazhdarchia), but in many cases the collapse of these clades, or alternative configurations, are unlikely to have a major impact on the distribution of character states or overall tree shape.

Comparison with previous studies

Traditional phylogenies. The main precladistic studies (Young 1964; Kuhn 1967; Wellnhofer 1975a, 1978) used general similarities, often based on the skull, to identify various lineages within “Rhamphorhynchoidea” and Pterodactyloidea, but were unable to determine the relationships of these lineages to one another (Figs 1 & 2). Several of these lineages, notably Rhamphorhynchinae, Dsungaripteroidea (*sensu* Wellnhofer 1978; Fig. 2) and Ctenochasmatoidea (in part) are supported by this study, but many others are not. In these cases, such as *Dimorphodon* and *Anurognathus*, the general similarities of the skull reflect the retention of features that appear to be plesiomorphic for pterosaurs. In other cases, such as the supposed relationship of *Scaphognathus* and *Istiodactylus*, this was partly based on a misunderstanding of the skull anatomy in the latter taxon, which was erroneously thought by Hooley (1913) to have a maxillo-nasal bar as in “rhamphorhynchoids”. Notwithstanding the above, most of the contrasts between the strict consensus tree generated by this analysis (Fig. 7a) and the traditional phylogenies can be attributed to new fossil finds in the last two decades, and the attempt here, as in other cladistic studies, to distinguish between derived and primitive characters.

Cladistic studies. Insofar as comparisons can be made, the results of this study share more in common with other cladistic studies than with earlier precladistic schemes. Howse (1986) recognized three clades that correspond fairly well with the Ctenochasmatoidea, Ornithocheiroidea and Azhdarchoidea as defined here, the main difference being the grouping of †*Doratorhynchus* (= *Gnathosaurus*) and Greensand vertebrae (= *Lonchodectes*) with the latter clade rather than the former. In Howse’s study most Jurassic pterodactyloids clustered at or near the base of Pterodactyloidea, which is to be expected considering their relatively uniform postcranial anatomy and the limited extent of his analysis. Greater resolution was achieved in this study, but as the bootstrap and other analyses show, evidence in support of these relationships is relatively fragile.

Where comparable, the main tree resulting from the first analysis by Bennett (1989) is generally similar to the consensus tree presented here (cf. Figs 3a & 7a). The content of Bennett’s *Pteranodontidae* and Azhdarchidae largely overlap with that of Ornithocheiroidea and Azhdarchoidea, and Dsungaripteridae is also recognized as a distinct taxon, although with a different content from Dsungaripteroidea. The placement of †*Doratorhynchus* in Azhdarchidae is perhaps inevitable in that only one other relatively basal ctenochasmatoid

(*Pterodactylus kochi*) was included in the taxon list, although interestingly the latter falls outside all other pterodactyloid clades.

The main difference is in the placement of *Nyctosaurus* near the base of Pterodactyloidea, well away from *Pteranodon* and even well outside the clade equivalent to Ornithocheiroidea. This is because, in Bennett's study, *Nyctosaurus* lacks some features of the shoulder girdle—notarium complex present in other pterosaurs (possibly related to the relatively small size of *Nyctosaurus*) and has a highly derived type of humerus wherein ornithocheiroid features have been further transformed. As shown here, many other features not included in Bennett's character analysis support a relationship within Ornithocheiroidea, as a sister-taxon to Pteranodontidae. This result is also far more consistent with the stratigraphic occurrence of *Nyctosaurus* than that of previous studies, since a basal position within Pterodactyloidea implies a remarkably long ghost range (Unwin 2001, fig. 14).

The cladogram presented in the second analysis by Bennett (1994) is topologically similar to that of the 1989 study, differs mainly in the inclusion of more taxa and is similar in many respects to the tree presented here. One significant difference, not discussed with regard to the 1989 analysis, is the exclusion of *Ornithocheirus* and *Brasileodactylus* from the *Pteranodontidae* (= Ornithocheiroidea here). The main reason for this appears to be the absence of data for these taxa in this study (only three entries for the 37 characters) and thus a lack of evidence supporting their assignment to *Pteranodontidae* (*sensu* Bennett 1989, 1994). A second apparent difference concerns the row of Late Jurassic and Early Cretaceous pterodactyloids clustered at or near the base of Pterodactyloidea. Inspection of this list shows, however, that most of these taxa (with the exception of *Germanodactylus*) belong in what was identified in the present study as Ctenochasmatoidea. This taxon was not supported in the bootstrap analysis (Fig. 6c) and the resulting cladogram is thus topologically similar to that presented by Bennett (1994, fig. 8). The lack of resolution in Bennett's 1994 tree is probably for the same reason as that proposed to account for the same phenomenon in Howse's 1986 study (see above).

The two studies published by Unwin (1992, 1995a) used earlier versions of the data set shown in Table 3; thus, not surprisingly, the resulting trees are remarkably similar to that obtained here. The 1992 tree differs in three ways:

- (1) Long-necked pterodactyloids were lumped together in a single clade principally because that study did not include *Tapejara* or *Tupuxuara*, or characters of the skull that distinguish ctenochasmatoids from azhdarchoids.
- (2) *Nyctosaurus* emerged as the most basal taxon within Ornithocheiroidea, principally because it lacked some ornithocheiroid characters pertaining to the humerus, several features that link Pteranodontidae and *Nyctosaurus* here were not included in the data set (e.g. hyperelongate wing metacarpal IV, shape of the mandible) and one feature (narrow, elongate, frontal crest) was not then known in *Nyctosaurus*.
- (3) Dsungaripteroids formed the most basal pterodactyloid group, rather than the Ornithocheiroidea. Only a single character (pneumatization of the limb bones) supported the clade uniting Azhdarchoidea (including Ctenochasmatoidea) and Ornithocheiroidea. This character is problematic, however, in that limb-bone pneumatization is difficult to identify in many Jurassic pterodactyloids and appears to follow a different pathway in ornithocheiroids than, for example, in azhdarchids, raising doubts as to its homology. If this character is ignored, the resulting trichotomy closely reflects the topology of the consensus tree (Fig. 7a).

In the cladogram described by Kellner (1996a; Fig. 5a), the topology crownwards from the clade uniting *Dimorphodon* with derived "rhamphorhynchoids" and pterodactyloids is almost identical to that of the consensus cladogram presented here (cf. Figs 5a & 7a). The only difference is that in Kellner's tree Nyctosauridae is placed at the base of a clade equivalent to Ornithocheiroidea, and this clade forms a sister-group to Dsungaripteridae + Azhdarchoidea rather than a sister-group to all other pterodactyloids. Both these arrangements have already been discussed above.

Kellner's cladogram (Fig. 5a) is clearly distinguished from the strict consensus cladogram presented here in that Anurognathidae forms the most basal taxon and three rhamphorhynchids (*Sordes*, *Scaphognathus*, *Dorygnathus*) lie near the base of the tree and outside Rhamphorhynchidae. According to Kellner (1996a) pterosaurs other than anurognathids are united by a posteriorly displaced external narial opening. This is certainly true of Campylognathoididae and other more derived forms (Figs 9 & 13), but an anteriorly located narial opening is also present in *Preondactylus* and dimorphodontids (Fig. 8a, b); thus, while the apparent distribution of states for this character support the results of this analysis, that anurognathids occur among basal forms (Figs 6 & 7), it does not necessarily support the placement of this group as the most basal taxon. Kellner (1996a) mentions that the placement of the other taxa, including the basal position of the three rhamphorhynchids, is dependent on derived states for the proportions of postcranial

bones, especially the wing elements, but does not describe or discuss these characters.

The relationships described by Viscardi *et al.* (1999) largely match those evident in the consensus tree (Fig. 7a). According to these authors Ornithocheiroidea is the sister-group to Azhdarchoidea, rather than Ctenochasmatoidea but, as already discussed, only one or two character states provide evidence regarding the relationships of the major pterodactyloid clades. Therefore alternative topologies are only slightly less parsimonious than the scheme shown in Fig. 7a, although this particular grouping did not occur in any of the six MPTs found in this study.

Pterosaur evolutionary history

At a general level, the basic pattern evident in the 'standard' pterosaur evolutionary tree (Wellnhofer 1978; Fig. 2) is similar to that seen in the evolutionary history shown in Fig. 21. There is a basal radiation in the Late Triassic–Early Jurassic, followed by a second radiation, of pterodactyloids, in the Late Jurassic. At finer scales, however, there are many differences: the new study reveals a more complex history and helps to clarify several important events.

The first, basal, radiation of pterosaurs seems to have been well established by the Late Triassic and may have begun earlier. According to the results of this study at least five distinct clades existed prior to the Triassic–Jurassic boundary, although only three of these are known from the fossil record (Appendix 1). Notably, the majority of Triassic records appear to belong to the Campylognathoididae (Wild 1978, 1984b; Dalla Vecchia 1995, 1996; Jenkins *et al.* 1999, 2001; Wellnhofer 2001, 2003), one of two lonchognathan lineages that existed contemporaneously with various clades of basal pterosaurs.

An important event occurred in the Early Jurassic with the replacement of several basal clades (*Preondactylus*, dimorphodontids, campylognathoidids) by a more derived and highly successful clade of "rhamphorhynchoids": the Rhamphorhynchidae. Rhamphorhynchids are unreported prior to the Toarcian (Appendix 1) but, apart from a few anurognathids, the numerous records of Middle and Late Jurassic "rhamphorhynchoids" all appear to belong to this clade. A striking feature of Jurassic "rhamphorhynchoids", when compared to Late Jurassic and Cretaceous pterodactyloids, is the relatively restricted degree of morphological and taxonomic diversity and their typically small size, with wing spans of no more than 2.5–3m.

The basal radiation of pterodactyloids is first documented in the Late Jurassic (Fig. 21), although this clade probably dates back to at least the Early Jurassic. Two of the four major clades (Cteno-

chasmatoidea and Dsungaripteroidea) are recorded in the Late Jurassic, and were already diverse and widely distributed by this time (Appendix 1). Pterosaurs seem to have achieved their highest levels of taxonomic, morphological and ecological diversity during the Early Cretaceous, when all four major pterodactyloid clades coexisted simultaneously (Unwin *et al.* 2000), although two of these clades, Ctenochasmatoidea and Dsungaripteroidea, do not appear to have survived much beyond the end of this interval.

An important, previously unrecognized event seems to have taken place in the early Late Cretaceous, resulting, principally, in a strong reduction in pterosaur diversity, with the complete disappearance of toothed forms (represented in the Cenomanian by ornithocheirids and lonchodectids) and some edentulous taxa (tapejarids and tupuxuarids). Among the two surviving lineages, pteranodontians are only known from the middle Upper Cretaceous of North America (Bennett 1994) and a single record from the Maastrichtian of South America (Price 1953); thus, counter to popular notions (e.g. Carroll 1987), *Pteranodon* was probably not the dominant or even a typical Late Cretaceous pterosaur. Recent fossil finds and revision of older discoveries (Unwin & Lü 1997; Company *et al.* 1999) show that almost all Campanian and Maastrichtian records represent azhdarchoids and this group seems to have dominated the last 20 Ma of pterosaur history.

Conclusions

The reconstruction of pterosaur phylogeny using cladistic techniques is still in its infancy but already some basic patterns, evident to some extent in pre-cladistic studies, are beginning to emerge. Pterosauria, Pterodactyloidea and Ornithocheiroidea are well supported and other relationships, such as a basal position for *Preondactylus* and dimorphodontids, and the monophyly of Dsungaripteroidea and Azhdarchoidea, are unlikely to be substantially modified. Together, these relationships impose considerable constraints on tree shape. Future studies are likely to focus on areas of greater uncertainty, aiming to clarify the relationship of clades of derived "rhamphorhynchoids" to the Pterodactyloidea, to test the monophyly of Ctenochasmatoidea and to resolve the relationships of taxa within all four major pterodactyloid lineages.

Redescriptions of older material and detailed accounts of the many new taxa named, but often only briefly described, in recent years, will be important for such studies. Utilizing species, or even specimens, as terminal taxa would reduce the number of untested hypotheses of relationships, although a pre-

liminary attempt by the author resulted in a character data set with a high proportion of missing data, a large number of MPTs and relatively poor resolution of relationships. One partial solution to these problems might be to partition the data set, treating “rhamphorhynchoids” and pterodactyls separately. Exploration and refinement of characters offers another promising approach. Recent studies have identified more than 100 characters and, while some of these are now well understood, most, especially those related to morphometric data, would benefit from further analysis. Doubtless, many further characters remain to be described: the pelvis, for example, exhibits considerable variation, but character states based on this have yet to be cited.

Beyond the task of improving and refining cladograms, understanding of pterosaur phylogeny could be used as a framework for investigations of other aspects of these animals. In recent years, pterosaur anatomy, functional morphology, locomotory abilities, growth and physiology have been the subject of intense scrutiny and debate (see Wellnhofer 1991a; Unwin 1999 for reviews) but with some rare exceptions (e.g. Bennett 2003), these studies have been conducted practically without reference to pterosaur phylogeny. Indeed, it is often implied, though perhaps not intentionally, that what holds true for one pterosaur holds true for them all, even though the basic construction of, e.g. “rhamphorhynchoids” and pterodactyls, differs in many fundamental ways (Schaller 1985). In addition to the fresh insights that it might yield, integration with phylogenetic studies would help to avoid this problem.

I am grateful to the many museums and institute staff who permitted me to inspect their collections and generously loaned material. Special thanks go to A. Milner, C. Walker and S. Chapman of The Natural History Museum, London, UK; C. Forbes, S. Etchells-Butler and D. Norman, Sedgwick Museum, Cambridge, UK; T. Kemp and P. Powell, Oxford University Museum, Oxford, UK; P. Wellnhofer, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; E. Frey, Staatliches Museum für Naturkunde, Karlsruhe, Germany; R. Wild, Staatliches Museum für Naturkunde, Stuttgart, Germany; the late L. Nesov, Department of Geology, St Petersburg University, Russia; W. Langston Jr, University of Texas, Austin, Texas, USA; M. Manabe and Y. Tomida, National Science Museum, Tokyo, Japan; S. Nabana, Iwaki Museum of Coal and Fossils, Iwaki, Japan; Y. Hasegawa and Y. Takakura, Gunma Museum of Natural History, Gunma, Japan; Y. Okazaki and Y. Yabumoto, Kita-Kyushu City Museum of Natural History, Kita-Kyushu, Japan; H. Taru, Kanagawa Prefectural Museum of Natural History, Kanagawa, Japan; E. Gaffney, M. Norell and A. Kellner, American Museum of Natural History, New York, USA; K. Carpenter, Denver Museum of Natural History, Denver, USA; P. Currie, Royal Tyrrell Museum of Palaeontology, Drumheller, Canada; D. Zhiming and J. Lü, Institute for Vertebrate Paleontology and Paleoanthropology, Beijing,

China; and Z. Cai, Zhejiang Museum of Natural History, Hangzhou, China. The Department of Earth Sciences, Bristol University, Institut für Paläontologie, Museum für Naturkunde, Humboldt Universität, the Royal Society, NERC and the British Council are thanked for funding aspects of this work. I thank N. Bakhurina, C. Bennett, M. Benton, S. Howse, M. Fastnacht, E. Frey, D. Martill, K. Padian, D. Peters, P. Wellnhofer and M. Wilkinson for useful discussions of pterosaur phylogeny; G. Arratia and T. Pfeiffer for help with PAUP; E. Siebert, J. Mendonça and D. Lazarus for assistance with the production of the figures; and R. Schoch and, in particular, B. Creisler for advice regarding the formulation of taxonomic names. I am especially grateful to M. Benton and C. Bennett for their constructive reviews and to E. Buffetaut for his editorial advice. This paper is dedicated to P. Wellnhofer, the father of modern pterosaurology.

Appendix 1 Terminal taxa used in this analysis

Content, diagnosis and where appropriate comments are given for each taxon. The heading ‘Source of phylogenetic data’ lists the specimens examined. Casts are indicated by ‘c’. Where additional information was collected from the literature, or only the literature was used, all citations examined are listed.

Preondactylus Wild 1984a

Content. *Preondactylus* Wild 1984a

Diagnosis. (Modified from Dalla Vecchia [1998] to include only characters found in *Preondactylus*.) Two or three enlarged, triangular maxillary teeth between the naris and the antorbital fenestra followed distally by 10 triangular teeth decreasing regularly in size; dentary less than half the length of the complete lower jaw.

Remarks. The relatively low, elongate snout shown in recent reconstructions (Wellnhofer 1991a; Dalla Vecchia 1998) does not match with details of the skull as illustrated by Wild (1984a, figs 1 & 2). The elongate, subvertically oriented nasal process of the maxilla, angle between dorsal and maxillary processes of the premaxilla and reinterpretation, as the nasal (Fig. 8a), of the element labelled as a frontal by Wild (1984b, fig. 3) indicate that the snout region was much higher than shown by Wellnhofer (1991a) and Dalla Vecchia (1998), with large narial and antorbital fenestrae similar to the condition in dimorphodontids. Moreover, since the premaxilla and maxilla reach 80% of the length of skull (calculated from the length of the mandible), the region from the anterior edge of the orbit to the posterior margin of the occiput must have formed less than 20% of the skull length. Since the orbit must have been accommodated in this space it is likely to have been considerably smaller than the narial or antorbital fenestrae.

Recorded temporal range. Late Triassic (Norian).

Source of phylogenetic data. *Preondactylus bufarini* (Wild 1984a; Dalla Vecchia *et al.* 1989; Dalla Vecchia 1998, 2001).

Dimorphodontidae Seeley 1870

Definition. *Dimorphodon macronyx*, *Peteinosaurus zambellii*, their most recent common ancestor, and all its descendants.

Content. *Dimorphodon* Owen 1859; *Peteinosaurus* Wild 1978; Charmouth dimorphodontid (Unwin unpub. data).

Diagnosis. (See also Wellnhofer 1978) External narial opening forms the largest skull opening; mandible with true dimorphodontid dentition: two large teeth followed by at least 30 small, close-set, lancet-shaped teeth (Owen 1870; Wild 1978; Dalla Vecchia 1998, fig. 5); deltopectoral crest of humerus subtriangular with apex directed proximally (Wild 1978, fig. 43; Dalla Vecchia 1998, fig. 6); strongly broadened proximal end of wing phalanx 1, with short extensor tendon process (Wild 1978, p. 241); phalanx 2 of pes digit V straight and equal in length to the first phalanx. Phalanx 2 is relatively long in some rhamphorhynchids (*Sordes Scaphognathus*, *Rhamphorhynchus*), but in these pterosaurs it is curved or bent (Sharov 1971; Wellnhofer 1975a).

Recorded temporal range. Late Triassic (Norian) to ?Mid-Jurassic (Aalenian–Bajocian).

Source of phylogenetic data. *Dimorphodon macronyx* (BMNH 41212, BMNH 41213, BMNH 41346, BMNH 41347b, BMNH 43051, BMNH 43974, BMNH R1034, BMNH R1035, BMNH R1596, BMNH R1598, GSM 1546; Owen 1870; Padian 1983; Unwin 1988a). *Dimorphodon weintraubi* (Clark *et al.* 1994, 1996, 1997, 1998). *Peteinosaurus zambellii* (Wild 1978; Dalla Vecchia 1998, 2001). Charmouth dimorphodontid (OUM J.53070).

Anurognathidae Nopcsa 1928

Definition. *Anurognathus ammoni*, *Batrachognathus volans*, their most recent common ancestor, and all its descendants.

Content. *Anurognathus* Döderlein 1923, *Batrachognathus* Ryabinin 1948, *Dendrorhynchoides* Ji *et al.* 1999, *Jeholopterus* Wan *et al.* 2002, unnamed anurognathid Bakhurina & Unwin 1995.

Diagnosis. Skull very short, high and broad (Döderlein 1923; Ryabinin 1948; Kuhn 1967; Wellnhofer 1975b, 1978), possibly kinetic and with palatal elements reduced to thin bars of bone (Bakhurina 1988; Unwin *et al.* 2000); teeth are small, peg-like, widely spaced and greatly reduced in number to only three on the premaxilla and eight or less on the maxilla (Ryabinin 1948; Unwin *et al.* 2000); combined length of the dorsal + sacral vertebrae is almost the same length as the ulna (Döderlein

1923; Unwin *et al.* 2000); tail reduced to 11 vertebrae or less (Döderlein 1923; Ryabinin 1948; Unwin *et al.* 2000); subsymmetric, angular profile of the proximal end of the humerus in dorsal view (Ryabinin 1948, fig. 1; Wellnhofer 1975b, fig. 37; Unwin *et al.* 2000, fig. 3); metacarpal IV relatively short and only 33% the length of the humerus; digit III of manus reduced to only three phalanges, not four as in other pterosaurs and archosaurs. Both Döderlein (1923) and more recently Wellnhofer (1975b) have restored the third digit of *Anurognathus* with four phalanges, but the author's observations suggest that as a result of either loss or fusion, only three phalanges were present. Furthermore, even though slightly disarticulated, the third digit of *Batrachognathus* also appears to contain only three phalanges (Unwin & Bakhurina 2000). Further putative apomorphies include: wing phalanx 1 longer than the combined length of the ulna + wing metacarpal and wing phalanx 2 longer than the ulna (Ji & Ji 1998; Unwin *et al.* 2000, table 2).

Recorded temporal range. Mid-Jurassic (?Aalenian–Bajocian) to Lower Cretaceous (Barremian).

Source of phylogenetic data. *Anurognathus ammoni* (BSP 1922 I 42; undescribed specimen in SMNS collections; Döderlein 1923, 1929; Petronievics 1928, Wellnhofer 1975b). *Batrachognathus volans* (PIN 52–2, PIN 2585/4a; Ryabinin 1948; Bakhurina 1988; Bakhurina & Unwin 1995; Unwin & Bakhurina 2000). *Dendrorhynchoides curvidentatus* (Ji & Ji 1998; Ji *et al.* 1999; Unwin *et al.* 2000). *Jeholopterus ningchengensis* (Wang *et al.* 2002). Undescribed Mongolian anurognathid (Bakhurina & Unwin 1995; Unwin & Bakhurina 2000).

Campylognathoididae (*Campylognathoidinae*) Kuhn 1967

Definition. *Eudimorphodon ranzii*, *Campylognathoides liasicus*, their most recent common ancestor, and all its descendants.

Content. *Campylognathoides* Strand 1928; *Eudimorphodon* Zambelli 1973.

Diagnosis. Anterior tip of the mandible downturned; supratemporal fenestra largest skull opening after the orbit (Wild 1978); humerus with a large rectangular deltopectoral crest and relatively large medial crest (Wild 1978, fig. 45); rectangular sternum with short cristospine and short rectangular processes on each posterolateral corner (Wild 1978); wing finger from 67–79% of total wing length.

Remarks. *Austriadactylus* (Dalla Vecchia *et al.* 2002) and *Eudimorphodon* share one derived character state – multicusped teeth (Jenkins *et al.* 2001; Wellnhofer 2001) and *Austriadactylus* also appears to have a relatively elongate wing finger, a condition otherwise found only in campylognathoidids and rhamphorhynchids. Weak as it is, the available evidence suggests that *Austriadactylus* should be

referred to the Campylognathoididae, a proposal that is consistent with the general similarity of this pterosaur to *Eudimorphodon*.

Recorded temporal range. Late Triassic (Norian) to Lower Jurassic (Toarcian).

Source of phylogenetic data. *Austriadactylus cristatus* (Dalla Vecchia *et al.* 2002). *Campylognathoides liasicus* (MT, MNHN, SMNS; Plieninger 1907; Wiman 1923; Wild 1971; Wellnhofer 1974). *Campylognathoides zitteli* (SMNS; Plieninger 1895, 1907; Wild 1971). *Eudimorphodon cromptonellus* (Jenkins *et al.* 1999, 2001). *Eudimorphodon ranzii* (Zambelli 1973; Wild 1978, 1994; Dalla Vecchia 2001). *Eudimorphodon rosenfeldi* (Dalla Vecchia 1995, 1996, 2001). *Eudimorphodon* sp. (Wellnhofer 2001).

Rhamphorhynchinae Nopsca 1928

Definition. *Dorygnathus banthensis*, *Rhamphorhynchus muensteri*, their most recent common ancestor, and all its descendants.

Content. *Angustinaripterus* He *et al.* 1983; *Dorygnathus* Wagner 1860; *Nesodactylus* Colbert 1969; *Parapsicephalus* (= *Dorygnathus*) Arthaber 1919; *Rhamphocephalus* Seeley 1880; *Rhamphorhynchus* Meyer 1847.

Diagnosis. Antorbital fenestra lies behind and below the naris; elongate antorbital fenestra twice as long as it is deep; mandible tips fused into a short symphysis bearing a forward-projecting prow and a number of large, fang-like, procumbent teeth forming a fish grab; wing finger 63% or more of total wing length; rear margin of wing finger grooved (see also Wellnhofer 1975b, 1975c, 1978).

Recorded temporal range. Early Jurassic (Toarcian) to Late Jurassic (Tithonian).

Source of phylogenetic data. *Angustinaripterus longicephalus* (He *et al.* 1983). *Dorygnathus banthensis* (MB 1905.15, 1986.6 [c], SMNS 18969, SMNS 18880, SMNS SO164, SMNS SO702, Tübingen 1536; Arthaber 1919; Wiman 1923; Saleé 1928; Wild 1975; Padian & Wild 1992). *Dorygnathus mistelgauensis* (Wild 1971). *Dorygnathus* (= †*Parapsicephalus*) *purdoni* (GSM); Newton 1888). *Nesodactylus hesperius* (Colbert 1969). *Rhamphocephalus bucklandi* (BMNH 47991; Huxley 1859; Owen 1874; Unwin 1996). *Rhamphorhynchus 'longiceps'* (BMNH R37002, MT unnumb.; Smith Woodward 1902; Plieninger 1907; Wellnhofer 1975a). *Rhamphorhynchus muensteri* (= *R. †gemmingi*, *R. †intermedius*, *R. †longicaudus*) (AMNH 1943, BMNH 37002, BMNH 37787, BMNH 42738, BMNH R2786, BSP AS VI 34, BSP AS I 771, BSP 1867 II 2, BSP 1877 X 1, BSP 1889 XI 1, BSP 1927 I 36, BSP 1929 I 69, BSP 1934 I 36, BSP 1938 I 503, BSP 1955 I 28, BSP 1960 I 470, MB 3965, MB 3966, MB 3967, MB 69/2191b, MGUH VP2304, MGUH V45/1, MMK V. 45/1,

MMK 1891.470, MMK 1891.738, NSMT 1776–8, PTH 1951.14, PTH 1954.39, PTH 1966.66, PTH unnumb., SMF R4128, SMF R4158; Meyer 1859; Zittel 1882; Winkler 1883; Plieninger 1907; Broili 1927; Koh 1937; Wellnhofer 1975a).

Scaphognathinae Hooley 1913

Definition. *Sordes pilosus*, *Scaphognathus crassirostris*, their most recent common ancestor, and all its descendants.

Content. *Scaphognathus* Wagner 1861; *Sordes* Sharov 1971; Morrison Formation scaphognathine (see Carpenter *et al.* 2003).

Diagnosis. Only nine, or less, relatively straight (or slightly recurved), widely spaced pairs of teeth in the rostrum (Sharov 1971, pl. 5, fig. 2; Wellnhofer 1975b, fig. 33; Ivakhnenko & Korabelnikov 1987, fig. 262; Carpenter *et al.*, 2003). Only six, or less, widely spaced, vertically oriented pairs of teeth in the lower jaw (Sharov, 1971, pl. 5, fig. 2; Wellnhofer 1975b, fig. 33). Phalanx 2 of pedal digit V has a distinctive angular flexure at mid-length, such that the distal half of the phalanx lies at 40–45° to the proximal half (Sharov 1971, fig. 2; Wellnhofer 1975b, fig. 36d). See also Wellnhofer (1975b, 1978), Bakhurina & Unwin (1995) and Carpenter *et al.* (2003).

Recorded temporal range. Late Jurassic (Oxfordian–Tithonian).

Source of phylogenetic data. *Scaphognathus crassirostris* (GPIB 1304 [c]; MSA 110; SMNS 59395; Wellnhofer 1975b). *Sordes pilosus* (PIN 104/73, PIN 2470/1, PIN 2585/3, PIN 2585/25, PIN 2585/36, PIN 2585/37; Sharov 1971; Bakhurina 1986; Unwin & Bakhurina 1994, 2000; Bakhurina & Unwin 1995). New genus and species of scaphognathine (NAMAL 101; Cloward & Carpenter 2001; Carpenter *et al.* 2003).

Istiodactylus Howse *et al.* 2001.

Content. *Istiodactylus* (= *Ornithodesmus*) Howse *et al.* 2001.

Diagnosis. (Modified from Wellnhofer 1978, Howse *et al.* 2001.) Unusually extensive nasoantorbital fenestra occupying much of the snout. Orbit continuous with long, narrow suborbital vacuity. Teeth labiolingually compressed with sharply pointed crowns, sharp anterior and posterior edges, a vertical ridge on the lingual surface and truncated triangular roots shorter than crowns. The rear-most pairs of teeth on the mandible fit into deep embayments in the lower jaw. See also Hooley (1913).

Recorded Temporal Range. Early Cretaceous (Barremian).

Source of phylogenetic data. *Istiodactylus* (= *Ornithodesmus*) *latidens* (BMNH 3877, BMNH 3878, BMNH R176, CAMMZ T706; Seeley 1901; Hooley 1913; Howse & Milner 1993; Howse *et al.* 2001).

Ornithocheiridae Seeley 1870

Definition. *Haopterus gracilis*, *Ornithocheirus simus*, their most recent common ancestor, and all its descendants.

Content. *Anhanguera* Campos & Kellner 1985; *Brasileodactylus* Kellner 1984; *Coloborhynchus* Owen 1874; *Haopterus* Wang & Lü 2001; *Ornithocheirus* Seeley 1869; new genus and species of ornithocheirid (Frey *et al.* 2003).

Diagnosis. (Modified from Bakhurina & Unwin 1995; Unwin 2001.) The first three pairs of teeth in the rostrum are relatively large, forming a terminal rosette and show a marked increase in size posteriorly. The fourth and fifth tooth pairs are much reduced in size and smaller than the first pair of teeth. Proceeding posteriorly, there is a steady increase in tooth size up to, typically, the ninth pair, which are of similar basal dimensions to the largest teeth in the terminal rosette. Further posteriorly, tooth size declines again. Consequently, the rostrum has an expanded anterior tip that accommodates the large anterior teeth, is narrowest in the region of the fourth or fifth tooth pair, and gradually widens posteriorly (e.g. Fastnacht 2001, figs 2–5; Fig. 10b, d, e). The expansion of the anterior end of the rostrum is most marked in large species and adult individuals, but may be practically absent in small species (e.g. *Haopterus*) and juveniles. The mandibular dentition and symphysis show similar morphological patterns to the rostrum.

Remarks. Various taxa from the Santana Formation ('*Araripesaurus*' and '*Santanadactylus*') and the Crato Formation (*Arthurdactylus*) of Brazil probably also belong in the Ornithocheiridae (Unwin 2001), but their taxonomic status and precise relationships to other ornithocheirids are uncertain (Bakhurina & Unwin 1995; Unwin & Lü 1997; Unwin & Bakhurina 2000; Unwin *et al.* 2000; Fastnacht 2001). *Anhangueridae* has a content (e.g. Kellner & Tomida 2000) and diagnosis (Campos & Kellner 1985) similar to that of Ornithocheiridae and is treated here as a junior synonym of the latter taxon (Unwin 2001).

Recorded temporal range. Early Cretaceous (Valanginian) to Late Cretaceous (Cenomanian).

Source of phylogenetic data. *Anhanguera araripensis* (BSP 1982 I 89; Wellnhofer 1985; Kellner & Tomida 2000). *Anhanguera blittersdorffi* (BMNH R11978; Campos & Kellner 1985; Kellner & Tomida 2000). *Anhanguera cuvieri* (BMNH 39409, CAMSM B54.431; Bowerbank 1851; Owen 1859; Unwin 2001). *Anhanguera fittoni* (CAMSM B54.423, CAMSM B54.556; Owen 1859; Unwin 2001). *Anhanguera santanae* (AMNH 22555, BSP 1982 I 90; BSP 1982 I 91, IMCF 1053; Wellnhofer 1985, 1991b). *Anhanguera* sp. (SMNK 1136 PAL; Frey & Martill 1994). *Arthurdactylus conandoylei* (SMNK 1132 PAL, Frey & Martill 1994). *Brasileo-*

dactylus araripensis (Kellner 1984; Sayão & Kellner 2000). *Coloborhynchus capito* (BMNH R481, CAMSM B54.625; Unwin 2001). *Coloborhynchus clavirostris* (BMNH R1822; Owen 1874; Lee 1994; Fastnacht 2001, Unwin 2001). *Coloborhynchus* (= †*Siroccopteryx*) *moroccensis* (Mader & Kellner 1999; Unwin 2001). *Coloborhynchus robustus* (= †*Anhanguera piscator*, †*Tropeognathus robustus*) (BSP 1987 I 47, NSM-PV 19892, SMNK 1133 PAL, SMNK 2302 PAL; Wellnhofer 1987; Kellner & Tomida 2000, Fastnacht 2001; Unwin 2001). *Coloborhynchus sedgwickii* (CAMSM B54.422; Owen 1859; Unwin 2001). *Coloborhynchus wadleighi* (Lee 1994); *Haopterus gracilis* (Wang & Lü 2001; see also Unwin 2001). *Ornithocheirus mesembrinus* (BSP 1987 I 46; Wellnhofer 1987; Fastnacht 2001). *Ornithocheirus simus* (CAMSM B54.428, MANCH L10832; Owen 1861; Unwin 2001). *Ornithocheirus* sp. (CAMSM B54.890). Khuren-Dukh ornithocheirid (Bakhurina & Unwin 1995). New genus and species of ornithocheirid (Viohl 2000, pl. 9, fig. 3; Frey *et al.* 2003).

Pteranodontidae Marsh 1876

Definition. *Ornithostoma sedgwicki*, *Pteranodon longiceps*, their most recent common ancestor, and all its descendants.

Content. *Pteranodon* Marsh 1876; *Ornithostoma* Seeley 1871.

Diagnosis. (Modified from Bennett 1994.) Cranial crest formed by frontals and directed upwards and backwards from skull. Premaxillary crest with relatively straight dorsal margin, not rounded in profile. Edentulous jaws with raised marginal ridges. Premaxillae extending beyond the end of the mandible. Ceratobranchials of hyoid apparatus greatly reduced or unossified. Notarial and synsacral supraneural plates formed of ossified interspinous ligaments. Postacetabular process of ilium contacting neural spines of posterior synsacral vertebrae and fused with them in mature adults. Proximal caudal vertebrae with duplex centra. Distal caudal vertebrae reduced and co-ossified to form caudal rod. Distal end of wing-metacarpal without an elevation between condyles. See also Bennett (2001) and Unwin (2001).

Recorded temporal range. Early Cretaceous (Albian) to Late Cretaceous (Campanian).

Source of phylogenetic data. *Ornithostoma sedgwicki* (CAMSM B54.485, Owen 1859; Seeley 1871; Unwin 2001). *Pteranodon longiceps* (AMNH 149, AMNH 4908, AMNH 6158, FMNH PR 464, FMNH PR 468–470, FMNH PR 494, FMNH PR 676, FMNH PR 1332; Eaton 1910; Bennett 1994, 2001). *Pteranodon sternbergi* (Harksen 1966; Bennett 1994, 2001). *Pteranodon* sp. (AMNH 5840, BMNH 2959, BMNH 4006, BMNH 4008, BMNH 4534, BMNH 4538; Eaton 1910; Bennett 1994, 2001).

Nyctosaurus Marsh 1876

Content. *Nyctosaurus* Marsh 1876.

Diagnosis. (Based on Brown 1986; Bennett 1989, 1994, 2000.) Neural spines of mid-notarial vertebrae T-shaped in anterior view. Dorsal centra crescentic in cross-section. Humerus with hatchet-shaped deltopectoral crest. Loss of manus digits I–III. Reduction of the wing finger to just three phalanges. *Recorded temporal range.* Late Cretaceous (Santonian–Maastrichtian).

Source of phylogenetic data. *Nyctosaurus gracilis* (FMNH 25026; Williston 1902, 1903; Miller 1972; Bennett 1989, 1994, 2000). *Nyctosaurus lamegoi* (Price 1953; Bennett 1989). *Nyctosaurus nanus* (Miller 1972; Bennett 1994).

Cynorhamphus Seeley 1870

Content. *Cynorhamphus* Seeley 1870.

Diagnosis. Reduction of the dentition to a few, slender, curved teeth on the tips of the jaws (Wellnhofer 1978). A large, deep, wing-like, parietal crest projecting backwards from the occiput (Wellnhofer 1978; Bennett 1996c). Relatively long terminal wing phalanx (Padian & Warheit 1989).

Recorded temporal range. Late Jurassic (Tithonian). *Source of phylogenetic data.* *Cynorhamphus canjeunsensis* (MNHN CNJ-71; Fabre 1974, 1976). *Cynorhamphus suevicus* (MT unnumb.; Quenstedt 1855; Wagner 1858; Fraas 1878, Plieninger 1907; Wellnhofer 1970, Bennett 1996c).

Pterodactylus Cuvier 1809

Content. *Pterodactylus* Cuvier 1809 (*partim*).

Remarks. In the last major review of this genus Wellnhofer (1968, 1970, 1978) included the following species from the Solnhofen Limestone: *P. antiquus*, *P. kochi*, *P. micronyx*, *P. elegans* and *P. longicollum*. Bennett (1996a) has suggested that ‘*P.*’ *micronyx* may be a juvenile form of *Gnathosaurus subulatus*. This is not unreasonable but, in any case, ‘*P.*’ *micronyx* is quite distinct from other species of *Pterodactylus* (Wellnhofer 1968, 1970; Unwin 1995b) and for the present the author prefers not to include ‘*P.*’ *micronyx* in *Pterodactylus sensu stricto* (see also Atanassov 2000). Bennett (1996a) also proposed that specimens of †*P. elegans* represent juveniles of *Ctenochasma gracile*, an idea that is accepted here. ‘*Pterodactylus*’ *longicollum* has at least one diagnostic character of gnathosaurines: expanded spatulate jaw tips with a rosette composed of numerous elongate teeth; however, its exact taxonomic status, a distinct species of *Gnathosaurus*, or perhaps a representative of another genus (?*Diopcecephalus* Seeley 1871), has yet to be established. In any case, ‘*P.*’ *longicollum* cannot be retained in *Pterodactylus*. Consequently, in this study, *Pterodactylus* contains just two species: *P. antiquus* and *P. kochi*. Whether these species are truly distinct

from one another, and how they differ from other similar taxa, such as *Germanodactylus rhamphastinus*, requires further study (see also Atanassov 2000).

Other taxa assigned to this genus, including †*P. arningi*, †*P. brancai* and †*P. maximus*, are *nomina dubia* (Unwin & Heinrich 1999), as are †*P. manselli* and †*P. pleydelli*.

Diagnosis. None of the characters previously used to define *Pterodactylus* (e.g. Wellnhofer 1968, 1970, 1978) are truly diagnostic because they occur in other pterosaurs. A group including *P. antiquus* and *P. kochi* is distinguished by the rostral dentition: 16 or more tall-triangular teeth, the largest located in the mid-region of the tooth row, which extends from the jaw tips posteriorly to a point beneath the nasoantorbital fenestra. While this excludes other ctenochasmatoids, it also holds true for *Germanodactylus rhamphastinus*, although not *G. cristatus*.

Recorded temporal range. Late Jurassic (Tithonian). *Source of phylogenetic data.* *Pterodactylus antiquus* (BMNH R388, BSP AS I 739, BSP 1968 I 95, Wellnhofer 1970). *Pterodactylus kochi* (AMNH 1942, BMNH 42736, BSP AS V 29, BSP AS XIX 3, BSP 1878 VI 1, BSP 1883 XVI 1, BSP 1924 V 1, BSP 1929 I 18, BSP 1937 I 18, BSP 1967 I 276, MB 1876.2059, NSMT PV19893, SM R4702, SM R4074; Zittel 1882; Abel 1925; Broili 1938; Huene 1951; Wellnhofer 1970, 1987; Tischlinger 1994; Frey & Martill 1998).

Lonchodectidae Unwin *et al.* 2000

Definition. *Lonchodectes giganteus*, *Lonchodectes machaerorhynchus*, their most recent common ancestor, and all its descendants.

Content. *Lonchodectes* Hooley 1913.

Diagnosis. (Modified from Unwin 2001.) Pterosaurs with distinctive, parapet-like alveolar borders to the jaws. Each border bears small, subequal sized, sub-circular, well-spaced alveoli with margins raised into a low collar, and containing teeth with constricted bases. There is a prominent, sharply ridged, median keel on the occlusal surface of the rostrum which corresponds with a deep, V-shaped median sulcus on the occlusal surface of the mandibular symphysis.

Recorded temporal range. Early Cretaceous (Valanginian) to Late Cretaceous (Cenomanian).

Source of phylogenetic data. *Lonchodectes compressirostris* (BMNH 39410, CAMSM B54.584; Owen 1851, pl. XXVIII, figs 8–10; Seeley 1870, p.114). *Lonchodectes giganteus* (BMNH 39412; Bowerbank 1846, pl. I, figs 1 & 2; Bowerbank 1848, pl. I, fig. 1; Owen 1851). *Lonchodectes machaerorhynchus* (CAMSM B54.885; Seeley 1870, pl. XII, figs 1 & 2). *Lonchodectes microdon* (BMNH R2268, BMNH R2269, CAMSM B54.439, CAMSM B54.486, GSM 87822; Seeley 1870, pl. XII, figs 6 &

7). *Lonchodectes platystomus* (BMNH 43074, CAMSM B54.835, YORM 1983/113F; Seeley 1870; Owen 1874, pl. I, figs 5 & 6). *Lonchodectes* sp. indet. (BMNH R2287c, BMNH R2296, BMNH R3019, BMNH R3694, BMNH 35229, CAMSM B54.074, CAMSM B54.075, CAMSM B54.081, CAMSM B54.262, CAMSM B54.536, CAMSM B55030, GSM 87850, GSM 87887, HMG V1487/2, HMG 1486/3, HMG V1486/4, HMG V1487/4, HMG V1488/3, HMG 1505/3). ?*Lonchodectes sagittirostris* (BMNH R1823; Owen 1874, pl. II, figs 1–8).

Ctenochasmatidae Nopcsa 1928

Definition. *Gnathosaurus subulatus*, *Pterodaustro guinazui*, their most recent common ancestor, and all its descendants.

Content. *Cearadactylus Leonardi* & Borgomanero 1985; *Ctenochasma* Meyer 1851; ?*Eosipterus* Ji & Ji 1997; *Gnathosaurus* Meyer 1834; *Huanhepterus* Dong 1982; *Plataleorhynchus* Howse & Milner 1995; '*Pterodactylus*' *longicollum* Meyer, 1854; *Pterodaustro* Bonaparte 1970.

Diagnosis. (Modified from Wellnhofer 1978; Buissonjé 1981; Howse & Milner 1995; Unwin 2002.) Rostrum anterior to nasoantorbital fenestra forms more than half the total length of the skull (tip of rostrum to occipital condyle). Anterior end of rostrum dorsoventrally compressed and rounded (Wellnhofer 1970, 1978). At least 25 teeth per side in the rostrum. Seven or more pairs of teeth in the premaxillae. Teeth project laterally from the dental border of the rostrum at least in the anterior part of the dentition (Wellnhofer 1970, 1978). Teeth in anterior part of dentition relatively elongate, with a long cylindrical crown of even width and a short tapering distal tip (Buissonjé 1981; Knoll 2000). Metatarsal III more than one-third the length of the tibia (Unwin *et al.* 2000, fig. 6a).

Recorded temporal range. Late Jurassic (Tithonian) to Early Cretaceous (Albian).

Source of phylogenetic data. *Cearadactylus atrox* (Leonardi & Borgomanero 1985). *Ctenochasma gracile* (= ?*Pterodactylus elegans*) (BSP AS VI 30, BSP 1867 II 1, BSP 1875 XIV 501, BSP 1920 I 57, BSP 1935 I 24, PTH 1950.33, PTH unnumb.; Zittel 1882, Broili 1919, 1924, 1936; Wellnhofer 1970; Buissonjé 1981; Bennett 1996a). *Ctenochasma porocristata* (JM SoS-2179; Buissonjé 1981). *Ctenochasma roemeri* (Meyer 1851; Broili 1924; Buissonjé 1981). *Ctenochasma* sp. (Taquet 1972). *Eosipterus yangi* (Ji & Ji 1997, Ji *et al.* 1999; Unwin *et al.* 2000). *Gnathosaurus macrurus* (CAMSM J5339; Howse & Milner 1995). *Gnathosaurus subulatus* (BSP AS VII 369, PTH 1951.84; Wellnhofer 1970). *Huanhepterus quingyangensis* (IVPP V 9070; Dong 1982). *Plataleorhynchus streptophorodon* (Howse & Milner 1995). '*Pterodactylus*' *longicollum*

(BMNH Wellnhofer 1970, Exemplar 55 [c]; SMNS Wellnhofer 1970, Exemplar 58; Meyer 1859; Plieninger 1907; Wellnhofer 1970). *Pterodaustro guinazui* (PVL 3860 [c], PVL 3968 [c]; Bonaparte 1970, 1971; Sanchez 1973; Chiappe *et al.* 2000; Davila & Chiappe 2000).

Germanodactylus Young 1964

Content. *Germanodactylus* Young 1964.

Diagnosis. True synapomorphies uniting *Germanodactylus cristatus* and *G. rhamphastinus*, have yet to be identified; thus *Germanodactylus* is treated here as a metataxon (Gauthier 1986).

Recorded temporal range. Late Jurassic (Tithonian). **Source of phylogenetic data.** *Germanodactylus cristatus* (BSP 1892 IV 1, NMING F15005, SMNK unnumb.; Plieninger 1901; Wellnhofer 1968, 1970). *Germanodactylus rhamphastinus* (BSP AS I 745, BSP 1977 XIX 1; Wellnhofer 1970).

Dsungaripteridae Young 1964

Definition. *Dsungaripterus weii*, *Noriopterus complicidens*, their most recent common ancestor, and all its descendants.

Content. *Dsungaripterus* Young 1964; *Noriopterus* Young 1973; '*Phobator*' Bakhurina 1986. *Domeykodactylus* Martill *et al.* 2000.

Diagnosis. Strong variation in tooth size with the largest teeth located at the caudal end of the dentition. Ventral region of the orbit partially ossified: the postorbital process of the jugal sends forward a bar of bone to the lacrimal enclosing a small suborbital slit. Presence of a short, rectangular sagittal crest projecting backwards from the posterodorsal apex of the skull. (See also Kuhn 1967; Bennett 1989, 1994; Martill *et al.* 2000.)

Recorded temporal range. Early Cretaceous.

Source of phylogenetic data. *Domeykodactylus ceciliae* (Martill *et al.* 2000). *Dsungaripterus weii* (IVPP V. 2776, IVPP V. 2777, IVPP 64041–1, IVPP 64041–3, IVPP 64043–4, IVPP 64043–12, IVPP 64045–1, IVPP 64045–2, IVPP 64045–3, IVPP 64045–5, IVPP 64045–9; Young 1964, 1973). *Noriopterus complicidens* (IVPP 64043–3; Young 1973). '*Phobator*' *parvus* (Bakhurina 1982, 1983, 1986, 1993; Ivakhnenko & Korabelnikov 1987; Bakhurina & Unwin 1995; Unwin & Bakhurina 2000).

Tapejara Kellner, 1989.

Content. *Tapejara* Kellner 1989.

Diagnosis. (Modified from Kellner 1989; Wellnhofer & Kellner 1991.) High premaxillary sagittal crest on anterior part of skull tapering to a low posterior extension closely following the midline of the skull roof. Short frontoparietal crest. Rostrum inclined downwards with concave depression in palatal view. Upper margin of symphysis

inclined downwards with concave depression dorsally.

Recorded temporal range. Early Cretaceous (Aptian) to Late Upper Cretaceous (Cenomanian).

Source of phylogenetic data. *Tapejara imperator* (Campos & Kellner 1997). *Tapejara wellnhoferi* (AMNH 24440, SMNK unnumb.; IMCF unnumb.; Kellner 1989; Kellner 1991; Wellnhofer & Kellner 1991). *Tapejara* sp. (SMNK 2343 PAL; Martill & Frey 1998).

Tupuxuara Kellner & Campos 1988.

Content. *Tupuxuara* Kellner & Campos 1988.

Diagnosis. Large sagittal cranial crest involving the premaxillae, frontals and parietals, and forming a prominent sail-like structure with an origin extending from a little posterior to the tip of the rostrum over the cranium, round onto the occipital plate. See also Kellner & Campos (1988).

Recorded temporal range. Early Cretaceous (Albian).

Source of phylogenetic data. *Tupuxuara longicristatus* (IMCF 1052; Kellner & Campos 1988). *Tupuxuara leonardii* (Kellner & Campos 1994).

Azhdarchidae Nesov 1984

Definition. *Azhdarcho lancicollis*, *Quetzalcoatlus northropi*, their most recent common ancestor, and all its descendants.

Content. *Arambourgiania* Nesov & Yarkov 1989; *Azhdarcho* Nesov 1984; *Hatzegopteryx* Buffetaut *et al.* 2002; *Montanazhdarcho* Padian *et al.* 1995; *Quetzalcoatlus* Lawson 1975a; *Zhejiangopterus* Cai & Wei 1994.

Diagnosis. Orbit reduced in size (only one-third the height of the nasoantorbital fenestra), subcircular and located entirely below the mid-height level of the nasoantorbital fenestra. The fifth cervical is at least 8 times longer than it is broad and the neural arch merges with the centrum to form a tube-like structure (Lawson 1975a; Nesov 1984; Padian 1984a, 1986; Howse 1986; Bennett 1994; Frey & Martill 1996; Martill *et al.* 1998). The neural spine is absent in the mid-section of the fifth cervical, but forms low crests anteriorly and posteriorly. Expanded coracoidal flange occupying more than half the length of the coracoid (Kellner & Langston 1996). Extremely shallow concavity of the caudal region of the distal end of wing phalanx 1 (Frey & Martill 1996). Longitudinal ridge on the ventral surface of wing phalanges 2 and 3, resulting in a T-shaped cross-section (Nesov 1991; Bennett 1994). Femur more than 1.6 times the length of the humerus (Table 2).

Remarks. Padian (1986) suggested that azhdarchids might also be distinguished by the absence of ossification of the neural canal, at least in the mid-series cervicals, but an ossified neural canal is clearly present in some forms, including *Azhdarcho* (Unwin

& Bakhurina 2000) and *Arambourgiania* (Martill *et al.* 1998, fig. 5; see also Bennett 1994). Other putative diagnostic characters include: an elongate nasoantorbital fenestra (Unwin & Lü 1997); occiput that faces ventrally; a relatively short wing finger (~50% total wing length) and various features of the humerus (Padian & Smith 1992). Many of these characters also seem to be present in *Tupuxuara* and may thus be apomorphies of Neoazhdarchia.

Recorded temporal range. Late Cretaceous (?Cenomanian–Maastrichtian).

Source of phylogenetic data. *Arambourgiania philadelphiae* (BSP 1978/1 [c]; Arambourg 1959; Frey & Martill 1996; Martill *et al.* 1998). *Azhdarcho lancicollis* (Ch.B.I 12454, 1/11915, 3/11915, 4/11915, 5/11915, 6/11915, 7/11915, 8/11915, 9/11915, 10/11915, 17/11915, 18/11915, 41/11915; Nesov 1984, pl. 7, figs 1–11 & 13; Nesov 1986, pl. 2, fig. 1; Nesov 1991; Nesov & Yarkov 1989, pl. 2, figs 2–8; Bakhurina & Unwin 1995). cf. *Azhdarcho* (Buffetaut 1999). *Hatzegopteryx thambema* (Buffetaut *et al.* 2002). *Montanazhdarcho minor* (Padian *et al.* 1995). *Quetzalcoatlus* sp. (TMM 41450, TMM 41541, TMM 41544, TMM 41546, TMM 41547, TMM 41954, TMM 41961, TMM 42138, TMM 42157, TMM 42161, TMM 42180, TMM 42422–30, TMM 42462; Lawson 1975a, b; Langston 1981; Kellner & Langston 1996). *Quetzalcoatlus northropi* (TMM 4150–3; Lawson 1975a, b; Langston 1981). ?*Quetzalcoatlus* (YPM-PU 22446 [c], MOR 553, MOR 656, MOR 1071; Padian 1984, 1986; Padian & Smith 1992). *Solana azhdarchid* (MGUV 2271, MGUV 2194, MGUV 2195, MGUV 2239, MGUV 2271, MGUV 3207, MGUV 3209, MGUV 3210, MPV TT48, MPV TT49; Company *et al.* 1999). *Zhejiangopterus linhaiensis* (ZMNH M1323, ZMNH 1328, ZMNH 1330; Cai & Wei 1994; Unwin & Lü 1997).

Appendix 2. List of characters that vary within Pterosauria, used in this analysis

1. Dentary: less (0), or more than 75% length of lower jaw (1).
2. Coracoid: less than (0), or at least 75% length of scapula (1).
3. Unguals of manus and pes: similar in size (0), manual unguals twice the size, or more, of pedal unguals (1).
4. Forelimb length: less (0), or at least 2.5 times the length of hindlimb (femur + tibia + metatarsals) (1).
5. Humerus: shorter (0), or longer than femur (1).
6. Quadrate: vertical (0), inclined anteriorly (1).
7. Ulna: shorter (0), subequal or longer than tibia (1).

8. Fibula: subequal in length (0), or less than 80% the length of the tibia (1).
9. Rostrum: high, with convex outline (0), low with straight or concave dorsal outline (1), anterior region of rostrum low, but antorbital region expanded dorsally (2).
10. Posterior extent of premaxilla: terminates at (0), or interfingers between frontals (1).
11. External nasal opening: height similar to or greater than anteroposterior length (0), low and elongate (1).
12. Nasal process of maxilla: vertical-subvertical (0), inclined backwards (1).
13. Maxilla-nasal contact: narrow (0), broad (1).
14. Orbit: smaller than (0) or larger than the antorbital opening (1).
15. Ventral margin of skull: straight (0), curved downwards caudally (1).
16. Caudal end of mandible with distinct dorsal 'coronoid' eminence: present (0), absent (1).
17. Bony mandibular symphysis: absent (0), present (1).
18. Mandibular symphysis: less than (0), or more than 30% the length of the mandible (1).
19. Two, large, fang-like mandibular teeth: present (0), absent (1).
20. Metacarpals I-III: disparate lengths (0), or the same length (1).
21. Length of metatarsal IV: subequal (0), shorter than metatarsals I-III (1).
22. Rostral dentition: more than (0) or less than 11 pairs of teeth (1).
23. Deltopectoral crest of humerus tongue-shaped, with necked base: absent (0), present (1).
24. Narial and antorbital fenestrae: separate (0), confluent (1).
25. Basipterygoids: separate (0), or united to form a median bar of bone (1).
26. Cervical ribs: present (0), strongly reduced or absent (1).
27. Combined length of caudal vertebrae: longer (0), or shorter than the dorsal series (1).
28. Pteroid: short and stubby (0), or long and slender (1).
29. Metacarpal IV: less (0), or 80%, or more, of humerus length (1).
30. Pes digit V: two phalanges (0), one or less (1).
31. Notarium: absent (0), present (1).
32. Coracoid: shorter than (0), longer than scapula (1).
33. Humerus with warped deltopectoral crest: absent (0), present (1).
34. Pneumatopore on anconal surface of humerus: absent (0), present (1).
35. Distal end of humerus: D-shaped (0), triangular (1).
36. Ornithocheiroid carpus: absent (0), present (1).
37. Contact between distal syncarpal and metacarpals I-IV: all four in contact (0), only I and IV contact syncarpal (1), only IV contacts the syncarpal (2).
38. Femur with stout neck and steeply directed caput: absent (0), present (1).
39. Posterior margin of nasoantorbital fenestra: straight (0), concave (1).
40. Basal region of orbit: open (0), infilled (1).
41. Coracoid facets on sternum: one anterior to the other (0), lateral to each other (1).
42. Tall, narrow, frontal crest: absent (0), present (1).
43. Dentition: present (0), absent (1).
44. Mandibular rami: at same level (0), or elevated well above symphysis (1).
45. Pneumatic opening in palmar surface of humerus: absent (0), present (1).
46. Metacarpal IV: less (0), or more than twice the length of the humerus (1).
47. Deltopectoral crest of humerus with elongate rectangular profile: absent (0), present (1).
48. Sagittal cranial crest continued dorsally in soft tissues and extending from anterior to nasoantorbital fenestra to apex of skull, or beyond: absent (0), present (1).
49. Quadrate: vertical or inclined (0), subhorizontal position (1).
50. Squamosal above (0), level with or below base of lacrimal process of jugal (1).
51. Occiput faces posteriorly or posteroventrally (0), ventrally (1).
52. Neural arch of cervicals: high with high neural spine (0), or low with low neural spine (1).
53. Elongate mid-series cervicals: absent (0), present (1).
54. Distal ends of paroccipital processes: unexpanded (0), expanded (1).
55. Dsungaripteroid teeth: absent (0), present (1).
56. Dentition: extends to jaw tips (0), jaw tips toothless, but followed by tooth row (1).
57. Location of largest teeth: rostral half of dentition (0), caudal half (1).
58. Appendicular bones: with thick cortex and narrow or absent lumen (0), thin cortex and wide lumen (1), secondarily thickened cortex (2).
59. Strongly bowed femur: absent (0), present (1).
60. Dorsal margin of orbit: level with dorsal margin of nasoantorbital fenestra (0) or located well below it (1).

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